Received: 14 October 2022 | Revised: 31 January 2023 | Accepted: 11 April 2023

DOI: 10.1002/ecy.4062

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Host insect specificity and interspecific competition drive parasitoid diversification in a plant–insect community

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Funding information
China Postdoctoral Science Foundation, Grant/Award Number: 2021M700472; Program of Introducing Talents of Discipline to Universities, Grant/Award Number: B13008; State Key Laboratory of Earth Surface Processes and Resource Ecology, Grant/Award Number: 2022-KF-10; National Natural Science Foundation of China, Grant/Award Number: 32261123001

Handling Editor: William E. Snyder

Abstract

Ecological interactions among plants, insect herbivores, and parasitoids are pervasive in nature and play important roles in community assembling, but the codiversification of tri-trophic interactions has received less attention. Here we compare pairwise codiversification patterns between a set of 22 fig species, their herbivorous pollinating and galling wasps, and their parasitoids. The parasitoid phylogeny showed significant congruence and more cospeciation events with host insects phylogeny than with host plants. These results suggest that parasitoid phylogeny and speciation is more closely related to their host insects than to their host plants. The pollinating wasps hosted more parasitoid species than gallers and indicated a more intense interspecific competition among parasitoids associated with pollinators. Closer matching and fewer evolutionary host shifts were found between parasitoids and galler hosts than between parasitoids and pollinator hosts. These results suggest that interspecific competition among parasitoids, rather than resource availability of host wasps, is the main driver of the codiversification pattern in this community. Therefore, our study highlights the important role of interspecific competition among high trophic level insects in plant–insect tri-trophic community assembling.

KEYWORDS
codiversification, fig, fig parasitoid wasp, host switching, interspecific competition, tri-trophic community

INTRODUCTION

Vast numbers of species are involved in the tri-trophic interactions between plants, insect herbivores, and insect parasitoids (e.g., Lopez-Vaamonde et al., 2005; Nelson et al., 2014). However, the understanding of parasitoids and host insects specificity is not well developed (but see McLeish et al., 2010a). Nevertheless, it is well known that plant–herbivore and parasitoid–host interactions have important ecological consequences (Bustos-Segura

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et al., 2020; Fortuna et al., 2014) and strong evolutionary consequences (Hembry & Weber, 2020). The coevolution of hosts and parasites has been studied at the microevolutionary level within and across extant populations of interacting species (Hu et al., 2022; Kraaijeveld & Godfray, 1999). However, understanding insect–plant interactions needs to consider the third trophic level effects (Cuny et al., 2021; Price et al., 1980). With the rapid development of molecular markers, the advent of molecular phylogeny have greatly facilitated our ability to study macroevolutionary patterns by comparing the phylogenies of hosts and their natural enemies to test for evidence of cospeciation and patterns of host shifts (Agrawal & Zhang, 2021).

The macroevolutionary patterns of radiation by insect herbivores and their host plants have been studied in a wide range of insect and plant taxa (Agrawal & Zhang, 2021; Janz, 2011; Marquis et al., 2016; Yoder & Nuismer, 2010). These are antagonistic relationships and, while coevolution is expected in terms of plant defenses and insect resistance, there is not a general expectation of cospeciation (Hardy & Otto, 2014). Indeed, the focus is often on the frequency and patterns of host shifts which are widely considered to play a key role in the speciation of insect herbivores (Wilson et al., 2012), as discussed in the classic work of Ehrlich and Raven (1964), who emphasized the "arms race" between plants and insect herbivores and the possibility of "escape and radiate" coevolutionary patterns (Thompson, 1989). However, it is also common that closely related insects attack the same or closely related plants (e.g., Lopez-Vaamonde et al., 2005; Weiblen et al., 2006), suggesting that when a plant lineage is colonized the herbivores often radiate to some extent, but that host shifts, not long-term cospeciation, explain their use of a wide range of plants. While most insect–plant interactions are antagonistic, some insect lineages are both pollinators and herbivores of their host plants, so they impart both costs and benefits. In nursery pollination mutualisms, adult female insects pollinate the plant, but their offspring feed on and destroy some seeds. The most famous case involves figs (*Ficus*) and fig-pollinating wasps (Agaonidae), which are found throughout the global tropics and subtropics (Cook & Rasplus, 2003; Weiblen, 2002; Yang et al., 2015). Cospeciation has long been suspected in this system due to the extreme host specificity of the wasps and intricate coadaptations of the insect and plant morphology and development (Hayward et al., 2021; Weiblen & Bush, 2002); however, there were occasional host shifts at both deep and shallow nodes (Cruaud et al., 2012).

