

# Changes in temperature alter competitive interactions and overall structure of fig wasp communities

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**Changes in temperature alter competitive interactions and overall structure of fig wasp communities**

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## 21 Abstract

- 22 1. Organisms exist within ecological networks, connected through interactions such as  
23 parasitism, predation and mutualism which can modify their abundance and distribution  
24 within habitat patches. Differential species responses make it hard to predict the influence of  
25 climate change at the community scale. Understanding the interplay between climate and  
26 biotic interactions can improve our predictions of how ecosystems will respond to current  
27 global warming.
- 28 2. We aim to understand how climate affects the multi-trophic biotic interactions as well as the  
29 community structure using the enclosed communities of wasps associated with figs as study  
30 system.
- 31 3. To examine the presence and strength of multi-trophic species interactions, we first  
32 characterized the multi-trophic community of fig wasps associated with *Ficus racemosa* and  
33 then applied hierarchical joint species distribution models, fitted to community monitoring  
34 data. We further evaluated the effect of climate on individual species trends as well as inter-  
35 specific interactions.
- 36 4. We found that the competitive balance shifted to favour non-pollinating galling wasps and  
37 disadvantage the dominant pollinator in sub-optimal conditions. Further, sub-optimal  
38 conditions for galling wasps facilitated the occurrence of their specialized parasitoid, as  
39 changes cascaded across trophic levels and led to alternative community structures. Our  
40 results highlight the role of how species interactions can be modified across multiple trophic  
41 levels in a fig wasp community according to climate.

42 **Keywords:** biotic interactions, climate change, multi-trophic communities, fig wasps, joint  
43 species distribution model, temporal and spatial scale

## 44    **Abstract in Chinese**

45    生态系统中的各类生物通过寄生、捕食、互惠等相互作用组成的生态网络，并相互影响与  
46    制约。由于不同物种外界变化的响应存在差异，在群落水平上预测气候变化对生物的影响  
47    一直是个难点。了解气候与物种间相互作用怎样共同作用于群落中的物种，有助于完善生  
48    态系统如何响应当前气候变暖的预测。在该研究中，我们选用榕小蜂群落作为研究系统，  
49    目标揭示气候怎样影响多营养级生物互作体及其群落结构。我们首先通过应用层级联合物  
50    种分布模型（Hierarchical joint species distribution models）分析了群落监测数据，检测了  
51    聚果榕多营养级榕小蜂群落多种种间互作的关系与强度。再进一步评估气候对单个物种动  
52    态及种间互作的影响。研究发现：当处于非最佳气候条件时，同一营养级之间的种间竞争  
53    更倾向于非优势的非传粉造瘿小蜂，对优势的传粉榕小蜂不利；而且同一营养级之间竞争  
54    平衡的倾斜，通过跨营养级的级联效应促进了非传粉造瘿小蜂专性复寄生蜂的发生，从而  
55    导致群落结构的改变。结果强调了气候通过级联效应影响种间的不同互作关系，最终影响  
56    多营养级的榕小蜂群落。

57

## 1 INTRODUCTION

*“There is an urgent need to understand the impacts of climate change on species interactions within ecological communities”* (Ockendon et al., 2014).

Global climate change is already affecting individual species worldwide (IPCC, 2021), and is projected to become an even more severe threat to global biodiversity and ecosystem functioning (Bellard et al., 2012; Thomas et al., 2004). Although the impacts of climate change on the distribution, phenology, and the population size of many species are well documented (Chen et al., 2011; Martay et al., 2017; Menzel et al., 2006; Parmesan & Yohe, 2003; Thackeray et al., 2010; Walther et al., 2002), there have been fewer studies of its impacts on species interactions within ecological communities (Araújo et al., 2011; Blois et al., 2013; Gilman et al., 2010; Ockendon et al., 2014). This is unfortunate because organisms do not persist in isolation. Direct and indirect interactions within ecological networks can modify, mitigate or enhance the effects of climate change (Walther, 2010)

Species interactions, including trophic associations play an important role in shaping ecological communities and their outcome and intensity can be influenced by changing abiotic conditions (Ockendon et al., 2014). Yet, most studies of climate effects on species ignore biotic interactions and instead only consider one species at a time using a “bioclimate envelope” approach that typically correlates species’ distribution and abundance with climate variables (Araújo et al., 2011; Zarnetske et al., 2012). As it stands, the strict “bioclimate envelope” approach is problematic because it fails to incorporate the interdependencies of species in the communities (Tylianakis et al., 2008). Some species in the community may have strong effects on others through trophic interactions and the effects of climate change on those species can

have cascading effects upon others still (Araújo et al., 2011; Ebenman & Jonsson, 2005; Zarnetske et al., 2012). For example, the removal or changes in density of the top consumer caused by climate change can lead to disproportionate changes in species composition across trophic levels (Antiqueira et al., 2018; Devlin et al., 2015; Harley, 2011; Zarnetske et al., 2012). In addition to the effects on antagonistic interactions between consumers and their resources, climate change can also affect the competitive interactions between species within the same trophic level by shifting the competitive balances (Alba et al., 2019; Alexander et al. 2015; Gilman et al., 2010; Lord & Whitlatch, 2015). For example, it has been shown in a wide range of taxa that competitively dominant species are often more susceptible to climate change (Davis et al., 1998a, 1998b; Dunson & Travis, 1991). Climate clearly affects the strength and direction of species interactions within and across trophic levels. Quantifying how biotic interactions respond to a changing climate is a central step as we seek to move towards a predictive framework at the level of ecological community and above (Gilman et al., 2010; Zarnetske et al., 2012). However, it is often difficult to accommodate different types of species interactions and evaluate the response of those interactions to climate change due to the inherent complexity of species interaction networks. Here, we examine the effects of climate on species interactions and community structure using a multitrophic fig wasp community.

The fig-fig wasp system is well suited for studying the impacts of climate change on species interactions due to the clear community boundaries of communities, high number of replicates, and the relatively simple nature of enclosed multitrophic interaction networks (Kerdelhué et al., 2000; Segar & Cook, 2012; Segar et al., 2013). Fig trees (*Ficus*, Moraceae) are pollinated by one or a few highly host-specific pollinating wasp(s) (Hymenoptera: Agaonidae). Both partners are totally co-dependent in terms of reproductive success. Fig flowers are located

inside the enclosed inflorescences (syconia, hereafter figs), which can only be pollinated by pollen-carrying fig wasps. In return, fig wasps use part of the flower as the space and food for wasp larvae to develop (Weiblen, 2002). In addition to pollinating wasps, fig species also host several non-pollinating wasps (NPFWs, Chalcidoidea), including herbivorous gall-makers and up to two levels of parasitoids (Borges, 2015; Cook & Segar, 2010). In the fig-fig wasp system, each fig is a clearly bounded empty patch with limited resources (female flowers). The primary exploiters are herbivorous gall-makers including the pollinators and NPFWs, some of which compete for the discrete fig flowers as a nursery for their larvae. A subset of these gallers form large galls early in fig development and preempt pollinators. The next trophic level comprises parasitoid wasps whose larval develop at the expense of gall-makers. Those parasitoids arrive later than their hosts and can exhibit host preference (Kerdelhué et al., 2000). Therefore, there are two types of species interactions within fig wasp communities (Supplementary material; Figure S1): (i) the (sometimes asymmetric) competitive interactions among all the gall-makers (including pollinators), and (ii) the antagonistic interactions among parasitoids and their specific herbivore hosts (gall-makers). Non-pollinating gall making wasps form two community modules, large gallers that oviposit early can reduce accessibility for subsequent smaller gallers and pollinators (that oviposit simultaneously and can compete directly for ovules). Parasitoids are generally specific in that they are restricted to large or small galling hosts.

Pollinator wasps are competitively dominant in the small wasp module, and their density can determine that of other small gall-makers and their specific parasitoids. However, early arriving large gallers can determine small galler abundance. Moreover, it has been shown that pollinating fig wasps are sensitive to changes in climate and persist within a narrow range of temperature. Small changes in ambient temperature can severely decrease their lifespan

(Jevanandam et al. 2013). Consequently, any climate change resulting in suboptimal climate conditions for pollinators would have cascading effects on all NPFWs and therefore overall community structure.

Here, we evaluated the effect of climate on both competing and antagonistic interactions as well as species composition in the fig wasp community associated with a monoecious fig species *Ficus racemosa* by using a combination of community monitoring and a joint species modelling framework. First, we assessed the presence of trophic interaction networks within fig wasp communities. Second, we tested (i) whether seasonal, regional, and medium-term climate shifts changed the competitive balance to favor non-dominant small gall-makers (NPFWs) over the competitively dominant pollinator and (ii) whether parasitoids are more sensitive to such climate shifts, with the expectation that the loss of the top trophic level would increase the abundance of their host gall-makers. Finally, we investigated the potential consequences for restructuring of the entire community. We predict that altered species interactions cause by climate change will lead to shifts in community structure.

