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Research

Variation in trophic cascade strength is triggered by top–down process in an ant–wasp-fig system

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Changes in the strength of trophic cascades over time have been associated with dramatic shifts in community structure and function. However, the pattern, process, and potential underlying mechanism of temporal variation in trophic cascades remains relatively unexplored. A top–down trophic cascade has been documented for the effects of predacious weaver ants *Oecophylla smaragdina* on the success of fig tree *Ficus racemosa* seed production. Ants cause high mortality of non-pollinating fig wasps *Sycophaga mayri* that parasitize fruits, leading to greater success for the pollinating fig wasp–fig tree mutualists. Here, using a design in which pairs of branches were selected on a tree, and ants were excluded from one of each pair, we quantified the magnitude of the trophic cascade in the cool–dry, hot–dry and rainy (hot–wet) seasons in Xishuangbanna, southwest China. We also recorded the daily behavioral dynamics of ants and fig wasps in different seasons and analyzed the correlation between behavioral, activity and trophic cascade strength. We found that the strength of the trophic cascade was strong in the hot–dry season, diminished in the rainy season and disappeared in the cool–dry season in this system. The strength of species interactions between ants and non-pollinating fig wasps, is positively correlated with trophic cascade strength, indicating that trophic cascade strength is determined by a top–down process when the community is well established. Moreover, because pollinating fig wasps, *Ceratosolen fuscicep*s, play a central role in the establishment of fig wasp communities, when *C. fuscicep*s wasps are absent, the community quickly disassembles as is the case in the cool–dry season. In summary, the strength of the trophic cascade is triggered by top–down processes, however, the occurrence of the trophic cascade is determined by a keystone species that plays a central role in assembly of the community.

Keywords: trophic cascade strength, predator-exclusion, predation, fig, fig wasp

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Introduction

Trophic cascades occur because of connectivity between species within the community. Strong inter-dependence means that changes in one trophic level are propagated through entire food chains and have both direct and indirect effects on other trophic levels (Pace et al. 1999, Polis et al. 2000). Top–down trophic cascades are initiated from top predators through herbivores to plants, and even microbes. Trophic cascades can also be bottom–up if initiated by changes in basal resources such as the nutrient supply to plants (Kagata and Ohgushi 2006, Heath et al. 2014). Although trophic cascades appear to be a ubiquitous property of food webs, strong trophic cascades are often transient, indicating temporal variation in trophic cascade strength (Piovia-Scott et al. 2017). However, temporal variation in trophic cascades and their mechanisms remain relatively unexplored (Piovia-Scott et al. 2017), although changes in the strength of the trophic cascade have been associated with dramatic shifts in community structure and function (Folke et al. 2004).

Theoretically, the occurrence and strength of trophic cascades are likely to be context dependent, relying on the specific nature of interactions among biotic and abiotic variables and their effects on species interactions (Sih et al. 2000, Shurin et al. 2002). Factors that drive population dynamics or affect behavioral variation in interacting species (Knape and de Valpine 2011) can then affect the strength of species interactions, and ultimately the strength of the trophic cascade. Specifically, trophic cascades can be density mediated and/or trait mediated, indicating that they are determined by both population density and behavioral traits of predator and prey species (Schmitz et al. 2004). Changes in population density and behavior of predator and prey species may initially affect interactions between these two components and subsequently be transmitted down to lower trophic levels, showing a top–down process (Norrdahl et al. 2002, Spiller and Schoener 2008, Terborgh and Estes 2010). On the other hand, bottom–up indirect interactions have also been reported, where the population dynamics of species at higher trophic levels is driven through resource supply mediated by primary productivity (Price and Hunter 2005). Although this seems straightforward, the variation in trophic cascade strength and the corresponding shift in predator and prey population dynamics and behavior are rarely tested empirically.

Generally, trophic cascades can be observed and detected when ‘initial consumers’ (predators) directly affect the population density or behavior of ‘transmitting consumers’ (herbivores), which in turn has a direct effect on productivity of the lower level, the ‘receiving resource’ (plants) (Abrams 1995). The strength of a trophic cascade is usually determined by comparing a quantitative measure of lower-level resource between areas with and without the initiating consumer (Wootton and Emmerson 2005). The log response ratio for the lower-level resource is used as a measure of trophic cascade strength with these data (Shurin et al. 2002, Borer et al. 2005).

Weaver ants, *Oecophylla smaragdina*, often build their nests in fig trees (Fig. 1a), forming a mutualistic relationship with treehoppers (Fig. 1b) (Wang et al. 2018). These ants are voracious predators of other small insects (Ranganathan and Borges 2009, Peng et al. 2013). Weaver ants are an especially important predator of parasitic gall making non-pollinating fig wasps (Fig. 1d), and they can even alleviate competition for female flowers between gall-makers and pollinating fig wasps (the obligate pollinators of figs) because these flowers are the only oviposition and larval nourishment resource for both fig wasp species (Segar and Cook 2012, Wang et al. 2014). In our previous work, which was conducted only in the rainy season, we showed that predation by weaver ants on gall making fig wasps can have cascading effects on the overall reproductive output of a given fig tree (Wang et al. 2014, Wang et al. 2018). Our previous results therefore demonstrate that a predacious guild can favorably influence the interaction between two mutualists (figs and wasps) by eliminating parasites. However, the composition of the arthropod communities associated with fig trees may change between seasons (Wang and Sun 2009), which can affect the strength