Although fig–pollinator mutualism is a major focus of evolutionary studies, figs also host many other wasp taxa with different ecological roles. Most *Ficus* species are attacked by several species of gall-inducing wasps that do not contribute to pollination (Borges, 2015, 2021; Cook & Rasplus, 2003). In fact, galling insects more generally (not just those on figs) are often very host-specific (Cook & Segar, 2010), probably due to the fact that precise adaptation is needed to reprogram the host genome to produce galls in which the insect larvae feed. Few studies have compared phylogenies of figs and gallers, but in tune with their antagonistic relationship and lack of vertical transmission (Hayward et al., 2021), there is little support for cospeciation (Wang, Peng, et al., 2019; Weiblen, 2002). Fig-pollinating wasps and the various lineages of non-pollinating gallers are all insect herbivores and, as such, are attacked by a range of insect parasitoids (DeGabriel et al., 2022; Kerdelhue et al., 2000; Marussich & Machado, 2007). Existing evidence suggests that these parasitoid fig wasps are also highly host–plant specific (Jousselin et al., 2008), but at least some of them attack insects on more than one *Ficus* species (Jiang et al., 2006; Marussich & Machado, 2007), and relatively few studies have probed this issue of host plant specificity.

In this tri-trophic community, when we consider resource (host) availability, one important difference between pollinators and gallers as hosts is that essentially every fig contains many pollinator offspring, while the offspring of any given galler species are patchier in space and time and, on average, much less numerous in the figs where they do occur. Different galler species may be either common or rare across fig fruits and have high or low numbers of individuals in occupied figs (DeGabriel et al., 2022; Segar et al., 2013). However, in general, from a parasitoid perspective, gallers represent a less abundant and patchier host resource than pollinators (Segar et al., 2013), and this may favor a wider host range for parasitoids of gallers than for parasitoids of pollinators. Under the host abundance hypothesis, we might predict more cospeciation between parasitoids and pollinator hosts than between parasitoids and galler hosts. Alternatively, if we consider competition between parasitoid species, then pollinators are usually attacked by more parasitoid species than gallers (e.g., Compton et al., 2018; Peng et al., 2005). From a parasitoid perspective, attacking host pollinators may therefore lead to more intense competition, and potentially competitive exclusion. Under the parasitoid competition hypothesis, we might predict the opposite pattern—more cospeciation between parasitoids and galler hosts than between parasitoids and pollinator hosts. Very few studies have compared phylogenies of parasitoids with host figs, pollinator or gallers, and most have not supported cospeciation (Jiang et al., 2006; Lopez-Vaamonde et al., 2001; Silvieus et al., 2008). Indeed, to our knowledge, only one study, involving wasps from African figs of *Galoglychia* (Jousselin et al., 2008), has reported evidence for the cospeciation of parasitoids, with both galling wasps and host figs.

In this paper, we focus on macroevolutionary patterns of host association and cophylogeny for 63 parasitoid morphospecies that attack either pollinating or galling wasps associated with a community of 22 *Ficus* species in southwestern China. We present phylogenies of the parasitoids sampled from host insects on these fig species and use these, along with phylogenies of their host insects and host plants, to address the following questions: (1) Do the parasitoids show evidence of codiversification with either (a) their host insects or (b) their host plants? Here, we predict that parasitoid codiversification with host insects is more likely due to the more intimate and direct physical association; (2) Does evidence for codiversification vary between two ecological subsets of parasitoids (a) those attacking fig-pollinating wasps and (b) those attacking (non-pollinating) galling insects? Here, we test two alternative hypotheses: (i) the host abundance hypothesis which predicts that parasitoids attacking pollinators are more likely to cospeciate than parasitoids attacking gallers. This is because pollinators (present in every fig in large numbers) represent a more abundant and consistent resource than gallers (present in some figs in smaller numbers) so parasitoids can persist long-term on pollinator hosts without host shifts; and (ii) the parasitoid competition hypothesis, which predicts the opposite, since more parasitoid species attack each pollinator species than attack each galler species. This creates more potential for competitive exclusion between parasitoids of pollinators and thus favors species that can also shift to new host.

MATERIALS AND METHODS

Taxonomic sampling, sequencing, and phylogenetic reconstruction

Parasitoid wasps were collected in the tropical rainforest at Xishuangbanna, China (21°41′ N, 101°25′ E) between 2008 and 2018. Parasitoid wasps occupy high trophic levels in the fig–fig wasp community; thus, their population sizes are generally smaller than those of pollinators and most gallers, and some parasitoids are rare species (e.g., DeGabriel et al., 2022). Mature figs were sampled from trees, and the wasps were allowed to emerge in mesh bags at ambient temperature. From the very large number of emerged wasps, we first identified insects to genus level and then sorted them into wasp morphospecies associated with each fig species. We included insects morphologically and included multiple representatives of all morphospecies from each fig species in our sequencing to test species identities and check for the likely presence of some cryptic species. This resulted in a sample of 247 parasitoid individuals belonging to 63 wasp morphospecies (50 Sycoryctinae; 5 Ormyridae; 7 Eurytomidae; 1 Sycophaginae: Appendix S1: Table S1) from 22 local fig species. To infer the host wasp species of parasitoid wasps, we searched the literature to determine the likely or confirmed host wasp species. The evidence for each host-parasitoid link was based on at least one of the following: experimental wasp introductions, oviposition timing, population size, gall size, and statistical pathway analyses (see Kerdelhue et al., 2000; Segar et al., 2013, 2014 for similar approaches). There is uncertainty for some of these links, as with most studies of parasitoids of concealed endophytic hosts, and the nature and source of evidence for each link is summarized in Appendix S1: Table S2.