## 2 MATERIALS AND METHODS

### 2.1 Study system

*Ficus racemosa* is a functionally monoecious fig species. It is naturally distributed from India to Australia. Being the sole species of sub-section *Sycomorus* in this region, the associated fig wasp species are well known and strictly associated with *F. racemosa* (Supplementary material; Figure S1). Recent molecular evidence shows that *F. racemosa* is actively pollinated by an undescribed species *Ceratosolen* sp. in continental South-East Asia (Bain et al., 2016). In addition to the pollinating wasp, *F. racemosa* supports five other species of non-pollinating fig wasps (NPFWs).



These include two gall-maker species (*Sycophaga mayri* and *S. testacea*) and three parasitoid wasps (*S. agraensis*, *Apocrypta westwoodi* and *Apocrypta* sp.) in the Indo-China peninsula. The *Ceratosolen* pollinator and *S. mayri* (small gallers) compete directly for access to flower resources while *S. testacea*, a large gall that oviposits before either, reduces the number of available flowers for both small gallers. Competition is therefore asymmetric between modules but is symmetric within them. The top consumers *S. agraensis*, *A. westwoodi* and *Apocrypta* sp. are thought to be the specific parasitoids of *Ceratosolen* sp. *S. mayri* and *S. testacea*, respectively in China (Wang & Zheng, 2008, Xu et al., 2008) while in Indian peninsula *A. westwoodi* also attacks *S. testacea* (Yadav and Broges, 2018). While we do not rule out undetected generalism in our study region this would not affect our conclusions. The early gall *S. testacea* produces large galls that can reduce the potential number of pollinator offspring through a reduction of numbers of accessible ovules. However, all NPFWs on *F. racemosa* need the pollinator males to cut an exit hole from the fig so that they can leave the natal figs (Sun et al., 2009). The biology of fig wasp species and their interactions can be found in Supplementary material Table S1.

## 2.2 Fig wasp community sampling

We sampled figs of *F. racemosa* from a total of 34 trees and five localities. We sampled one site in Laos, Myanmar, one in Thailand, and two sites in China (Supplementary material; Figure S2). Sampling events at Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG) in China were distributed across a continuous period between 2002-2004, 2013-2014, and 2018-2019. We also conducted continuous sampling at Liuku (China) between 2013-2014. In addition, we sampled figs from Laos, Myanmar, and Thailand in 2018. More detailed sampling information can be found in Supplementary material Table S2. Among those sampling localities, Liuku represents the northernmost point of *F. racemosa*'s natural range. When

available, 30 mature figs from each tree were collected at the wasp-emerging phase. Each fig was placed into a  $200 \times 200$  mm mesh bag until the wasps emerged. All the wasps were collected and preserved in 75% ethanol, and were then identified to species. We counted the abundance of fig wasps as the total number of male and female wasps. All the specimens are currently located in YQP's collection at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. All six fig wasp species were collected in all the sampling sites.

#### Climate variables

Bioclimate data, including monthly average temperature ( $T_{ave}$ ), monthly maximum temperature ( $T_{max}$ ), monthly minimum temperature ( $T_{min}$ ), and monthly average precipitation ( $P_{ave}$ ) of Xishuangbanna and Liuku during the sampling period, were obtained from the Xishuangbanna Station for Tropical Rainforest Ecosystem at Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Bioclimate variables of the sampling localities in Laos, Myanmar, Thailand were obtained from WorldClim (Hijmans et al., 2005). We note that the climate data obtained from WorldClim may be less accurate than data taken from the ecological station; however, we assume that even these coarser measurements will approximate well the general differences across sites. To ensure the combination of climate data from data from meteorological stations and WorldClim did not affect our results, we extracted the monthly minimum temperature, monthly maximum temperature, and monthly total precipitation from WorldClim for XTBG and Liuku, and then compared both datasets. We found that the data from meteorological stations and WorldClim are highly correlated with a Spearman correlation coefficient  $r > 0.9$  (Supplementary material; Figure S3). All the climate variables were first divided into temperature- and precipitation-related subsets. For each subset, we first removed variables with weak explanatory power (Spearman correlation coefficients between variables and

pollinating fig wasp abundance  $|r| < 0.1$ ). We then addressed collinearity for each climatic subset by investigating the bivariate correlations between all possible pairs of variables. If  $|r| > 0.7$ , the variable with lower explanatory power (lower Spearman correlation coefficient between the variable and pollinating fig wasp abundance) was removed (see Dormann et al., 2013; Liu et al., 2017) for details). Finally, we selected monthly maximum temperature ( $T_{\max}$ ), and monthly average precipitation ( $P_{\text{ave}}$ ) as unique subsets of temperature- and humidity-related variables. Details on the correlation results can be found in Supplementary material Table S3 and Table S4. Moreover, because of the narrow range of temperature that the pollinator can tolerate, the optimal temperature for the pollinator was inferred by the ambient temperature where the pollinator's abundance peaks.

#### 2.4 Hierarchical modelling of species communities framework (HMSC)

Most evidence for the trophic interactions among fig wasp species associated with *F. racemosa* comes from manipulative field experiments (Ghara & Borges, 2010; Wang et al., 2014; Yadav & Borges, 2018). Joint species distribution models combine community-scale data alongside species responses to environmental variation. They have emerged as a powerful tool to detect the influence of environmental variables on species association networks (Dallas et al., 2019; Ovaskainen et al., 2017; Warton et al., 2015). Here, we apply the hierarchical modelling of species communities (HMSC) approach (Ovaskainen et al., 2017) to characterize the trophic interaction networks within the fig wasp communities.

The data (Y matrix) comprises the abundance of six fig wasp species surveyed in 773 mature *F. racemosa* figs (communities) from five localities between 2002 and 2019. We included  $T_{\max}$  and  $P_{\text{ave}}$  as fixed effects (X matrix). We added a community-level random effects

that related to spatial and temporal variations by including the year of sampling (seven levels), the season of sampling (three levels), study sites (five levels), and the tree sampled (34 levels).

We fitted the HMSC model using the R-package '*Hmsc*' (Tikhonov et al., 2020). We sampled the posterior distribution with four MCMC chains, each of which was run for 150,000 iterations with first 50,000 as burn-in. Each chain was thinned by 100 to yield 1,000 posterior sample per chain, and 4,000 posterior samples in total. We examined the model performance and convergence using species-specific AUC and Tjur's  $R^2$  values. To cross-validate the model, we applied 5-fold cross-validation by randomly assigning the total 773 sampling communities into five equally sized folds. More detail on HMSC model fitting procedure can be found in Tikhonov et al. 2020 (Tikhonov et al., 2020).

We characterized trophic associations of all six fig wasp species through the species association matrix provided by HMSC with values ranging from -1 to 1, indicating that the two species are more likely to co-occur (reaching 1) or less likely to co-occur (reaching -1) in comparison random expectations (Ovaskainen et al., 2017). Therefore, a negative association between species within the same trophic level in the fig wasp community can be considered as interspecific competition, and a positive association between species across trophic levels in the fig wasp community indicate host-parasite interactions. We visualized the trophic associations with more than 80% posterior support for either a negative or positive interaction.

## 2.5 Multiple regression analyses

To examine whether climate shifts change the competitive balance to favor non-dominant gall-makers over the dominant pollinators (and whether parasitoids are more sensitive to such climate shift) we investigate the importance of each climate variable on the abundance of the six fig wasp species. We assessed variable importance using an AICc-based model averaging approach

as described in Burnham and Anderson 2002 and Wagner et al. 2012. For each fig wasp species dataset, we first fitted the Generalized Linear Mixed Model (GLMM, with a Poisson error structure) that included the full set of additive models given the predictor variables, with random effects including the year of sampling, the season of sampling, study sites, and the tree of samplings using the R function ‘*lmer*’ (Bates et al., 2015). The temperature variable was represented as the square of Tmax as a quadratic term in all the models. All continuous covariates were z-transformed to get standardized effect sizes. Second, we calculated the Akaike weights of each model using the function ‘*akaike.weights*’ (Barton, 2009). We then calculated the relative importance (RI) of each variable, as the sum of the Akaike weights of the models in which the variable appears. RI values range from 0 to 1, indicating that the variables contribute more (more important, reaching 1) or less (less important, reaching 0) to fit the model. Since better models will have larger Akaike weights, any variable that contributes more to this model will thus have a higher relative importance value. Finally, we calculated model-averaged parameter estimates and standard errors for each predictor, as the sum of the estimates for each model in which the predictor appears, multiplied by the relative Akaike weight of each of those models. A predictor variable was considered to be significant for a particular dataset if the 95% confidence interval for its parameter estimate did not include 0. Moreover, we include the model selection details in Supplementary Material Table S5.