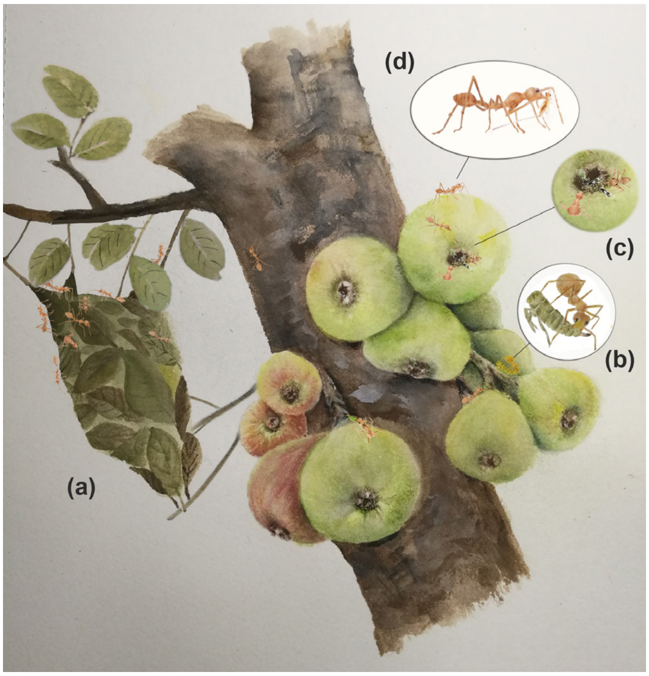

Figure 1. A schematic diagram of the interaction network among weaver ants, treehoppers, fig wasps, and *Ficus racemosa*. Weaver ants build nests using leaves of *Ficus racemosa* (a). Chemical camouflage helps maintain the mutually beneficial interaction between weaver ants and treehoppers (b), and ants facilitate the reproductive success of both sides of fig tree and pollinator mutualists by mainly preying on the non-pollinating fig wasps (d), although they also prey on pollinating fig wasps (c), and reduce their opportunities for oviposition.

of both direct and indirect inter-specific interactions. A cross-seasons ant exclusion experiment can potentially demonstrate the variation in trophic cascade strength. Moreover, comparisons of seasonal variation in weaver ant and fig wasp abundance and behavioral activity will help to uncover mechanisms driving such variations. These natural temporal variations in mutualist and parasite density provide an ideal model with which to explore the possible variation in the strength of trophic cascades across the seasons as well as their underlying mechanisms.

In this study, we addressed the following specific questions: 1) is there temporal variation in trophic cascade strength in the ant–wasp–fig system? 2) what are the possible mechanisms affecting trophic cascade strength in this system? For the first question, we conducted across-season field exclusion experiments using a paired design to reveal the seasonal variation in fig wasp community composition between treatments (two levels: with predacious weaver ants and ant exclusion). We then used the log response ratio as a measure of strength of trophic cascade and compared these responses among seasons. Parasitic wasp oviposition attempts can be detected on the surface of syconia (enclosed inflorescences), while ovipositing mutualist wasps can be retrieved from within syconia. For the second question, we therefore 1) recorded and compared oviposition scars of non-pollinating fig wasps (parasite activity) and foundress number (pollinator activity) in each syconium (enclosed inflorescence) to reveal the processes governing the trophic cascade; 2) we also compared the correlation of species interaction strength (log response ratio as a measure of species interaction strength) and trophic cascade strength; 3) analyzed the correlation between air temperature, light (illumination) and fig wasp and ant behavioral activity at the experimental sites, because fig wasp behavior activity is sensitive to temperature and light. The nature of temporal variation in trophic cascade strength will have important implications for evaluating the role of predators in community dynamics and will inform our understanding of how species interactions mediate the effects of environmental change on ecological communities. The constrained nature of the fig wasp system naturally results in a higher signal noise ratio because most of the interaction network can be accurately quantified, for example, through the dissection of figs.

Methods

Location and study system

The study was carried out in the Xishuangbanna tropical botanical garden (XTBG) (21°41′N, 101°25′E), which covers an area of 11.25 km^2, including a well-preserved 2.5 km^2 section of primary tropical rainforest, in Yunnan province, southwest China. The climate in Xishuangbanna is strongly seasonal and is classified into three seasons (Cao et al. 2006). The cool–dry season lasts November–February and is characterized by a high frequency of heavy radiation fog during the night and in the morning. The hot–dry season lasts March–April, it is characterized by dry and hot weather during the afternoon and heavy radiation fog during the morning. The rainy season lasts May–October, in this period XTBG receives high rainfall from the southwest summer monsoon.

We performed all experiments using *Ficus racemosa*, which is a native monoecious fig species distributed throughout south-east Asia and reaching Australia, pollinated by *Ceratosolen fusciceps* (Mayr 1885). *Ficus racemosa* produces large crops of figs (syconia: approx. 40 mm in diameter when mature), which are borne on small fruiting branches that grow from the trunk and larger branches (Fig. 1). Syconia are enclosed inflorescences, each contains about 4000–5000 flowers. The syconia have five distinct developmental stages (Galil and Eisikowitch 1968): A phase: pre-receptive, B phase: receptive to pollination, C phase: inter-floral, D phase: male floral (pollinators mature, acquire pollen and disperse), and E phase: seed dispersal. During the last stage the figs become attractive to frugivorous seed dispersers.

Five non-pollinating (effectively parasitic) fig wasp species reproduce in the syconia of *F. racemosa* in Xishuangbanna; three species of *Sycophaga* (*S. mayri*, *S. testacea* and *S. agraensis*) and two of *Apocrypta* (*Apocrypta* sp. and *A. westwoodi*) (Wang et al. 2010). *Sycophaga mayri* and *S. testacea* gall fig flowers and have herbivorous larvae, whereas *S. agraensis* is a parasitoid of the pollinators. *Apocrypta* sp. and *A. westwoodi* are parasitoids of *S. testacea and S. mayri*, respectively.

When the flowers are receptive to pollen, the syconium emits volatiles that attract gravid female pollinating wasps (foundresses) which enter through a bract-lined tunnel to spread pollen and oviposit. Foundress then die inside the syconium and the wasp offspring develop into adults in galled female flowers in synchrony with fig maturation. The new generation of adult wasps emerge into the fig cavity, males emerge first and mate with female wasps, females then collect pollen and exit the syconium from exit tunnels excavated by male wasps to start a new cycle. Foundresses are vulnerable to temperature (Jevanandam et al. 2013), which leads to a population decline during the cool–dry season. Syconia are aborted if they are not pollinated during the cool–dry season. However, a part of the pollinating fig wasp population survive as larvae (inside figs) during the cool–dry season when the development of syconia and wasps slows. Adult pollinating fig wasps emerge in the dry–hot season.