We purified the whole genomic DNA from the whole body of each single parasitoid wasp and sequenced the nuclear ribosomal genes 18S rRNA (variable regions V3–V5) and 28S rRNA (D4–D5 expansion regions) and the mitochondrial cytochrome c oxidase subunit I (COI) gene. All gene sequences have been deposited in GenBank (see Appendix S1: Table S1). To reconstruct phylogenetic trees of host wasp and host fig species, we downloaded the published sequence data from Wang, Peng, et al. (2019) from GenBank. Using these sequences, we inferred the parasitoid, host wasp, and host fig phylogenies with Bayesian inference (details in Appendix S1: Section S1). The trees were all rooted using appropriate outgroups (e.g., three species of *Ceratosolen* fig pollinating wasps for the parasitoid phylogeny) (Appendix S1: Section S1). The parasitoid molecular phylogenies revealed a few cases where a putative morphospecies had surprisingly high interspecific genetic distances, or two putatively different species had very low genetic distances (details in Appendix S1: Section S1). For our cophylogenetic analyses, we interpreted the former cases as two different (cryptic) species. We also treated the latter cases as two different species as the cases involved different host plants, so may represent recent host shifts.

Pairwise cophylogenetic analyses

We used two approaches to quantify the degree of pairwise codiversification of parasitoid wasps with their host wasps or host figs: (1) a Procrustean distance-based approach to infer cophylogenetic concordance (PACo: Balbuena et al., 2013), and (2) a parsimony event-based approach for cophylogeny reconstruction (Jane: Conow et al., 2010), based on the costs of different underlying evolutionary events. Pairwise cophylogenetic analyses were conducted for the parasitoids and their inferred or confirmed host wasps.

We conducted PACo analyses with the paco (Hutchinson, Cagua, Balbuena, et al., 2017) and ape packages (Paradis et al., 2004) in R version 3.6.1 (R Core Team, 2021). In this approach, distances between species within a clade are measured based on the sum of their connecting branch lengths along the inferred phylogeny. To assess congruence between parasitoids and their hosts, we assumed contingent codivergence with parasitoid wasps as the reactive clade, given their unilateral dependence on hosts. The congruence of our best estimates of parasitoid and host phylogeny was then compared with a null distribution, generated from congruence values for 1000 parasitoid phylogenies created by random permutation of the parasite matrix.

We used two sets of event costs to conduct phylogeny reconciliation in Jane analysis. One set was based on the default set in Jane (0 for cospeciation; 1 for duplication, loss, failure to diverge; and 2 for host switching). The other set followed the parameters used by Cruaud et al. (2012) in their first model analyzing the cophylogenies of *Ficus* and pollinating wasps for a global sample of species. Specifically, we set the costs as 0 for cospeciation and 1 for all other events, which also matches the classic TreeMap cost-model (Charleston & Page, 2002). All analyses were run for 40 generations and considered 1000 populations. In the cases where different event distributions were identified, we used the average of each event number in all minimal cost sets, weighted by their respective relative frequencies. We used averaged Fisher's exact tests across pairs of event distributions to compare the codiversification patterns.

RESULTS

Pairwise codivergence of parasitoids and their inferred hosts: Distance-based

Overall, the average number of parasitoid species per host insect species was higher ($t = 2.123$, $\mathrm{df} = 13$, $p = 0.053$) for pollinator hosts than for galler hosts (Figure 1a,c). Meanwhile, the PACo analysis identified significant congruence both for the parasitoid–pollinator association ($m^2_{XY} = 9.7 \times 10^{-5}$, $p = 0.021$; Figure 1a) and the parasitoid–galler association ($m^2_{XY} = 2.6 \times 10^{-6}$, $p = 0.001$; Figure 1c), but with greater significance for the parasitoid–galler association.