## 2.6 Shift in community structure

Although it is difficult to quantify the effects of climate on community structure, we used two-dimensional nonparametric multidimensional scales (NMDS) to visualize the community structure of fig wasp under different climate conditions. To do that, we first calculated the taxonomic beta diversity (TBD) among all fig wasp communities using abundance-based

262 pairwise Sørensen dissimilarity with R package ‘*betapart*’ (Baselga & Orme, 2012). We then  
263 used the R function ‘*metaMDS*’ (Oksanen et al., 2015) to perform NMDS analyzes and plot the  
264 communities together with the climate variable Tmax.

265 All analyses were conducted using R software Version 3.6.3 (R Development Core Team, 2021).

266

## 3 RESULTS

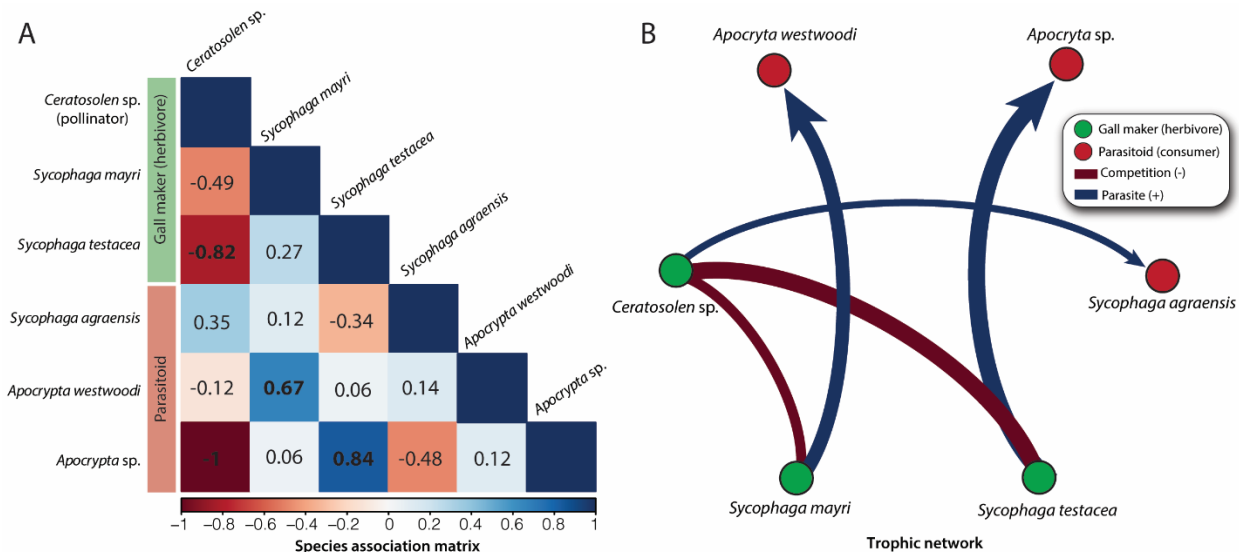
### 3.1 Sampling effects

A total of 951 figs (communities) were sampled from 2002 to 2019 with 680 figs from XTBG, 182 figs from Liuku, 17 figs from Laos, 40 figs from Myanmar, and 32 from Thailand (Supplementary materials Table S3). Overall, the pollinator *Ceratosolen* sp. dominates the fig wasp community with the average abundance of 713 individuals ( $713 \pm 26$ , mean  $\pm$  SE) per fig. The abundance of its two competing gall makers species *Sycophaga mayri* and *S. testacea* is 133 ( $133 \pm 4$ , mean  $\pm$  SE), and 104 ( $104 \pm 5$ , mean  $\pm$  SE) per fig, respectively. It is worth noting that *S. testacea* arrive at the fig much earlier than the pollinator and pre-empt the space for the pollinator (priority effect), while *S. mayri* competes directly with the pollinator by colonizing figs at the same time. All three parasitoids are less abundant compared to lower-trophic gall makers with 25 ( $25 \pm 1$ , mean  $\pm$  SE, per fig) for *S. agraensis*, 43 ( $43 \pm 4$ , mean  $\pm$  SE, per fig) for *Apocrypta* sp., and 39 ( $39 \pm 2$ , mean  $\pm$  SE, per fig) for *A. westwoodi*.

### 3.2 Fig wasp trophic interaction networks

After controlling for climate (both temperature and precipitation) and spatio-temporal differences (i.e., tree, locality, season, year), the species association matrix captures the potential association between fig wasp species with the values ranging from -1 to 1. We found strong negative species associations between the pollinator *Ceratosolen* sp. and other gall-makers *S. mayri* and *S. testacea*, suggesting those species are less likely to co-exist in the same fig, which may be due to competition (Figure 1A). The strong positive species associations across trophic levels indicated the specific host-parasite relationship between *Ceratosolen* sp. and *S. agraensis*, *S. mayri* and *Apocrypta westwoodi*, and *S. testacea* and *Apocrypta* sp. (Figure 1A). Based on this species

association matrix, we built the complete trophic interaction network for the fig wasp community associated with *F. racemosa*. This network included competitive interactions between the pollinator and the other two gall-makers, and three pairs of parasite-host interactions (Figure 1B).



**Figure 1.** Species interactions of fig wasps associated with *Ficus racemosa*. (A) Species association matrix based on the hierarchical model of species communities (HMSC) model, with blue (or red) depicting species pairs that are more likely to co-occur (or less often). The numbers are the species association values. (B) Trophic network of fig wasp species in the community based on A and our knowledge of the wasp biology. The edge width represented the species association value inferred from A. There are strong negative biotic interactions between the pollinator *Ceratosolen* sp. and the non-pollinating gall maker *Sycophaga testacea* and *S. mayri* due to competition. Parasitoid wasps *Apocrypta* sp. and *A. westwoodi* parasitise *S. testacea* and *S. mayri*, respectively.



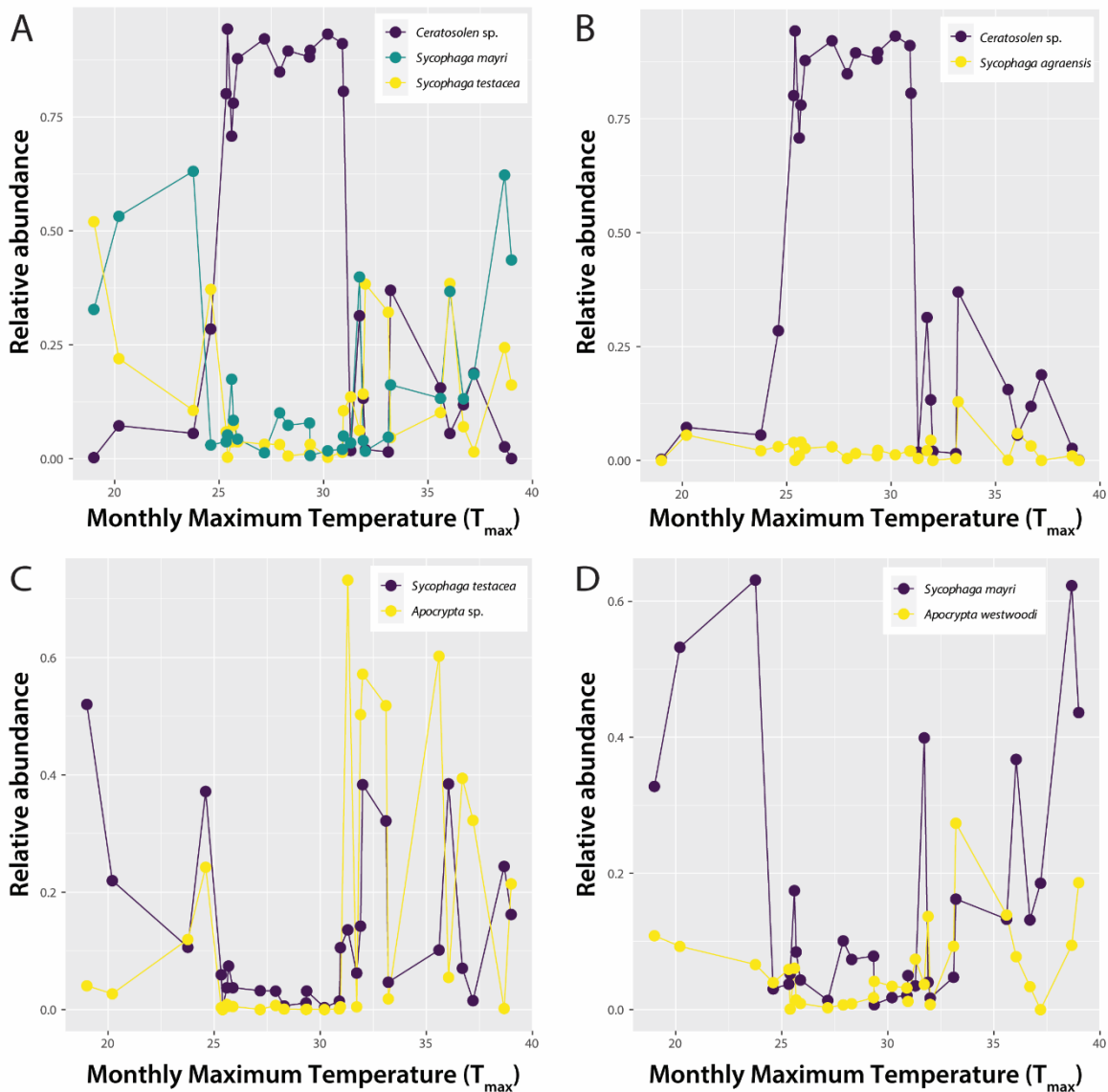
### 3.3 The effect of climate on species interactions