Each wasp species oviposits at a specific developmental stage (Wang et al. 2010). Broadly speaking herbivorous gallers lay their eggs before or slightly after pollinators while parasitoids come later. Of all non-pollinating fig wasps, *S. mayri* is the dominant species, and it oviposits at the same stage (B phase) as pollinating fig wasps. Because non-pollinating fig wasp species that gall fig flowers have herbivorous larvae, they may inflict costs on both mutualists by competing with the pollinators for oviposition sites and reduce fig seed production (Segar et al. 2018). Some wasps are parasitoid species that develop at the expense of pollinators or non-pollinating fig wasps. While pollinators enter the syconia to oviposit, thus avoiding intense predation by weaver ants (Fig. 1c), all of the non-pollinating fig wasp species associated with *F. racemosa* oviposit externally, which makes them vulnerable to predators (Fig. 1d) (Wang et al. 2014). *Oecophylla smaragdina* abundance peaks at B phase, effectively reducing ovipostion opportunities for *S. mayri* and alleviating competition between *S. mayri* and pollinating fig wasps (Wang et al. 2014). In this system trophic cascade strength through to pollinators (*C. fusciceps*) is dependent on the density and behavior of parasites (*S. mayri*) which is mediated by predators (*O. smaragdina*). Our primary consideration is how and why the strength of this trophic cascade varies across seasons.

Effects of ant exclusion on fig wasp community and fig seed production

Three trees with DBH (diameter breast high) over 40 cm, dominated by nesting weaver ants, *O. smaragdina*, were selected with which to perform the following experiments. For each tree, 3–4 pairs of fruiting branches were selected with which to conduct the experiment, two adjacent fruiting branches were randomly assigned as control and treatment. A round filter paper (12 cm in diameter) was placed around the proximal part of each branch and fixed using a stapler. For the treatment, flavorless, scentless, colorless glue (approximately 25 ml) was smeared on the surface of the filter paper to prevent ants from praying on the figs. The control branches were only surrounded by filter paper; ants could pass through and patrol figs. Branches were checked daily, additional glue was applied roughly every seven days until the experiment finished. The experiment started when the syconia were buds and finished when ripe syconia were collected. In the male floral phase, mature syconia (yellow or orange colored) without exit holes were checked and collected daily; collected syconia were put into mesh bags. The syconium and the wasps that emerged into the bags were killed and preserved in 75% ethanol. All wasps were sorted by species and sex, identified and counted. The syconia were finally cut into four equal parts; seeds from one quarter were scraped free and counted. The total number of seeds in the whole syconium was estimated by multiplying that result by four (Kerdelhue et al. 2000). The experiments were conducted on three trees per season.

Measurement of trophic cascade strength and species interactions

Otto et al. (2008) and Wootton and Emmerson (2005) proposed the following equation for calculating both species interaction strength and strength of the trophic cascade:

$$\mathrm{IS} = \log_{10}\left(\mathrm{B}^{+\mathrm{pred}} / \mathrm{B}^{-\mathrm{pred}}\right) \qquad (1)$$

Here, IS refers to interaction strength or the strength of the trophic cascade, $\mathrm{B}^{+\mathrm{pred}}$ refers to the performance of prey or plants in the presence of the predator, $\mathrm{B}^{-\mathrm{pred}}$ refers to performance of the prey or plants when the predator is absent. For each pair of branches assigned to treatment (without ants) or control (with ants), the numbers of *S. mayri* and seeds were averaged by syconium for each branch. For each pair of branches, interaction strengths were calculated by Eq. 1, $\mathrm{B}^{+\mathrm{pred}}$ is the averaged *S. mayri* number for the control branch and $\mathrm{B}^{-\mathrm{pred}}$ is the averaged *S. mayri* number for the treatment branch. Trophic cascade strength was calculated with the same equation, with $\mathrm{B}^{+\mathrm{pred}}$ representing the averaged seed number for the control branch and $\mathrm{B}^{-\mathrm{pred}}$ representing the averaged seed number for the treatment branch.

Seasonal variation in ant abundance, ant foraging in fruit branches, foundress number and non-pollinating fig wasp oviposition

The number of weaver ant nests in a tree was used as a proxy for weaver ant abundance. Nests in each tree were observed three times per season. Nests built with green leaves, or with ants active on the nest surface were counted. Observations were made using a pair of binoculars.

Weaver ants forage on fig-bearing branchlets in *F. racemosa*. During each season, three trees were selected, and we observed and recorded ant number on ten fig-bearing branchlets for each tree. All observations were conducted during the receptive phase between 09:30 and 11:30, the peak activity time for *C. fusciceps*.

In each season, the figs were collected one week after pollination. They were then dissected to reveal the number of foundresses inside, after external inspection of the number of oviposition scars made by non-pollinating wasps (Harrison 2014). These scars can be inspected after peeling back the surface of syconia using a sharp knife, they result from *S. mayri* using their long ovipositors to pierce the fig wall and lay eggs.

Correlation between air temperature, illumination and ant/fig wasp behavior activity

Sticky yellow boards were used to attract fig wasps during the receptive phase, giving a measure of local pollinator and competitive galler abundance. Yellow boards were hung on the branches close to the syconia. Each board was left in a tree for one hour, and then replaced, the fig wasps on each of the boards were counted. This experiment was conducted continuously during the receptive phase from 06:00 to 20:00. This experiment was not conducted for 24 h, because in the preliminary experiments no fig wasps were caught with the boards during the night from 20:00 to 06:00. For each tree, three boards per tree per hour were used. The number of ants on the main trunk of the fig tree, i.e. how many ants passed a fixed line (approximately breast high) for 10 min once per hour from 06:00 to 20:00 for one day per tree in each season was also recorded. This experiment was performed once per season for three trees. Air temperature (°C) and illumination (photosynthetic photon flux density, PPFD) under the trees were also recorded using a data logger with quantum sensors.

Average daily air temperature and PPFD data were obtained from Xishuangbanna Station for tropical rain forest ecosystem studies (XSTRE) to show the annual air temperature and PPFD variation in different seasons (Supplementary material Appendix 1 Fig. A1).

Data analysis

Effects of ant exclusion on fig wasp community and fig seed production

To compare the fig wasp community among different seasons, permutational multivariate analysis of variance (Permanova) using distance matrices were used (Warton et al. 2012). This analysis first obtains distance matrices from fig wasp communities, then fits linear models to distance matrices using a permutation test (Oksanen et al. 2018). The Permanova was based on Bray–Curtis distances and run for 999 permutations, permutations were constrained within each 'tree'. Nonmetric multidimensional scaling (NMDS) was used to graphically represent wasp community differences (Bray–Curtis distance) (Clarke 1993).