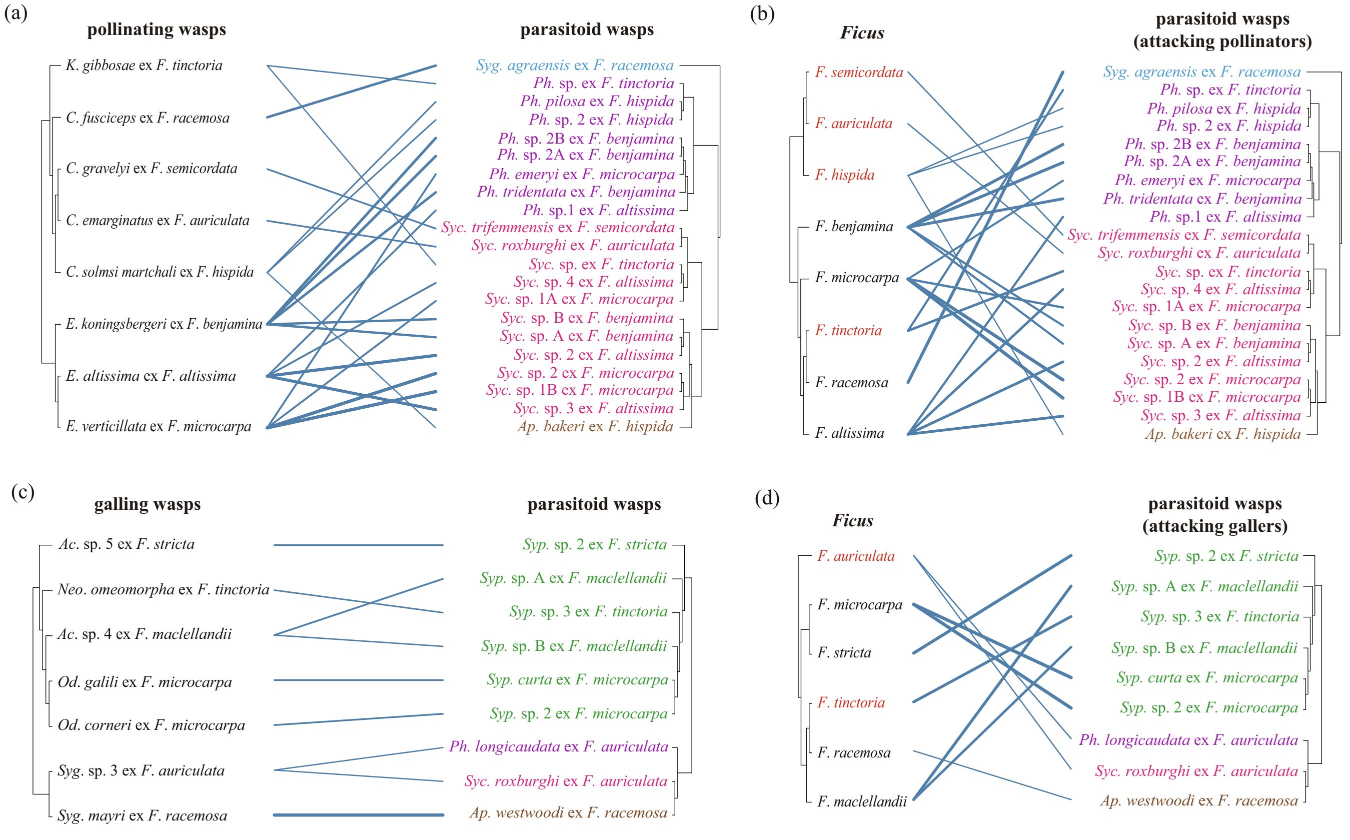

FIGURE 1 Cophylogenetic patterns between (a) pollinating and parasitoid wasps, (b) *Ficus* and parasitoid wasps associated with pollinator wasps, (c) galling and parasitoid wasps, and (d) *Ficus* and parasitoid wasps associated with galler wasps. For *Ficus*, red and black tip labels distinguish dioecious and monoecious species, respectively. For parasitoid wasps, the genera *Apocrypta*, *Sycoscapter*, *Philotrypesis*, *Sycophaga*, and *Sycophila* are shown in brown, pink, purple, blue, and green, respectively. Solid lines connecting species in the left- and right-hand phylogenetic trees indicate observed associations. Line thickness increases with the contribution of a particular association to overall phylogenetic congruence. The outgroups of each phylogeny were pruned in order to focus on the cophylogenetic pattern between parasitoids and their hosts. The "ex …" labels identify the host fig species of individual wasp species. *Ac.*, *Acophila*; *Ap.*, *Apocrypta*; *C.*, *Ceratosolen*; *E.*, *Eupristina*; *F.*, *Ficus*; *K.*, *Kradibia*; *Neo.*, *Neosycophila*; *Od.*, *Odontofroggatia*; *Ph.*, *Philotrypesis*; *Syc.*, *Sycoscapter*; *Syg.*, *Sycophaga*; *Syp.*, *Sycophila*.