The model averaged parameter estimates from multiple regression models indicated that the monthly maximum temperature ( $T_{\max}$ ) has a much stronger effect than the monthly average precipitation ( $P_{\text{ave}}$ , Table1). Therefore, we will only focus on the effects of  $T_{\max}$ .  $T_{\max}$  is a strong and significant predictor of abundance for the gall-making species (Table 1; *Ceratosolen* sp.: Relative Importance (RI) =1, adjusted  $R^2$ =0.66; *Sycophaga mayri*: RI=1, adjusted  $R^2$ = 0.40; *S. testacea*: RI=1, adjusted  $R^2$ =0.37). The pollinator *Ceratosolen* sp. dominates the community and its relative abundance peaks at  $25^{\circ}\text{C} < T_{\max} < 31^{\circ}\text{C}$  while declining dramatically on either side (Figure 2A, Supplementary material; Figure 3). The optimal temperature range for pollinator is from  $25^{\circ}\text{C}$  to  $31^{\circ}\text{C}$  based on this observation. On the other hand, the abundance of *S. testacea* showed the reverse pattern when compared to the pollinator (Supplementary material; Figure 3).

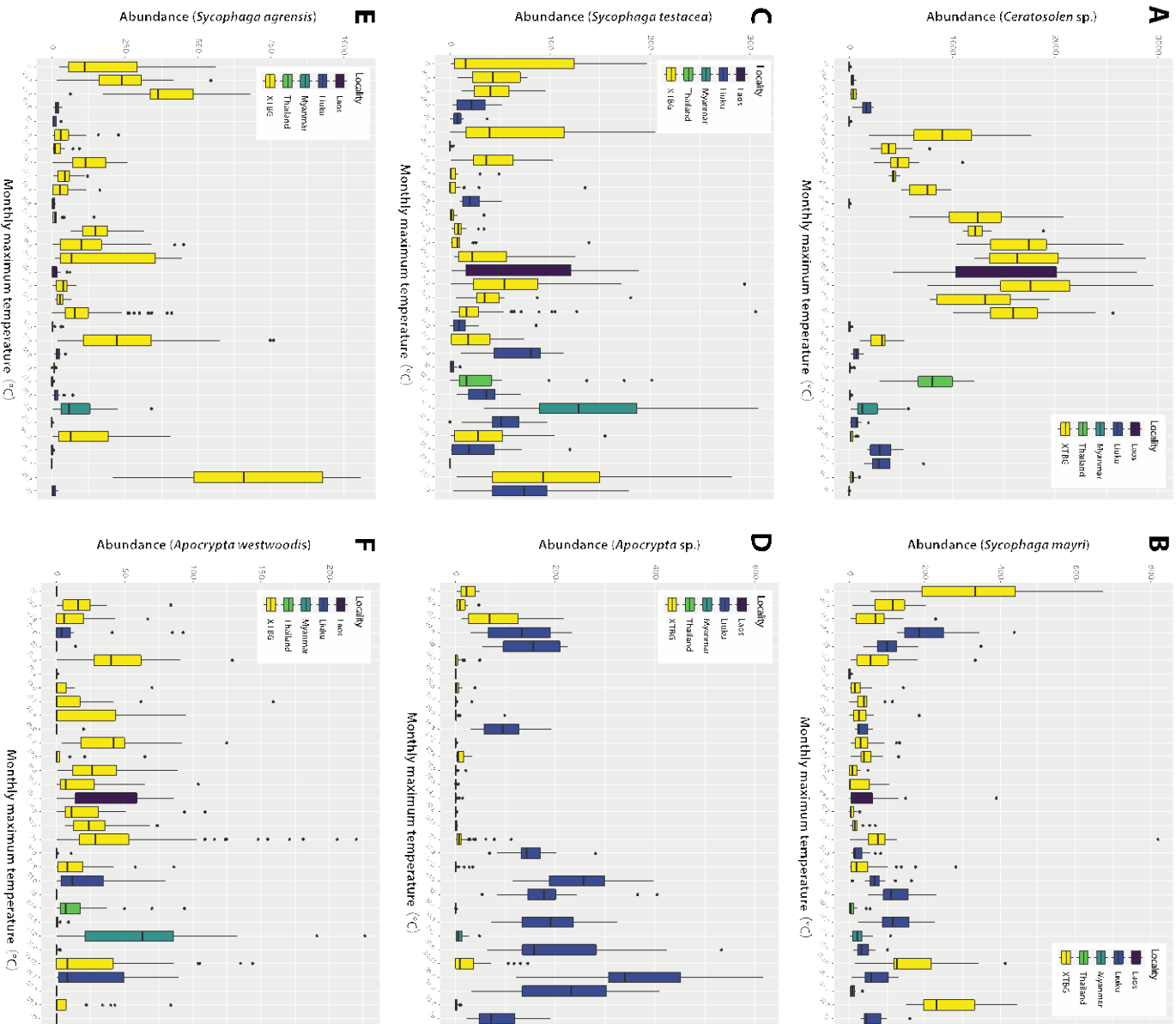
**Table 1.** Results of Multiple regression models including model-averaged parameter estimates, relative-importance values and adjusted  $R^2$  for each variable. \* The quadrat term of temperature.

Taxon	Temperature ( $T_{\max}^2$ ) *			Precipitation ( $P_{\text{ave}}$ )		
	Relative Importance	Estimate $\pm$ SE	Adjusted $R^2$	Relative Importance	Estimate $\pm$ SE	Adjusted $R^2$
<i>Ceratosolen</i> sp.	<b>1</b>	<b>-2.299 <math>\pm</math> 0.168</b>	<b>0.660***</b>	0.32	<b>-0.694 <math>\pm</math> 0.328</b>	<b>0.044*</b>
<i>Sycophaga agraensis</i>	0.10	0.007 $\pm$ 0.009	0.004	0.18	0.042 $\pm$ 0.877	0.03
<i>Sycophaga mayri</i>	<b>1</b>	<b>3.678 <math>\pm</math> 0.053</b>	<b>0.403***</b>	0.24	-3.549 $\pm$ 4.606	0.012
<i>Sycophaga testacea</i>	<b>1</b>	<b>2.1528 <math>\pm</math> 0.381</b>	<b>0.367***</b>	0.23	<b>0.8545 <math>\pm</math> 0.153</b>	<b>0.042*</b>
<i>Apocrypta westwoodi</i>	0.1	0.029 $\pm$ 0.033	0.026	0.16	-0.086 $\pm$ 0.133	0.058
<i>Apocrypta</i> sp.	0.12	-0.122 $\pm$ 0.230	0.024	0.37	<b>-0.327 <math>\pm</math> 0.041</b>	<b>0.036*</b>

320  $T_{\max}$  does not have strong effects on the abundance of any of the parasitoid wasps (Table 1; *S.*  
 321 *agraensis*:  $RI=0.10$ , adjusted  $R^2=0.004$ , *Apocrypta* sp.  $RI=0.12$ , adjusted  $R^2=0.002$ , and *A.*  
 322 *westwoodi*:  $RI=0.1$ , adjusted  $R^2=0.003$ ). The abundance of *S. agraensis* (parasite of *Ceratosolen*  
 323 sp.) and *A. westwoodi* (parasite of *S. mayri*) is relatively stable regardless of temperature  
 324 conditions and the abundance of their host species (Figure 2B, D). However, the abundance of  
 325 *Apocrypta* sp. (parasite of *S. testacea*) increases dramatically with the increasing abundance of  
 326 its host species only when  $T_{\max}$  is above  $32^{\circ}\text{C}$  (Figure 2C).