The numbers of wasps and seeds from branches with and without ants were analyzed using linear mixed effects models fitted by restricted maximum likelihood (Bates et al. 2015). These models were run for each species of fig wasp using wasp number or seed number as response variable, with 'branch' nested within 'tree' as random effects, and 'treatment' (two levels, with ants, ant exclusion) as the fixed effect.

Seasonal variation in trophic cascade strength and species interactions

The strength of inter-specific interactions and the strength of trophic cascades were each fitted using a linear mixed effects model. For each analysis, the strength of inter-specific interaction and the strength of the trophic cascade each was set as a response variable, we included 'season' (two levels 'hot–dry' and 'rainy') as the fixed effect, and 'tree' (three trees) as a random effect. Correlations between species interaction strength and trophic cascade strength were analyzed using Pearson's product–moment correlation.

Seasonal variation in foundress number, non-pollinating fig wasp oviposition, ant abundance and number of ant foraging in fruit branches

The seasonal variation in ant abundance and activity was modeled using a Poisson generalized estimating equation (GEE), with ant nest number as the response variable and 'season' and 'tree' as the explanatory variables. An AR1 autocorrelation structure was set for each observation and tree. We started with a model that contained all the explanatory variables and non-significant variables were excluded from the model by step wise simplification (Zuur et al. 2009). Pairwise comparisons were conducted using the Tukey and Kramer test.

Number of ant foraging in fruit branches, foundress number, and ovipostion scar fitted neither the Poisson distribution nor the negative binomial distribution. Therefore, the Kruskal–Wallis rank sum test was used to analyze ant activity, followed by a pairwise comparison using the Tukey and Kramer test (Rosner 2002, Pohlert 2014).

Correlation between air temperature, illumination and ant/fig wasp behavior activity

Because there is temporal auto-correlation between observations taken during a day for each tree, a Poisson generalized estimating equation (GEE) was fitted, with ant number as the response variable, with 'season' and 'tree' as explanatory variables. An AR1 auto-correlation structure was used for each observation for each tree. AR1 autocorrelation structure is the simplest correlation structure, it assumes that the number of ant or wasps in a tree at time s depends on those measured at time s – 1, and also less strong, on s – 2, etc. in the same tree (Zuur et al. 2009). We consider this to be the most relevant correlation structure in comparison to the 'unstructured correlation', 'exchangeable correlation', and 'stationary correlation' structures (Zuur et al. 2009). We started with a model that contained all the explanatory variables, and non-significant variables were excluded from model by step wise simplification. The correlation between temperature and ant activity, ant activity and light, light and temperature were analyzed using Spearman's rank order correlation. Data with missing records of temperature or light intensity were excluded from these correlation analyses.

Daily fig wasp activity data for each season fitted neither the Poisson distribution nor the negative binomial distribution. Therefore, a nonparametric rank-based analysis of longitudinal data with an Anova-type statistic (ATS) was used, the effects of 'tree' and 'season' (three levels 'hot–dry', 'rainy', and 'cool–dry') were tested (Noguchi et al. 2012). Fig wasp activity was correlated with temperature and light using Spearman's rank order correlation.

The above analyses were conducted using the 'lme4' package (Bates et al. 2015), 'geepack' (Halekoh et al. 2005) and 'vegan' (Oksanen et al. 2018) in R ver. 3.3.3 (<www.r-project.org>).

Data deposition

Data and R code for data analysis and additional boxplots to show data distribution for Fig. 2–4 are deposited in the Figshare repository: <https://doi.org/10.6084/m9.figshare.5596894.v1>.

Results

The effects of ants and season on fig wasp community variation and fig seed production

The fig wasp community structure differed significantly among seasons (Permanova, $R^2 = 0.24$, $p < 0.001$). NMDS comparisons of wasp communities among different seasons are shown in Supplementary material Appendix 1 Fig. A2 (stress value = 0.13, and $R^2 = 0.98$).

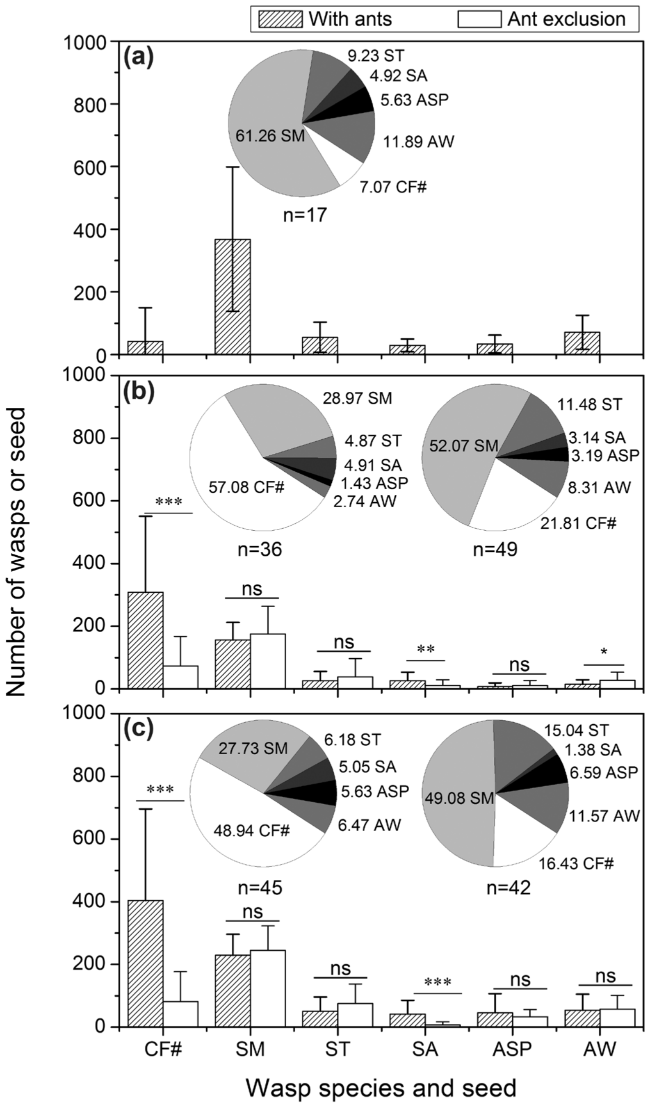

Figure 2. Number of wasps from branches with weaver ants or without ants in the cool–dry (A), hot–dry (B), and rainy (C) seasons. Species composition is shown on the top of bar plot for each season, left pie (with ants), right pie (ants excluded). Syconia in the cool–dry season in ant exclusion treatments were all aborted. Linear mixed-effects models were fitted, with the number of fig wasps as the response variable, with treatment (trees with or without *Oecophylla smaragdina*) as the fixed factor, tree as a random factor. * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$), NS = not significant. CF = *Ceratosolen fusciceps*; SM = *Sycophaga mayri*; ST = *S. testacea*; SA = *S. agraensis*; AS = *Apocrypta* sp.; AW = *A. westwoodi*. Columns and bars show mean ± SD. # represent pollinating fig wasp. Numbers under the pie represent replications of syconium sampled.