The corresponding pairwise associations between parasitoids and host figs differed between the mutualistic and antagonistic pairings. Each fig species hosted more parasitoids of pollinators than parasitoids of gallers ($t = 1.797$, df = 12, $p = 0.097$; Figure 1b,d). However, neither the phylogenies of figs and parasitoids of pollinators ($m^2_{XY} = 0.535$, $p = 0.250$; Figure 1b) nor those of figs and parasitoids of gallers ($m^2_{XY} = 0.128$, $p = 0.051$; Figure 1d) showed significant congruence.

Pairwise codivergence of parasitoids and their inferred hosts: Event-based

The pairwise codiversification event distribution inferred by Jane revealed differences in the underlying evolutionary processes. The association fitted much more parsimoniously under the Cruaud et al. (2012) cost set than the default set (total costs = 17 and 27, respectively; Figure 2a and Appendix S1: Figure S1). Consequently, we used the more parsimonious results under the Cruaud et al. (2012) cost set.

The event distributions differed for codiversification through direct parasitism on wasps and indirect parasitism on figs, although these differences were only statistically significant for parasitoids of gallers when comparing their fit with either host gallers or host figs (average Fisher's exact tests, $p < 0.05$). Specifically, diversification of parasitoids involved more cospeciation with their direct host wasps than with their indirect fig hosts (Figure 2a). Cospeciation accounted for 7/20 and 6/9 of all speciation events in codiversification between parasitoids with pollinators and gallers, respectively. In contrast, cospeciation only accounted for 3/20 and 1/8 speciation events in codiversification between parasitoids with indirect host figs, respectively.

Our estimation of codiversification event distributions of parasitoids with pollinators differed from parasitoids with gallers, but the difference was not significant (averaged Fisher's exact tests, $p = 0.099$; Figure 2a). Diversification of parasitoids with gallers involved a higher proportion of cospeciation events (6/9) than with pollinators (7/20). Moreover, parasitoids also showed fewer host shifts (2/9) with gallers than with pollinators (9/20).

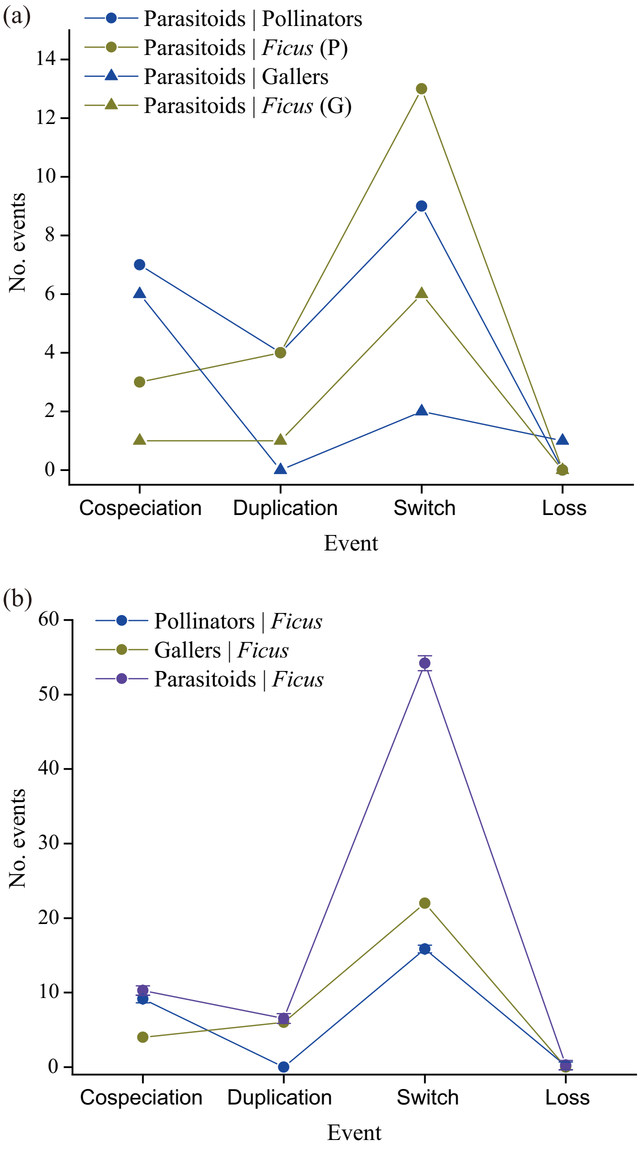

FIGURE 2 The frequencies of different types of co-phylogenetic events (cospeciation, duplication, association switch, association loss) between (a) various pairs of taxa (see inset legend) and (b) *Ficus* and different wasp types inferred by Jane, using the event cost set of Cruaud et al. (2012). X|Y denote that clade Y was the reference clade and clade X was the comparator clade; error bars indicate ±SD for cases in which Jane identified several different sets of outcomes associated with the same minimal cost. Lines linking events are provided to aid comparison of distributions for different taxa but convey no quantitative information.