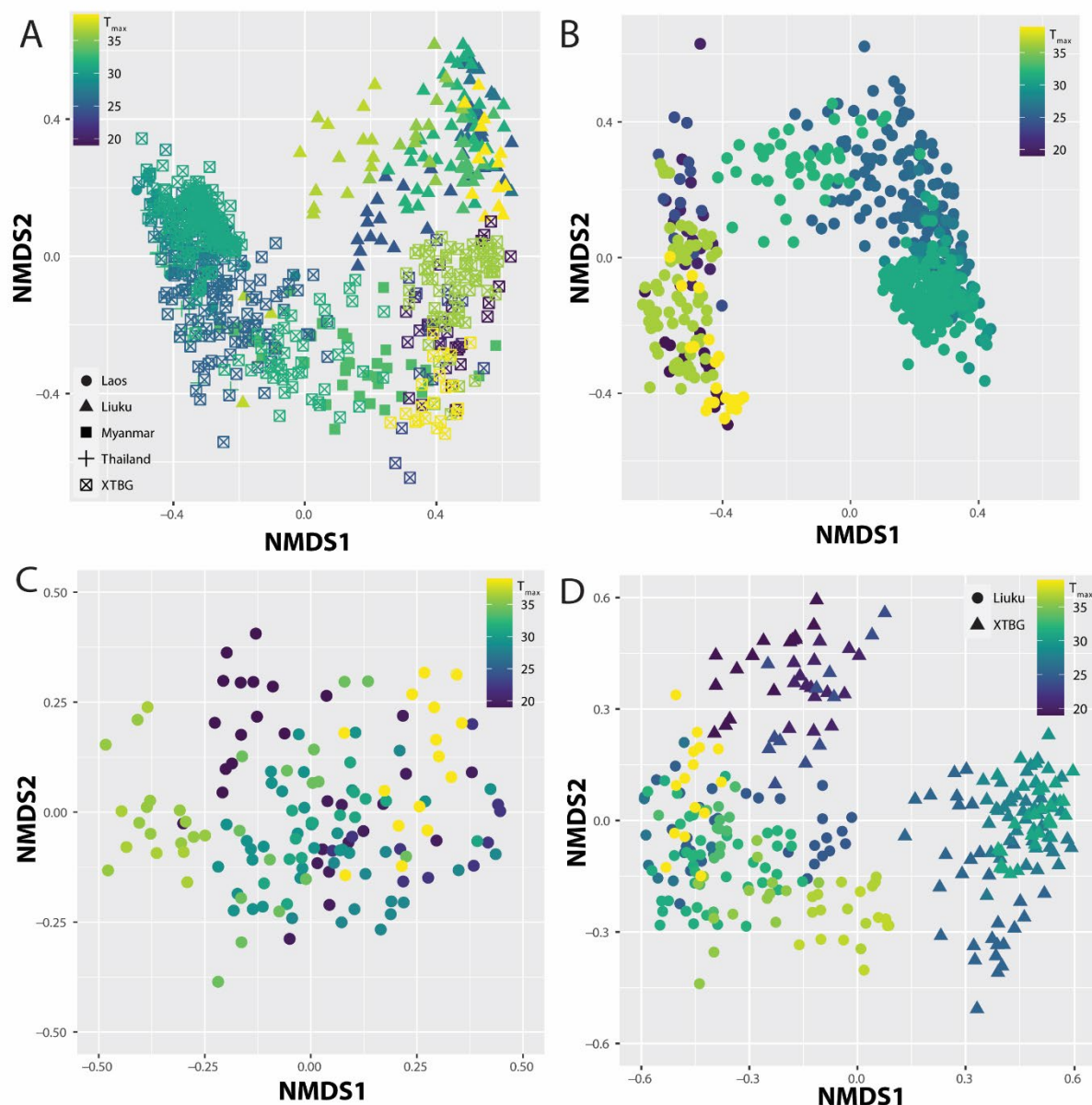
328 **Figure 2.** Relative abundance of fig wasp species with changing monthly maximum temperature  
 329 (T<sub>max</sub>). A. Relative abundance of three galler competitors. B-D. Relative abundance of three  
 330 parasitoid-host pairs: *Sycophaga agraeensis* and *Ceratosolen* sp., *Apocrypta* sp. and *S. testacea*,  
 331 and *A. westwoodi* and *S. mayri*.



**Figure 3.** The abundance of the 6 fig wasp species associated with *Ficus racemosa* with changing monthly maximum temperature. **(A).** *Ceratosolen* sp., **(B).** *Sycophaga mayri*, **(C).** *S. testacea*, **(D).** *Apocrypta* sp., **(E).** *S. agraensis*, and **(F).** *A. westwoodi*. The abundance of each fig wasp was counted at fig level. The boxes enclose the 25–75th percentiles of the values, the whiskers extend to 1.5 times the interquartile range.

### 3.4 The effects of climate change on community structure.

Overall, the results of NMDS ordination revealed a clear separation between the fig wasp communities from Liuku and the remaining localities (Figure 4A). Moreover, NMDS also indicates that the community structure within the tropics was significantly related to  $T_{\max}$  and can be separated into two clusters: with one cluster located in pollinator's optimal temperature range, and another located below or above the optimal temperature range (Figure 4A). This separation in community structure based on  $T_{\max}$  becomes even more obvious when only examining the fig wasp communities from XTBG, where sampling was most continuous (Figure 4B). This shift in community structure is consistent with the changing competitive interactions between pollinator and other gall-makers with the temperature shift into sub-optima (Figure 4A). Although, no clear separation in community composition with temperature was found in Liuku (Figure 4C), we found that Liuku communities were clustered with the sub-optimal XTBG communities across like-for-like temporal comparisons (Figure 4D).



**Figure 4.** Nonmetric multidimensional scaling (NMDS) ordination of fig wasp community under different monthly maximum temperature ( $T_{max}$ ) based on taxonomic beta diversity. A. All 773 communities that were collected from five localities during 2002-2019; B. Communities from XTBG; and C. Communities from Liuku. D. Communities from XTBG and Liuku that were collected from 2013-2014.

## 4 DISCUSSION

Our analysis of fig wasp communities based on joint species distribution models and monitoring data provides insights into the effect of climate on multiple species interactions within the same community. We suggest that long-term climate change might eventually lead to restructuring of the entire wasp community. First, our results show seasonal temperature shifts dramatically affect the abundance of the pollinator wasps, leading to a shift in the competitive balance to favor originally non-dominant NPFWs. Second, we document that parasitoids are not sensitive to the temperature variation; rather they are influenced by the availability of their hosts. Finally, we find a shift in community structure that reflects that of temperature. Together, our findings highlight the predominant role of temperature in affecting the fig wasp community structure by changing the strength of competitive interactions.

### 4.1 Trophic interaction networks in *F. racemosa*

Although the network of fig wasps associated with *F. racemosa* is relatively simple, precisely quantifying interaction strength is still difficult. By using joint species distribution models, which leverage observed community data, we detected both competitive interactions within and host-parasite interactions across trophic levels. While two NPFWs gall-makers (*S. testacea* and *S. mayri*) both compete with the pollinator *Ceratosolen* sp., *S. testacea* is a much stronger (although indirect) competitor than *S. mayri* (still an effective competitor, Supplementary material Figure S4). This result is likely due to the ecological differences stemming from arrival order. *S. testacea* arrives and lays their eggs at the very earliest stages of fig development, inhibiting the establishment of the later-arriving pollinators from the same trophic level due to a strong priority effect (Fukami, 2015). On the other hand, there are no priority effects between *S. mayri* and the pollinator since they arrive almost simultaneously. Interestingly, rather than competitive

exclusion, we found positive species association between *S. testacea* and *S. mayri*, suggesting that they co-occur more often than expected by chance. There may be little direct competition or priority effect influencing this interaction. Unlike the pollinator, which lays many eggs and as such prefers unoccupied figs, *S. mayri* has much smaller egg load and can tolerate any ovule regardless of how many neighbors it may have (Ghara & Borges, 2010). In fact, it is very likely that *S. mayri* even prefers figs partially exploited by *S. testacea* because this reduces potential competition with pollinators. Gallling wasps also require pollinator males to release them from figs, so total exploitation should be selected against. Despite this we found 76/771 figs containing *Sycophaga* individuals and no pollinators. Across trophic levels, we detected three specific host-parasitoid interactions, which are consistent with the field observations. Among these interactions, the species association between pollinators and *S. agraensis* is relatively weak in comparison to the association between *S. testacea* – *Apocrypta* sp., and *S. mayri* – *A. westwoodi*. It could be that the low abundance and occurrence of *S. agraensis* in our community data reduced the statistical power of the joint species distribution model (Dallas et al., 2019). In general, our models do not correct for low abundance or relate abundance directly to additional factors (e.g., phenology). However, it is likely that Northern populations are generally ‘slower’ (e.g., longer fig development times and intervals between fruiting) as a direct correlate of decreased temperature (Chen et al., 2018). Therefore, temperature drives these additional factors.