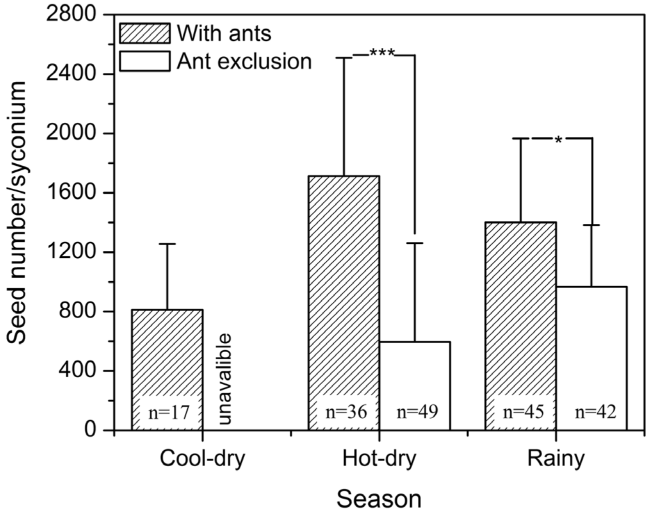

Figure 3. Number of seed from branches with weaver ants or ants excluded in cool–dry, hot–dry, and rainy seasons. * ($p < 0.05$), *** ($p < 0.001$). Numbers in the box represent replications of syconium sampled.

In the cool–dry season, the galling wasp *S. mayri* is the dominant species comprising up to 61.26% of the total fig wasp community, followed the parasitoid *A.* sp. (11.89%), and galling *A. testacea* (9.23%) (Fig. 2A). Pollinating fig wasps are scarce in the cool–dry season (7.07%). When ants were excluded in the cool–dry season, all the syconia dropped off, therefore fig wasp community data is unavailable. In the hot–dry season, when weaver ants exist, pollinating fig wasps are the most abundant species (57.08%), followed by galling *S. mayri* (28.97%), and the parasitoid *P. agraensis* (4.91%) (Fig. 2B). When we excluded weaver ants in the hot–dry season, *S. mayri* became the most abundant species (52.07%), followed by pollinating fig wasps (21.81%), *A. testacea* (11.48%), and *A. westwoodi* (8.31%). When weaver ants were present, pollinating fig wasp were the most abundant species (48.94%) in rainy season (Fig. 2C), followed by *S. mayri* (27.73%), and *A. westwoodi* (6.47%). When we excluded weaver ants in rainy season, *S. mayri* became the most abundant species (49.08%), followed by pollinating fig wasps (16.34%), *A. testacea* (15.04%), and *A.* sp. (6.59%).

In the hot dry season (Fig. 2B), the number of pollinating fig wasps and *S. agraensis* decreased significantly, but the number of *A. westwoodi* increased, when ants were excluded. The number of *S. mayri*, *A. testacea* and *A.* sp. did not differ significantly between the control and treatment (Table 1). In the rainy season (Fig. 2C), the number of pollinating fig wasps decreased significantly compared to the control (with ants) and the number of *S. agraensis* also decreased significantly, when ants were excluded. The number of *S. mayri*, *A. testacea*, *A.* sp. and *A. westwoodi* did not differ significantly.

Seed production (female reproductive function) was lowest in the cool–dry season (812 ± 443.80) and it increased in the hot–dry (1713.11 ± 796.13) and rainy seasons (1400.62 ± 565.61) (Fig. 3). Seed production decreased significantly when weaver ants were excluded in the rainy season, and seed production also decreased significantly when weaver ants were excluded in the hot–dry season (Table 1).

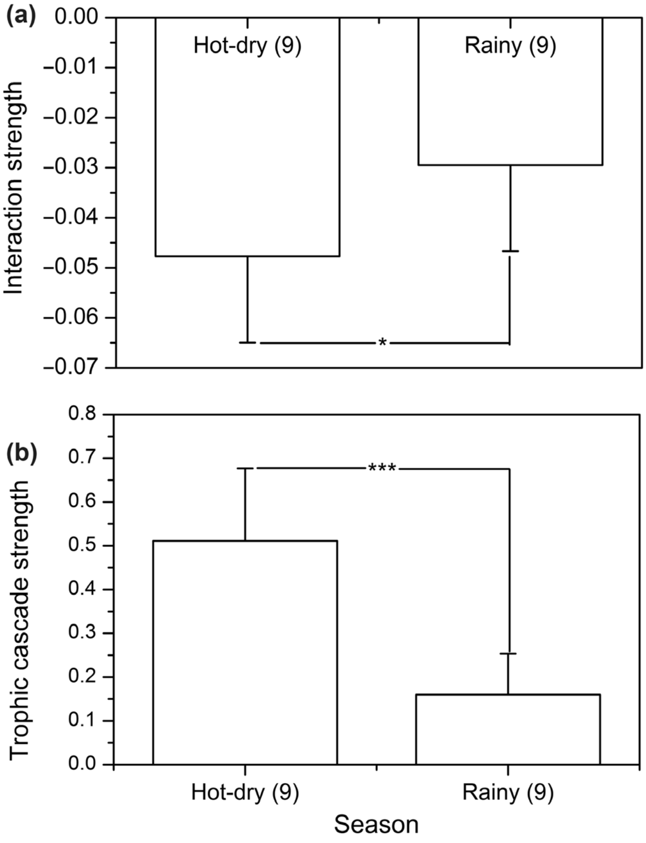

Figure 4. Mean (± SD) interaction strength (A) of weaver ant, *Oecophyla smaragdina*, on the gall making fig wasp, *Sycophagus mayri*, and the strength of the trophic cascade (B) in different seasons. * ($p < 0.05$), *** ($p < 0.001$). Numbers in the brackets represent replications of with ants/ant exclusion branchlets pairs.