Pairwise codivergence of all parasitoids and their host figs

Codiversification patterns were identified between all parasitoids (from both pollinator and galler hosts, including parasitoids not included in the analyses above; Appendix S1: Figure S2) and host figs. For the overall pairwise analyses between parasitoids and host figs, the phylogenies did not show significant congruence ($m^2_{XY} = 3.9637$, $p = 0.069$; Appendix S1: Figure S3). The distributions of event frequencies inferred by the Jane analyses revealed a majority of host switch events (57/72), as opposed to cospeciation (10/72) and duplication (5/72) events (Figure 2b).

DISCUSSION

We provide evidence from distance-based (PACo) and event-based (Jane) analyses that parasitoid wasps exhibit significant cospeciation with their direct wasp hosts but not with their indirect host figs. In addition, we found evidence that parasitoid wasps showed more cospeciation and fewer host switches with galler hosts than with pollinator hosts, as predicted by the parasitoid competition hypothesis and contradicting the host abundance hypothesis. Based on these patterns we suggest that interspecific competition between parasitoids for host insects is a significant force for codiversification patterns in this tri-trophic plant–insect community.

Host fig wasps have a strong influence on fig tri-trophic codiversification

Fig parasitoid wasps attack both fig pollinators and gallers, and depend on their galls to complete their life cycles. The significant congruence of the phylogenies of parasitoid wasps and their host wasps based on the PACo results reflects the dependency of this parasitic interaction (Figure 1), and reconstructions from Jane analyses suggest that the parasitoid–host wasp association involves more cospeciation than the parasitoid–host fig association (Figure 2a). In contrast, some other studies have found that parasitoid wasps show phylogenetic conservation of the use of host plant genera, but show no evidence of cospeciation with their host insects (e.g., Ives & Godfray, 2006; Lopez-Vaamonde et al., 2005). However, these cases indicated that host conservation between parasitoids and plants was mainly at the genus level, whereas our results focused on patterns within the *Ficus* genus. Furthermore, parasitism between fig parasitoid wasps and their host wasps may be even more intimately aligned than other parasitic interactions, because parasitoid wasps cannot finish their life cycle without the galls made by pollinators or gallers (Godfray, 1994).

Most fig parasitoids feed on pollinator or galler larvae, although there may also be rarer cases of hyperparasitoids. Based on our results, the antagonistic host–parasitoid interactions in these tri-trophic systems could show as much cospeciation as the mutualistic interactions between pollinators and figs (Figure 2b). Some fig parasitoids may show more host plant switching than other insect parasitoids, with high host-switching shown in a study on Asian *Philotrypesis* wasps (Jiang et al., 2006). However, another study on *Philotrypesis* wasps in Africa showed congruent topology with their *Galoglychia* host figs (Jousselin et al., 2008). These different patterns within wasps from the same genus, but from different continents, show that patterns can be lineage-specific, and more studies are needed for general patterns to emerge. Non-pollinating fig wasps may generally show less host-plant specificity than pollinators, because most of them lay their eggs directly through the fig wall, without the need to enter the fig, which may reduce host-specificity constraints (Lopez-Vaamonde et al., 2001; Wang, Peng, et al., 2019). Indeed, our results show that parasitoids switch between host figs more often than between host gallers (Figure 2b), and we found no evidence for significant cospeciation of parasitoids and host figs.

Previous studies have shown that volatile chemical cues are important for associations between host figs and fig wasps (Proffit et al., 2007), with parasitoids being attracted by a mix of herbivore-induced plant volatiles and oviposition-induced plant volatiles (Borges, 2015; Fatouros et al., 2012). Given the life histories of the different fig wasp functional groups, parasitoids usually oviposit later than their hosts, and may meet more complex and variable volatile cues that are less distinctive between fig species, and thus less likely to impede host shifts. Therefore, host specificity on the indirect hosts (plants) might often be lower for parasitoid wasps.

Finally, we note that, while it is straightforward to identify links between parasitoids and host plants based on rearing, definitive identification of the host insects of parasitoids is more challenging, especially for parasitoids of endophytic hosts (including many gall-inhabiting arthropods, such as fig wasps) that develop concealed within host plant tissues. Thus, inference of host-parasitoid links in fig wasp communities uses indirect evidence from statistical associations, relative timing of oviposition, and so forth, although results from experimental wasp introductions (Sun et al., 2008; Wu et al., 2013) and direct observations of larval parasitism (Zhen et al., 2004) are available for some taxa (see Appendix S1: Table S2).

In recent years, some studies have used polymerase chain reaction (PCR) -based methods to detect host DNA by analyzing the gut contents or frass of adult parasitoids (Hall et al., 2017; Rougerie et al., 2011). This can provide direct evidence of host-parasitoid links and has been used mainly for cases involving parasitoid wasps (Hymenoptera) whose hosts belong to other insect orders (Diptera, Lepidoptera, Hemiptera), permitting fairly straightforward design of taxon-specific primers (Hall et al., 2017; Rougerie et al., 2011), followed by direct Sanger sequencing. It would be interesting to test this approach with fig wasps, but more difficult, because both host and parasitoids are from the same hymenopteran superfamily (Chalcidoidea) making diagnostic primer design more challenging.