#### 4.2 Abortion of figs and associated uncertainty

Furthermore, the local abundance of *Ceratosolen* sp. and *S. mayri* has implications for rates of fig abortion and can result in over or under estimation of *S. testacea* abundance. It is important to discuss the evidence for multiple outcomes concerning *S. testacea*. To some extent *S. testacea* is capable of preventing abortion when present. For example, in our data set 24/594 figs contain *S.*

*testacea* and no pollinators, showing that this species can sometimes prevent abortion. Within these 24 figs we found between 4 and 376 wasps (mean = 86). As such, we may over-estimate the relative abundance of *S. testacea* when the pollinator is rare, because unpollinated figs visited by other NPFWs would not reach maturity and thus be excluded from our study. Wang et al. (2008) also present evidence that both *S. testacea* and *S. mayri* are able to prevent abortion of *F. racemosa* figs.

However, data from one of our study sites (Sun et al., 2009) shows that abortion rates were as high as 87% when 20 or over developing *S. testacea* are present in a fig. While we lack abortion data for our study, we suggest that this is an important objective in terms of confirming some of our conclusions concerning this species. Furthermore, Zhang and Li (2022) showed that 40-56% of figs with *S. testacea* aborted and demonstrated an average abortion rate of 48% in figs only containing *S. testacea*. These data suggest that we underestimate the numbers of *S. testacea* when pollinators are scarce (these NPFWs are not ‘rescued’). It is difficult to assess the opposing influences of *S. testacea* on fig abortion: it can both prevent and induce fig abortion. Perhaps abortion is contingent on the physiological condition, pollination rates at the tree level or among individual variation with respect to fig hosts. We are thus unable to quantify fully the impact that *S. testacea* has on abortion in our study, but we can say that abortion was prevented by *S. testacea* in 4% of cases in our study.

#### 4.3 Impact of climate change on species interactions

The previous study reported that the survival times of female pollinators were shorter than those of NPFWs, and the short-lived pollinators is more sensitive to host plant phenology mismatches so that the community structure of fig wasps is influenced by phenology (Chen et al., 2018, 2020). Our results from multiple regressions show that temperature strongly affects the



occurrence and the abundance of all the gall makers (pollinator: *Ceratosolen* sp.; NPFWs: *S. mayri*, and *S. testacea*). The optimal temperature for the pollinator is 24°C -31°C inferred from our observation, and colder or warmer temperatures led to a steep drop in abundance. Its competitors, *S. mayri* and *S. testacea* on the other hand followed completely the opposite pattern. These results are highly suggestive of the fact that seasonal temperature shifts altered the competitive balance to favor *S. mayri* and *S. testacea* by strongly reducing the relative abundance of the competitively dominant pollinators in the community. Previous studies on thermal tolerance have already shown that the NPFWs are less sensitive and more tolerant to the temperature change (e.g. Chen et al. 2020). We suggest that the relative abundance patterns of *S. mayri* and *S. testacea* are driven by alternative outcomes from competitive interactions, rather than by the direct effects of the changing temperature. Our results highlight the role of biotic interactions as a mediator of the impact of climate on species in the community (Ockendon et al., 2014).

Our results suggest that *Ceratosolen* sp. has a narrower thermal tolerance than the NPFWs, yet it appears to be an excellent disperser (populations across southern China and Thailand are not well differentiated genetically) (Kobmoo et al., 2010). This may be a result of contrasting dispersal heights. Pollinating fig wasps are known to disperse long distances using above canopy winds, whereas NPFWs likely disperse in the shaded understory (Harrison and Rasplus, 2006). The exposed nature of canopy dispersal provides little shelter in comparison to the shaded subcanopy, and we suggest that this buffers variation in temperature to an extent that NPFWs can be expected to be less adversely influenced by climate change in the absence of forest clearance. These results also have wider implications for how community assembly changes when confronted to climate change because responses across interacting species will not be uniform.

On average, we found that parasitoids (the highest trophic level in our focal community) were not sensitive to temperature shift. In contrast, a number of studies have shown that species in the higher trophic positions are more sensitive to climate change due to their greater metabolic needs or smaller population size (Yang et al., 2011; Zarnetske et al., 2012). However, the relative abundance of *S. agragensis* and *A. westwoodi* is stable regardless of the changing temperature and the abundance of their host species (the pollinator, and *S. mayri*, respectively). This may be due to their relatively small population size and strong top-down control by the weaver ant *Oecophylla smaragdina* (Wang et al., 2014). On the other hand, the abundance of *Apocrypta* sp. increases with the increasing abundance of its host species *S. testacea* only at the warmer temperatures (above the pollinator's optimal temperatures). It is unclear why *Apocrypta* sp. did not increase its abundance at lower temperatures (below the pollinator's peak temperature) where its host species is also abundant.

#### 4.4 Impact of climate change on community structure

We found significant changes in fig wasp community composition in response to changing temperature. This shift was mainly due to the shifts in the outcome of competitive interactions. Species level response to climate change may be hard to predict due to variation in intrinsic thermal tolerance across communities of interacting species. At the community level changing temperature will influence relative dominance and competitive ability, potentially 're-wiring' ecological networks (Post & Pedersen, 2008; Schleuning et al., 2020; Tylianakis & Morris, 2017; Woodward et al., 2010; Yang et al., 2011). For example, the relative abundance of the pollinators declined dramatically outside of the optimal temperature range, while its competitors *S. mayri* and *S. testacea* showed the inverse response to the same temperature change. Consequently, the shifts in the competitive interactions between the pollinator and the other gall-makers lead to two

alternative fig wasp community structures: i) pollinator-dominated communities and ii) NPFW-dominated communities. Notably, we did not detect any significant change in community structure in Liuku across a range of temperatures. The temperature in Liuku never falls into the optimal temperature for the pollinator and the abundance of pollinators is continuously low. Consequently, NPFWs dominated the community structure in Liuku. This was also confirmed by the NMDS analysis, which showed separations between the communities from Liuku and pollinator-dominated communities sampled from XTBG from the same year (e.g., Figure 3D), although we only sampled for one year in Liuku.

#### 4.5 Limitations and future research

Finally, we acknowledge some limitations to the current study and suggest ways of generalizing these results further. We highlight the imbalanced nature of our data set, with XTBG dominating our sampling effort. Future studies should ensure more even temporal and spatial coverage across the range of *F. racemosa* (ideally extending as far as Australasia to the south and India to the west). Moreover, although we believe that sampling 30 figs per tree is sufficient to address our questions due to the fairly simple nature of *F. racemosa* fig wasp community, more sampling would be ideal to detect the responses of fig wasp community to the changing climate. Furthermore, we would urge future studies to include additional explanatory variables beyond climatic ones. For example, Wang and Sun (2009) found decreased pollination, and community level changes, in the dry season and across forest fragments. Fig availability also changes across the seasons, with dry conditions reducing the proportion of fruiting trees. Variables related to the intensity of interspecific interactions and the abiotic environment beyond climate therefore need to be included, because these may have increased explanatory power and offer alternative interpretations. Specifically, we suggest that estimates of the number of fruiting trees, fig number

per tree, and/or the stage of development of the figs, and fig abortion rates need to be made. Our approach may overestimate the relative numbers of *S. testacea* at locations where pollinators are absent because figs colonized by this species may not abort at such high rates as those colonized by other NPFWs. However, we may also underestimate the abundance of the wasp if it leads to increased rates of abortion. Both outcomes are supported by evidence. The latter would mean that we underestimate the abundance of *S. testacea* in locations where it ‘replaces’ *Ceratosolen* and does not alter our conclusions as dramatically as increased abortion at localities climatically favorable for *Ceratosolen* would do. Ideally, we would control for variation in abortion rates across all sites.