Seasonal variation in interaction strength and trophic cascade strength

Because fruits in the cool–dry season were aborted during the experiment, we could not calculate the interaction strength and cascade strength during the cool–dry season. But the interaction strength was significantly stronger in the hot–dry (–0.05 ± 0.02) season in comparison to the rainy (–0.03 ± 0.02) season (Fig. 4A: $t=2.41$, $df=14.00$, $p < 0.05$), and the trophic cascade strength from predators to pollinators in the hot–dry season (0.51 ± 0.17) was also stronger than rainy season (0.16 ± 0.09) (Fig. 4B: $t=5.54$, $df=16$, $p < 0.001$). There is a significant positive correlation between interaction strength and trophic cascade strength ($t=2.29$, $df=16$, $p < 0.05$, $r=0.50$).

Seasonal variation in foundress number, non-pollinating fig wasp oviposition, ant abundance and number of ant foraging in fruit branches

Overall ant abundance measured as nest number (Fig. 5A) was significantly different between seasons ($\chi^2=22.7$, $df=2$, $p < 0.001$), with ant abundance being highest in the rainy season (mean ± SD: 11.11 ± 4.26) followed by the hot–dry (7.11 ± 2.42) and finally the cool–dry (7.33 ± 1.87) season. There were also significantly more ants in fig-bearing branchlets during the rainy season (16.9 ± 12.55) and hot–dry (17.27 ± 13.10) season in comparison to the cool–dry season (1.87 ± 2.43) (Kruskal–Wallis rank sum test: $\chi^2=41.51$, $df=2$, $p < 0.001$, Fig. 5B).

Foundress number (a measure of pollinator activity) differed significantly among seasons ($\chi^2=139.30$, $df=2$, $p < 0.001$), with a mean of 1.24 ± 1.93 (mean ± SD) foundresses per syconium being found in the cool–dry season, 9.38 ± 11.56 in the hot–dry season, and 16.21 ± 9.89 in the rainy season (Fig. 5C). The number of non-pollinating fig wasp oviposition scars (a proxy for parasite activity) was also significantly different between seasons ($\chi^2=118.66$, $df=2$, $p < 0.001$), with a mean of 49.62 ± 89 in the cool–dry season, 499.99 ± 413.6 in the hot–dry season, 260.88 ± 167.75 in the rainy season (Fig. 5D).

Correlation between air temperature, illumination and ant/fig wasp behavior activity

Ant activity on tree trunks was significantly different ($\chi^2=12.3$, $df=2$, $p < 0.01$) among seasons, ants were more active in the cool–dry season than the rainy season, the autocorrelation of ant activity was high over the course of each day with a value of 0.82 (Fig. 6A). Ant activity was positively correlated with temperature (Spearman's $\rho=0.55$, $p < 0.001$) and light (Spearman's $\rho=0.33$, $p < 0.01$). Light and temperature were positively and significantly positively correlated (Spearman's $\rho=0.73$, $p < 0.001$).

Table 1. Comparing the fig wasp and seed number between figs with ants and ant exclusion using linear mixed model fit by restricted maximum likelihood t-tests.

	Hot dry season					Rainy season				
Species	Estimates	SE	t	df	p	Estimates	SE	t	df	p
Ceratosolen fusciceps	242.78	48.45	5.01	11.19	< 0.001	319.92	57.73	5.54	13.89	< 0.001
Sycophaga mayri	15.29	15.99	0.96	81.38	0.34	16.23	16.37	0.99	15.9	0.34
Sycophaga testacea	17.57	13.80	1.27	13.32	0.22	23.60	15.33	1.54	15.57	0.14
Sycophaga agraensis	15.98	4.96	3.22	83	< 0.01	34.85	8.00	4.36	16.49	< 0.001
Apocrypta sp.	5.09	4.27	1.19	14.07	0.25	14.71	9.60	1.53	13.82	0.15
Apocrypta westwoodi	16.47	6.06	2.72	15.18	< 0.05	4.26	10.85	0.39	13.47	0.70
Seeds	1127.06	198.83	5.67	17.38	< 0.001	431.89	151.88	2.84	13.86	< 0.05

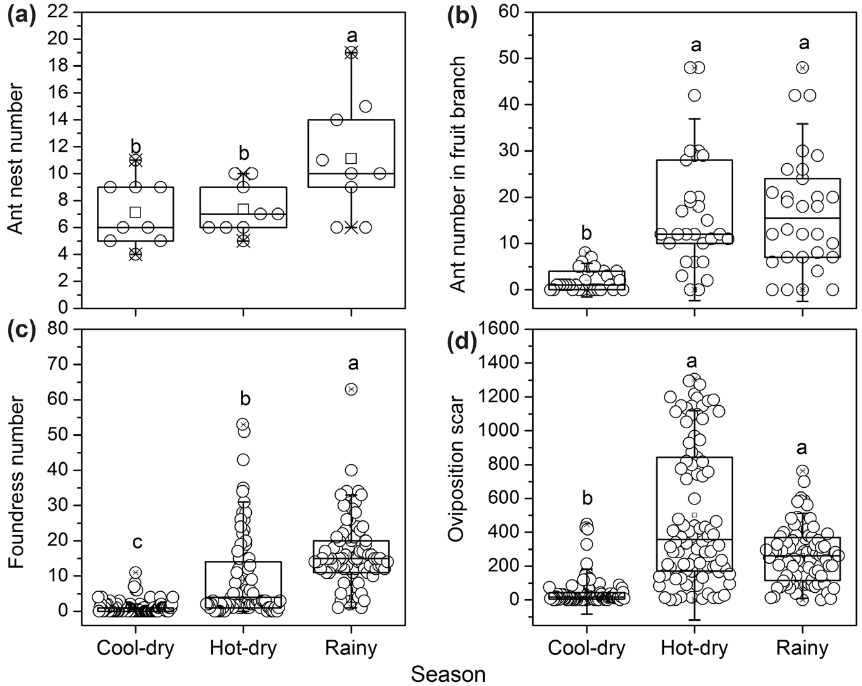

Figure 5. Box plot of the number of weaver ant nests (A), number of weaver ants foraging in fig-bearing branchlets (B), foundress number (C), and oviposition scars of non-pollinating fig wasps (D) in the fruits of *Ficus racemosa* after receptive stage of *Ficus racemosa* in different seasons. Different letters represent significant differences between each season, pairwise comparisons conducted using Tukey and Kramer test. Each circle represents a data point.