An alternative would be to just use the one set of primers and hope to produce amplicons from both host and parasitoid. This would no longer be suitable for

Sanger sequencing due to mixed template DNA, but might be resolved by cloning and sequencing. However, it would likely be costly and time-consuming as many more clones would need to be sequenced to have a good chance of including amplicons from the species that amplified less well. Consequently, it would probably be better for future studies attempting this to use next-generation sequencing of amplicons for more effective detection of minority PCR products.

Interspecific competition followed by host shifting is the main force in fig tri-trophic community codiversification

Antagonists can usually enhance their fitness by exploiting abundant and stable host resources. This may lead to intimate and species-specific host–parasitoid relationships, which might be expected to favor long-term cospeciation of hosts and parasites. In the fig microcosm, fig-pollinating wasps generally show much larger and more stable populations than galling wasps (e.g., Segar et al., 2013; Zhang et al., 2016). In addition, top-down trophic cascades involving predacious ants can cause high mortality of non-pollinating wasps and increase surviving pollinator numbers (Compton & Robertson, 1988; Wang, Segar, et al., 2019). Therefore, pollinators generally represent a more abundant and consistent host resource than non-pollinating gallers. However, using PACo analyses, we found greater congruence between the phylogenies of parasitoids and their host gallers than between parasitoids and their host pollinators (Figure 1), which contradicts this host abundance hypothesis. Moreover, using Jane analyses, parasitoids were inferred to have more host switches and fewer cospeciation events with host pollinators than with host gallers (Figure 2a), although the event-based differences were not significant (discussed below). Together, these results indicate that host abundance is probably not the main driver of codiversification between parasitoids and their host wasps.

Our Jane analyses suggest that cospeciation is about twice as common for parasitoids with galler hosts (6/9 events = 67%) as for those with pollinator hosts (7/20 = 35%), but this is not significant (Fisher's exact test). Given this, and the fact that PACo analyses also showed more cospeciation for parasitoids with gallers, we further explored the power of event-based analyses to reveal a significant difference. If we hold the 6/9 galler cospeciation events constant, then the number of pollinator cospeciation events must decrease to 2/20 before obtaining a significant difference. If we use the opposite approach and hold the 7/20 pollinator events constant, then even increasing to 9/9 galler events does not generate a significant difference. This illustrates that, even after sampling 22 fig wasp communities (and 69 parasitoid species), subsequent data filtering and event reconstructions may severely limit statistical power to detect differences. Nevertheless, the greater proportion of parasitoid-galler cospeciation events suggested by the Jane analyses is also supported by the higher level of significant congruence found in the PACo analyses.

Fewer switches between galler hosts could be explained by lower interspecific competition, because there are fewer parasitoid species per galler host than per pollinator host (Figure 1). Higher interspecific competition between parasitoids sharing the same host insect decreases parasitoid fitness and may lead to competitive exclusion. However, host shifts may enhance parasitoid fitness by providing a partial escape from such resource competition. Our results support this alternative parasitoid competition hypothesis and suggest that interspecific competition may play an important role in determining patterns of cospeciation and host shifts in this system. Most fig parasitoid wasps belong to subfamily Sycoryctinae, including two common genera *Philotrypesis* and *Sycoscapter* (Appendix S1: Figure S2). These parasitoids are often the most prevalent and numerous parasitoid species in Old World fig microcosms, and are generally reported to attack pollinators (Lopez-Vaamonde et al., 2001; Zhai et al., 2008). In contrast, most large galling wasps were attacked by parasitoids in the genus *Sycophila*, which only represents a small fraction of all fig parasitoid species (Compton, 1993). As a result, parasitoid wasp species attacking pollinators may encounter more interspecific competition than those attacking galling wasps. One study showed that parasitoid fig wasps in the Sycoryctinae, mainly those belonging to the genera *Sycoscapter* and *Philotrypesis*, have relatively low host fig specificity (Deng et al., 2021), although others have found very high host fig specificity in different lineages of the same genera (Lopez-Vaamonde et al., 2001). There is also some evidence for a long-term association between some large gallers and their parasitoids (Compton, 1993), which may have led to higher codiversification than seen between pollinators and their parasitoids. More generally, beyond fig systems, competition between parasitoid species for hosts has been considered a major mechanism influencing parasitoid speciation and extinction (Godfray, 1994).