## 5 CONCLUSIONS

Understanding the impacts of climate change on species interactions is crucial for us to predict the response of natural communities and ecosystems to a changing climate (Gilman et al., 2010). By investigating the responses of fig wasp species to temperature shifts, our study showed that shifts non-optimal temperatures alters the competitive ability of the usually dominant pollinator. This has cascading effects on other gall makers through competitive interactions, resulting in an entirely different community structure. Overall, our study highlights the central role of biotic interactions in determining the impact of climate on ecological communities.

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## 520 AUTHORS' CONTRIBUTIONS

521 Y.Q.P. and C.L. designed study; K.M.M.A., H.H.C., and B.G.M. collected the data; C.L.  
522 analyzed the data; Y.Q.P., S.S., and C.L. wrote paper; all gave final approval for publication.

## 523 CONFLICT OF INTEREST

524 No conflict of interest exists for all the authors

## 525 DATA AVAILABILITY STATEMENT

526 All data are available on Dryad.

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## REFERENCES

- Alba, C., Fahey, C., & Flory, S. L. (2019). Global change stressors alter resources and shift plant interactions from facilitation to competition over time. *Ecology*, *100*(12), e02859. <https://doi.org/10.1002/ecy.2859>
- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515-518. <https://doi.org/10.1038/nature14952>
- Antiqueira, P. A. P., Petchey, O. L., & Romero, G. Q. (2018). Warming and top predator loss drive ecosystem multifunctionality. *Ecology Letters*, *21*(1), 72-82. <https://doi.org/10.1111/ele.12873>
- Araújo, M. B., Rozenfeld, A., Rahbek, C., & Marquet, P. A. (2011). Using species co-occurrence networks to assess the impacts of climate change. *Ecography*, *34*(6), 897-908. <https://doi.org/10.1111/j.1600-0587.2011.06919.x>
- Bain, A., Borges, R. M., Chevallier, M. H., Vignes, H., Kobmoo, N., Peng, Y. Q., Cruaud, A., Rasplus, J. Y., Kjellberg, F., & Hossaert-McKey, M. (2016). Geographic structuring into vicariant species-pairs in a wide-ranging, high dispersal plant-insect mutualism: the case of *Ficus racemosa* and its pollinating wasps. *Evolutionary Ecology*, *30*, 663-684. <https://doi.org/10.1007/s10682-016-9836-5>
- Barton, K. (2009). Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18.
- Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808-812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>

556 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models  
 557 using lme4. *Journal of Statistical Software*, 67(1), 1-48.  
 558 <https://doi.org/10.18637/jss.v067.i01>

559 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of  
 560 climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365-377.  
 561 <https://doi.org/10.1111/j.1461-0248.2011.01736.x>

562 Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the  
 563 past, present, and future of biotic interactions. *Science*, 341(6145), 499-504.  
 564 <https://doi.org/10.1126/science.1237184>

565 Borges, R. M. (2015). How to be a fig wasp parasite on the fig-fig wasp mutualism. *Current*  
 566 *Opinion in Insect Science*, 8:34-40. <https://doi.org/10.1016/j.cois.2015.01.011>

567 Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a  
 568 practical information-theoretic approach. New York, NY: Springer.

569 Chen, H.H., Zhang, Y., Peng, Y.Q., & Corlett, R. T. (2018). Latitudinal effects on phenology near  
 570 the northern limit of figs in China. *Scientific Reports*, 8, 4320.  
 571 <https://doi.org/10.1038/s41598-018-22548-7>

572 Chen, H. H., Li, Z. M., & Tang, L. Z. (2020). Effects of fig wasp temperature tolerance on  
 573 interspecific coexistence. *Biodiversity Science*, 28(10), 1222-1228.  
 574 <https://doi.org/10.17520/biods.2019383>

575 Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts  
 576 of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.  
 577 <https://doi.org/10.1126/science.1206432>

578 Cook, J. M., & Segar, S. T. (2010). Speciation in fig wasps. *Ecological Entomology*,  
579 35(Supplement s1), 54-66. <https://doi.org/10.1111/j.1365-2311.2009.01148.x>

580 Dallas, T. A., Laine, A.-L., & Ovaskainen, O. (2019). Detecting parasite associations within  
581 multi-species host and parasite communities. *Proceedings of the Royal Society B:*  
582 *Biological Sciences*, 286(1912), 20191109. <https://doi.org/10.1098/rspb.2019.1109>

583 Davis, A. J., Lawton, J. H., Shorrocks, B., & Jenkinson, L. S. (1998a). Individualistic species  
584 responses invalidate simple physiological models of community dynamics under global  
585 environmental change. *Journal of Animal Ecology*, 67(4), 600-612.  
586 <https://doi.org/10.1046/j.1365-2656.1998.00223.x>

587 Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., & Wood, S. (1998b). Making  
588 mistakes when predicting shifts in species range in response to global warming. *Nature*,  
589 391(6669), 783-786. <https://doi.org/10.1038/35842>

590 Devlin, S. P., Saarenheimo, J., Syväranta, J., & Jones, R. I. (2015) Top consumer abundance  
591 influences lake methane efflux. *Nature Communications*, 6, 8787.  
592 <https://doi.org/10.1038/ncomms9787>

593 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G.,  
594 Gruber, B., Lafourcade, B., Leitão, P. J., M nkiem ller, T., McClean, C., Osborne, P. E.,  
595 Reineking, B., Schr der, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013).  
596 Collinearity: a review of methods to deal with it and a simulation study evaluating their  
597 performance. *Ecography*, 36(1), 27-46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

598 Dunson, W. A., & Travis, J. (1991). The role of abiotic factors in community organization. *The*  
599 *American Naturalist*, 138(5), 1067-1091. <https://doi.org/10.1086/285270>



- Ebenman, B., & Jonsson, T. (2005). Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution*, 20(10), 568-575.  
<https://doi.org/10.1016/j.tree.2005.06.011>
- Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1-23.  
<https://doi.org/10.1146/annurev-ecolsys-110411-160340>
- Ghara, M., & Borges, R. M. (2010). Comparative life-history traits in a fig wasp community: implications for community structure. *Ecological Entomology*, 35(2), 139-148.  
<https://doi.org/10.1111/j.1365-2311.2010.01176.x>
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, 25(6), 325-331. <https://doi.org/10.1016/j.tree.2010.03.002>
- Harley, C. D. G. (2011). Climate change, keystone predation, and biodiversity loss. *Science*, 334(6059), 1124-1127. <https://doi.org/10.1126/science.1210199>
- Harrison, R.D., & Rasplus, J.-Y. (2006). Dispersal of fig pollinators in Asian tropical rain forests. *Journal of Tropical Ecology*, 22(6), 631-639. <https://doi.org/10.1017/S0266467406003488>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965-1978. <https://doi.org/10.1002/joc.1276>
- IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K.

623 Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University  
 624 Press.  
 625 Jevanandam, N., Goh, A.G., & Corlett, R.T. (2013). Climate warming and the potential  
 626 extinction of fig wasps, the obligate pollinators of figs. *Biology Letters*, 9(3), 20130041.  
 627 <https://dx.doi.org/10.1098/rsbl.2013.0041>  
 628 Kerdelhué, C., Rossi, J.-P., & Rasplus, J.-Y. (2000). Comparative community ecology studies on  
 629 old world figs and fig wasps. *Ecology*, 81(10), 2832-2849. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2000)081[2832:CCESOO]2.0.CO;2)  
 630 [9658\(2000\)081\[2832:CCESOO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2832:CCESOO]2.0.CO;2)  
 631 Kobmoo, N., Hossaert-Mckey, M., Rasplus, J.-Y., & Kjellberg, F. (2010). *Ficus racemosa* is  
 632 pollinated by a single population of a single agaonid wasp species in continental South-East  
 633 Asia. *Molecular Ecology*, 19(13), 2700-2712. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2010.04654.x)  
 634 [294X.2010.04654.x](https://doi.org/10.1111/j.1365-294X.2010.04654.x)  
 635 Liu, C., Dudley, K. L., Xu, Z. H., & Economo, E. P. (2017). Mountain metacommunities:  
 636 climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*,  
 637 41(1), 101-112. <https://doi.org/10.1111/ecog.03067>  
 638 Lord, J., & Whitlatch, R. (2015). Predicting competitive shifts and responses to climate change  
 639 based on latitudinal distributions of species assemblages. *Ecology*, 96(5), 1264-1274.  
 640 <https://doi.org/10.1890/14-0403.1>  
 641 Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., Barlow, K.  
 642 E., Botham, M. S., & Pearce-Higgins, J. W. (2017). Impacts of climate change on national  
 643 biodiversity population trends. *Ecography*, 40(10), 1139-1151.  
 644 <https://doi.org/10.1111/ecog.02411>