Pollinating fig wasp activity was significantly different among seasons, and tree identity did not affect pollinating fig wasp activity (Table 2). Pollinating fig wasp activity did not differ significantly between rainy and hot–dry seasons, but did differ significantly between rainy and cool–dry, and between hot–dry and cool–dry seasons (Fig. 6B). Pollinating fig wasp activity was positively correlated with both temperature (Spearman's $\rho = 0.56$, $p < 0.001$), and light (Spearman's $\rho = 0.60$, $p < 0.001$).

The activity of the gall making fig wasp, *S. mayri,* also differed significantly among seasons, but tree identity did not affect gall maker activity (Table 2). The activity of *S. mayri* did not differ significantly between the rainy and hot–dry season and the hot–dry and cool–dry season, but did differ significantly between the rainy and cool–dry seasons (Fig. 6C). *S. mayri* activity was weakly correlated with both temperature (Spearman's $\rho = 0.17$, $p < 0.001$) and light (Spearman's $\rho = 0.30$, $p < 0.001$).

Discussion

The species composition of the fig wasp community differs among seasons (Fig. 2), with the pollinating fig wasp species dominating in the hot–dry and rainy seasons, and parasitic gall making *Sycophaga mayri* becoming dominant in the cool–dry season (Fig. 2A–C). The variation in fig wasp community composition parallels the results reported by Wang and Sun (2009), the difference in species composition may reflect the different tolerance of fig wasps to climactic factors (e.g. temperature and drought). Fig wasp populations showed seasonal dynamics in Xishuangbanna, possibly as a response to low temperature in cool–dry season (below 10°C in Xishuangbanna, Supplementary material Appendix 1 Fig. A1).

We could not obtain data in the cool–dry season, and cannot calculate interaction strength, because the syconia we used in the exclusion experiment all dropped off and almost no pollinating fig wasps were observed ovipositing during this period. We dissected the fallen syconia and found that there were no foundress wasps inside. Syconia will be aborted when there are no foundress to pollinate or lay eggs, and this is common in the cool–dry season in Xishuangbanna (Wang et al. 2010). Therefore, the ant–wasp–fig (predator–herbivore/pollinator–host) interaction network disassembled in the cool–dry season due to absence of pollinating fig wasps (Wang and Sun 2009), indicating that pollinating fig wasps play a control role in the organization of this interacting network. The ant exclusion experiment succeeded in hot–dry and rainy seasons and cascading effects are stronger in hot–dry season in comparison to the rainy season, which could be a direct result of the interaction strength between *Oecophyla smaragdina* and *S. mayri* (Fig. 4A). In this system, the occurrence of a trophic cascade is determined by the presence of pollinating fig wasps and the strength of the trophic cascade is positively correlated to the interaction strength between predacious weaver ants and parasitic non-pollinating fig wasps.

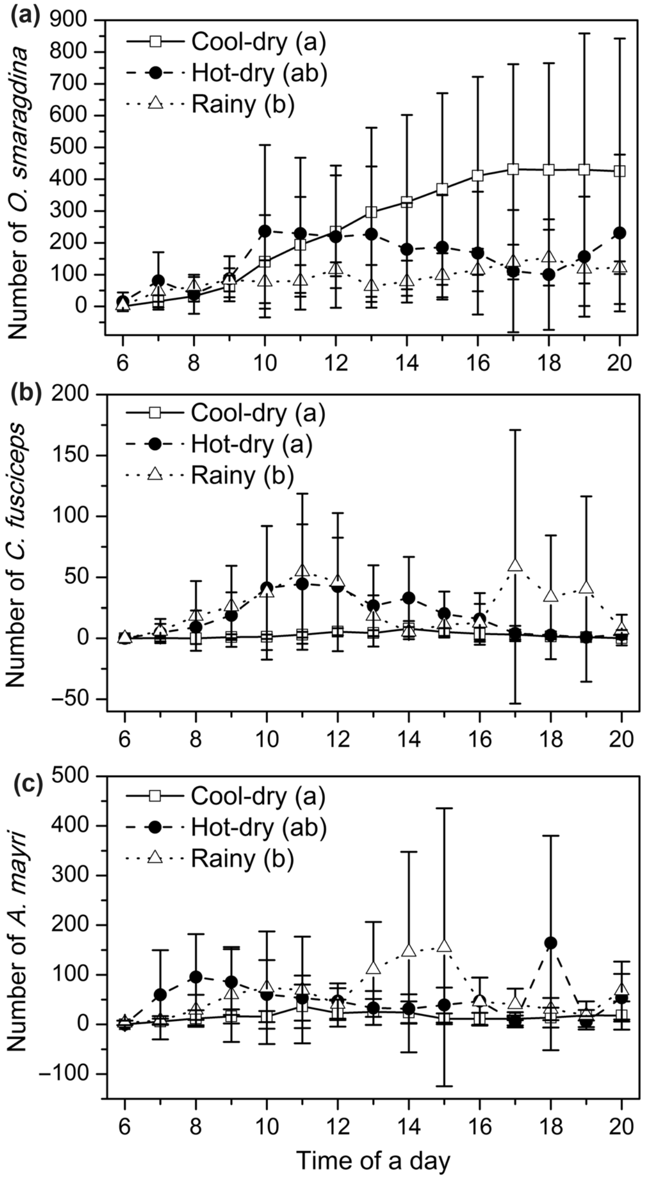

Figure 6. Number (mean ± SD) of weaver ants, *Oecophyla smaragdina* (A), pollinating fig wasp activity, *Ceratosolen fusciceps* (B), and gall making fig wasp, *Sycophagus mayri* activity (C) from 06:00 to 20:00 in different seasons. Symbols represent means and drop lines show the standard deviation. Different letters represent significant differences between each season, significance derived using non-parametric rank-based analysis of longitudinal data with Anova-type statistics (ATS).