645 Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,  
 646 Braslavská, O., Briede, A., Chmielewski, F. M., Črepinšek, Z., Curnel, Y., Dahl, Å., Defila,  
 647 C., Donnelly, A., Filella, Y., Jatzak, K., ... Züst, A. (2006). European phenological  
 648 response to climate change matches the warming pattern. *Global Change Biology*, 12(10),  
 649 1969-1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>  
 650 Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E.,  
 651 Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C.,  
 652 Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014).  
 653 Mechanisms underpinning climatic impacts on natural populations: altered species  
 654 interactions are more important than direct effects. *Global Change Biology*, 20(7), 2221-  
 655 2229. <https://doi.org/10.1111/gcb.12559>  
 656 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G.  
 657 L., Solymos, P., Stevens M. H. H., & Wagner, H. (2015). Vegan: community ecology  
 658 package. <http://CRAN.R-project.org/package=vegan>  
 659 Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T.,  
 660 Abrego, N., & Chave, J. (2017). How to make more out of community data? A conceptual  
 661 framework and its implementation as models and software. *Ecology Letters*, 20(5), 561-576.  
 662 <https://doi.org/10.1111/ele.12757>  
 663 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts  
 664 across natural systems. *Nature*, 421(6918), 37-42. <https://doi.org/10.1038/nature01286>  
 665 Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and  
 666 without herbivores. *Proceedings of the National Academy of Sciences of the United States*  
 667 *of America*, 105(34), 12353-12358. <https://doi.org/10.1073/pnas.0802421105>

668 R Development Core Team. (2021). R: A Language and Environment for Statistical Computing;  
 669 R Foundation for Statistical Computing: Vienna, Austria.

670 Schleuning, M., Neuschulz, E. L., Albrecht, J., Bender, I. M. A., Bowler, D. E., Dehling, D. M.,  
 671 Fritz, S. A., Hof, C., Mueller, T., Nowak, L., Sorensen, M. C., Böhning-Gaese, K., &  
 672 Kissling, W. D. (2020). Trait-based assessments of climate-change impacts on interacting  
 673 species. *Trends in Ecology & Evolution*, 35(4), 319-328.  
 674 <https://doi.org/10.1016/j.tree.2019.12.010>

675 Segar, S. T., & Cook, J. M. 2012 The dominant exploiters of the fig/pollinator mutualism vary  
 676 across continents, but their costs fall consistently on the male reproductive function of figs.  
 677 *Ecological Entomology*, 37(5), 342-349. <https://doi.org/10.1111/j.1365-2311.2012.01370.x>

678 Segar, S. T., Pereira, R. A. S., Compton, S. G., & Cook, J. M. 2013 Convergent structure of  
 679 multitrophic communities over three continents. *Ecology Letters*, 16(12), 1436-1445.  
 680 <https://doi.org/10.1111/ele.12183>

681 Su, B. F., Wang, R. W., Hu, Z., & Li, Y. T. (2009). Relation between two non pollinating wasps  
 682 oviposition and the fruit abscission on *Ficus racemosa*. *Acta Ecologica Sinica*, 29(4), 1770-  
 683 1776.

684 Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M.  
 685 S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards,  
 686 M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., Roy, D.  
 687 B., Scott, W. A., Smith, M., Smithers, R. J., Winfield, A. J., & Wanless, S. (2010). Trophic  
 688 level asynchrony in rates of phenological change for marine, freshwater and terrestrial  
 689 environments. *Global Change Biology*, 16(12), 3304-3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>  
 690

691 Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C.,  
 692 Erasmus, B. F. N., de Siqueira, M. F. M., Grainger, A., Hannah, L., Hughes, L., Huntley, B.,  
 693 van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T.,  
 694 Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*,  
 695 427(6970), 145-148. <https://doi.org/10.1038/nature02121>  
 696 Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge, M. M. J., Oksanen, J., &  
 697 Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc.  
 698 *Methods in Ecology and Evolution*, 11(3), 442-447. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13345)  
 699 [210X.13345](https://doi.org/10.1111/2041-210X.13345)  
 700 Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and  
 701 species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351-1363.  
 702 <https://doi.org/10.1111/j.1461-0248.2008.01250.x>  
 703 Tylianakis, J. M., & Morris, R. J. (2017). Ecological Networks Across Environmental Gradients.  
 704 *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 25-48.  
 705 <https://doi.org/10.1146/annurev-ecolsys-110316-022821>  
 706 Wagner, C. E., Harmon, L. J., & Seehausen, O. (2012). Ecological opportunity and sexual  
 707 selection together predict adaptive radiation. *Nature*, 487(7407), 366-369.  
 708 <https://doi.org/10.1038/nature11144>  
 709 Walther, G. R. (2010). Community and ecosystem responses to recent climate change.  
 710 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2019-  
 711 2024. <https://doi.org/10.1098/rstb.2010.0021>

712 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-  
 713 M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate  
 714 change. *Nature*, 416(6879), 389-395. <https://doi.org/10.1038/416389a>  
 715 Wang, B., Geng, X.-Z., Ma, L.-B., Cook, J. M., & Wang, R.W. (2014). A trophic cascade  
 716 induced by predatory ants in a fig-fig wasp mutualism. *Journal of Animal Ecology*, 83(5),  
 717 1149-1157. <https://doi.org/10.1111/1365-2656.12219>  
 718 Wang, R. W., & Zheng, Q. (2008). Structure of fig wasp community: temporal segregation of  
 719 oviposition and larval diets. *Symbiosis*, 45, 113-116.  
 720 Wang, R.W., & Sun, B. F., (2009). Seasonal change in the structure of fig-wasp community and  
 721 its implication for conservation. *Symbiosis*, 47(2):77-83.  
 722 <https://doi.org/10.1007/BF03182290>  
 723 Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., &  
 724 Hui, F. K. C. (2015). So many variables: joint modeling in community ecology. *Trends in*  
 725 *Ecology & Evolution*, 30(12), 766-779. <https://doi.org/10.1016/j.tree.2015.09.007>  
 726 Weiblen, G. D. (2002). How to be a fig wasp. *Annual Review of Entomology*. 47(47), 299-330.  
 727 <https://doi.org/10.1146/annurev.ento.47.091201.145213>  
 728 Woodward, G., Benstead, J. P., Beveridge, O. S., Blanchard, J., Brey, T., Brown, L. E., Cross, W.  
 729 F., Friberg, N., Ings, T. C., Jacob, U., Jennings, S., Ledger, M. E., Milner, A. M., Montoya,  
 730 J. M., O'Gorman, E., Olesen, J. M., Petchey, O. L., Pichler, D. E., Reuman, D. C.,  
 731 Thompson, M. S. A., Van Veen, F. J. F., & Yvon-Durocher, G. (2010). Chapter 2-  
 732 Ecological Networks in a Changing Climate. G. Woodward (Eds.), *Advances in Ecological*  
 733 *Research*, (pp. 71-138). Academic Press.

734 Xu, F. J., Yang D. R., Peng, Y. Q., Xu, L., & Chen, G. H. (2008). Study of the oviposition  
 735 behavior and the diet of the nonpollinating fig wasp of *Ficus racemosa*. *Journal of Yunnan*  
 736 *Agricultural University*, 23(1), 36-41.

737 Yadav, P., & Borges, R. M. (2018). Host-parasitoid development and survival strategies in a  
 738 non-pollinating fig wasp community. *Acta Oecologica*, 90, 60-68.  
 739 <https://doi.org/10.1016/j.actao.2017.04.001>

740 Yang, H., Wu, M., Liu, W., Zhang, Z., Zhang, N., & Wan, S. (2011). Community structure and  
 741 composition in response to climate change in a temperate steppe. *Global Change Biology*,  
 742 17(1), 452-465. <https://doi.org/10.1111/j.1365-2486.2010.02253.x>

743 Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic Multipliers of Climate Change.  
 744 *Science*, 336(6088), 1516-1518. <https://doi.org/10.1126/science.1222732>

745 Zhang, X. W., & Li, L. H. (2020). An early gall-inducing parasitic wasp adversely affects the  
 746 fitness of its host *Ficus* tree but not the pollinator. *Scientific Reports*, 10, 14941.  
 747 <https://doi.org/10.1038/s41598-020-71738-9>