Table 2. Comparing pollinating fig wasp *Ceratosolen fusciceps* and gall making fig wasp *Sycophaga mayri* activity among seasons using nonparametric rank-based analysis of longitudinal data with an Anova-type statistic (ATS).

	Ceratosolen fusciceps			*Sycophaga mayri*		
Species	ATS	df	p	ATS	df	p
Season	7.28	1.67	< 0.01	4.62	1.92	< 0.05
Tree	2.38	1.67	0.10	1.73	1.47	0.19
Rainy vs hot–dry	0.12	1	0.073	0.50	1	0.48
Rainy vs cool–dry	12.45	1	< 0.001	10.97	1	< 0.001
Hot–dry vs cool–dry	15.83	1	< 0.001	3.26	1	0.07

Pollinating fig wasps are more active in the rainy and hot–dry seasons than in the cool–dry season (Fig. 6B). Almost no foundresses were caught in a 15 h survey across three different trees in the cool–dry season, which is concordant with the high abortion rates in ant exclusion experiments conducted in the cool–dry season. Both foundress and oviposition scar counts supported the hypothesis that fig wasp abundance is low in the cool–dry season relative to the hot–dry and rainy seasons (Fig. 5C–D). The activity of pollinating fig wasps is strongly and positively correlated with temperature and illumination, which explains the absence of pollinating fig wasps during the cool–dry season. Compared to the rainy season, gall making fig wasps activity was not significantly different in the hot–dry season, but was significantly lower in the cool–dry season (Fig. 6C). The activity of gall making non-pollinating fig wasps was not strongly correlated with either temperature or illumination, indicating gall making fig wasps are more tolerant to low temperatures than pollinating fig wasps. Because Xishuangbanna is located close to the northern limits of the tropics, low temperatures during the cool–dry season will kill fig wasps and lead to population declines of both pollinating and gall making fig wasps population. However, the fig wasp populations will recover at the onset of the hot–dry season in the following year, fig wasp populations show significant seasonal fluctuations. In the more southerly parts of its range (e.g. Thailand, India, and Singapore), *Ficus racemosa* is less likely to be pollinator limited because seasonal variation in temperature is less pronounced than at Xishuangbanna. We therefore anticipate that species interaction and trophic cascade strength will be both stronger and more stable than at Xishuangbanna.

Weaver ant abundance was higher in the rainy season than in the hot–dry and cool–dry seasons according to ant nest number (Fig. 5A). However, high nest number did not correspond to strong predator–prey interaction strength and trophic cascade strength, which may reflect the fact that trophic cascade strength is determined more by effective predation and not just by the abundance of predators. Our results showed that ants were significantly more active on inflorescence branches in the hot–dry and rainy season than in the cool–dry season (Fig. 5B). However, in the fig tree trunk, ants are more active in the cool–dry season than in the rainy season (Fig. 6A), which may reflect the fact that weaver ants change food sources in the cool–dry seasons relative to the hot–dry and rainy season. In the hot–dry and rainy seasons, ants generally prey on fig wasps, feed on hemipteran honeydew, or extra-floral nectaries on the surface of syconia (Harrison 2014). In the cool–dry season ants may spend more time searching for food on the ground, because the abundance of fig wasps and hemiptera is low in the cool–dry season. Analysis of gut content using DNA based methods will allow us to test this hypothesis (King et al. 2008). Investigation of between branch interactions is also warranted. This species of

Ficus is known to employ host sanctions at the syconium level (in the event of non-pollination) and it is not unrealistic to expect overall resource allocation to reflect pollination success (Wang et al. 2014). Furthermore, differential rates of folivory across the tree, for example, may exacerbate between branch differences.

In the hot–dry season, ants will have more opportunity to prey on the surface of syconia and this will lead to stronger effects on fig wasps, because of a lack of rain fall in this season. In contrast, rain fall is frequent and heavy in the rainy season, which will temporarily stop ant predation and attenuate the ant's effects on gall making fig wasps. However, gall making fig wasps still stay on the surface of syconia laying eggs (Bo Wang personal observation), which might partly explain the stronger interaction strength and trophic cascade strength in the hot–dry season compared to the rainy season.

Not only do species population dynamics vary seasonally, but species interactions are also context-dependent, with outcomes varying in response to environmental factors (e.g. temperature, light, spatial heterogeneity) (Borer et al. 2005, Price and Hunter 2005, Laws and Joern 2013, 2015). Because predators exert considerable influence on structure and function in top–down systems, their responses to climate may shape responses at lower trophic levels. On the other hand, the population dynamics of higher trophic level species can also be driven through resource supply, so-called bottom effects (Price and Hunter 2005). However, our results indicated that the response to environmental change was universal, but species dependent, across the food chain. As a reaction to environmental change, predatory ants will shift their food source from fig wasps to ground living arthropods, and plants will not be capable of finishing development as the results of pollinator scarcity, gall-making non-pollinating fig wasps also die if the plant cannot continue developing and provide food source. The pollinating fig wasp–fig tree mutualism therefore plays a central role in this complex interaction network. When pollinating fig wasp numbers decline, the whole interaction network will disassemble and the weaver ant induced trophic cascade will disappear. With the recovery of the pollinating fig wasp population in the warm season, the strength of the interaction between weaver ants and gall making non-pollinating fig wasps increases, and the trophic cascade also strengthens in the warm season with the increase in pollinator wasp population. Variation in the trophic cascade may spread from the middle trophic level in this system, rather than from bottom or top trophic levels.

Abiotic conditions such as temperature may be especially important to predator–prey interactions among arthropods, which play critical functional roles in terrestrial ecosystems (Whiles and Charlton 2006). Temperature affects seasonal phenology, daily activity and physiological processing capabilities in arthropods (Harrison and Fewell 1995, Helmuth et al. 2005), where variability in any of these factors might alter the strength or direction of inter-species interaction paths (Schmitz 2008). For example, Norrdahl et al. (2002) found that strong seasonality may attenuate the strength of the trophic cascade. Spiller and Schoener (2008) reported that climate can control the strength of interactions between lizard predators and spider prey in an island ecosystem. The strength of inter-specific interactions can be transmitted along the food chain, the strength of the trophic cascade is therefore a result of variation in inter-specific interaction strength (Novak 2009).

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Supplementary material (available online as Appendix oik-05653 at <www.oikosjournal.org/appendix/oik-05653>). Appendix 1.