The observed parasitoid diversification patterns in our study might be better explained by interspecific competition followed by host shifts, somewhat like the classic "escape and radiate" coevolutionary model, but here more a case of "compete and host shift to radiate". Host shifting is thought to have a wide role in driving speciation or promoting increased diversification (Ricklefs et al., 2014; Sato et al., 2017). Long distance host shifts have also been shown to be important in the overall radiation of parasitoids, especially for the genus *Philotrypesis* (Jiang et al., 2006; Segar et al., 2012). There have also been studies showing pervasive host-switching among other parasitic organisms, whose phylogenies rarely mirror those of their hosts (Roy, 2001; Sorenson et al., 2003). Nevertheless, the diversification of parasitoid wasps or the whole community could also respond to several other biotic and abiotic factors under potential ecological opportunities (McLeish et al., 2010b).

Estimating parasitoid host specificity/generalism in host plant community

While fig parasitoid wasps may attack different kinds of fig wasps, they still ultimately rely (indirectly) on figs to complete their life cycles. We found that parasitoids did not show phylogenetic congruence with their host figs (Appendix S1: Figure S3). This is reflected in the significantly different distributions of event frequencies for parasitoid–fig associations (Figure 2b) compared with pollinator–fig associations (Wang, Peng, et al., 2019). Moreover, the parasitoid–fig event reconstructions involve more host switching and slightly more cospeciation (Figure 2b) than the corresponding antagonism between figs and gallers studied by Wang, Peng, et al. (2019).

Phylogenetic congruence and macroevolutionary events are both interpretations of the codiversification pattern from an evolutionary perspective. It is important to bridge evolution and ecology within communities, as community evolutionary processes and ecological interactions among species can influence each other (Johnson & Stinchcombe, 2007). The phylogenetic congruence and macroevolutionary events could suggest the contemporary ecological interactions among species are under coupled evolutionary history. In turn, the coupled evolutionary history may provide additional insights into how evolution determines contemporary ecological associations (Hutchinson, Cagua, & Stouffer, 2017). In our study, low phylogenetic congruence and high host switching between parasitoid wasps and figs (Figure 2b and Appendix S1: Figure S3) may suggest relatively low host fig specificity of parasitoid wasps. Indeed, we found that some parasitoids from different host figs showed similar sequences. Some *Apocrypta* species, *Philotrypesis* species, and *Sycoscapter* species sampled from different host fig species were found to have similar COI sequences (pairwise COI distance <0.04, even some pairs with <0.01 divergence; Appendix S1: Figures S4 and S5). These results may indicate lower host specificity in fig parasitoids than in gallers or pollinators. Lower host plant specificity of parasitoid fig wasps has also been reported in different geographic regions, such as Asia (Zhou et al., 2012), America (Farache et al., 2018), and Africa (McLeish et al., 2012). Even when low host specificity of parasitoids has been found in some ecological studies, the wasp community structure is still largely conserved (DeGabriel et al., 2022; Deng et al., 2021).

Codiversification pattern in tri-trophic community

The rich diversity of plant–herbivore interactions has itself facilitated the diversification of their parasitoids and these pervasive parasitoid–herbivore–plant tri-trophic interactions are important for community stability and evolution (e.g., Althoff, 2008; Leppanen et al., 2013; Wilson et al., 2012). Tri-trophic interactions also provide ideal systems to test for cascading speciation and diversification (Bracewell et al., 2018; Forister & Feldman, 2011). However, assessing phylogenetic congruence among three sets of phylogenetic trees has received relatively little attention and needs more exploration (Blasco-Costa et al., 2021). In fig microcosms, different types of interactions occur simultaneously in the same location (inside the figs). This complexity creates the possibility that the codiversification pattern of one type of interaction might be influenced by that of another. Specifically, we found that the parasitoid wasp phylogeny was more congruent with the host phylogeny when the hosts were galling wasps than when they were pollinating wasp hosts, and not congruent with host figs.

AUTHOR CONTRIBUTIONS

Wan-Jin Liao, Yan-Qiong Peng, and Da-Yong Zhang designed the research. Ai-Ying Wang, Yan-Qiong Peng, Da-Rong Yang, and Wan-Jin Liao conducted field sampling and identified fig and wasp species. Ai-Ying Wang performed the phylogenetic reconstruction and conducted the data analyses. Ai-Ying Wang, James M. Cook, Da-Yong Zhang, and Wan-Jin Liao wrote the manuscript.

ACKNOWLEDGMENTS

We thank Pei Yang and Jian-Feng Huang for helping with sample collection. This work was supported by China Postdoctoral Science Foundation (2021M700472), the State Key Laboratory of Earth Surface Processes and Resource Ecology (2022-KF-10), the “111” Program of Introducing Talents of Discipline to Universities (B13008), and National Natural Science Foundation of China (32261123001). We also thank Jean-Yves Rasplus for helping with fig wasp identification.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Gene sequences used for parasitoid wasp phylogeny are available in GenBank (https://www.ncbi.nlm.nih.gov/genbank/); see Appendix S1: Table S1 for accession numbers. Sequences used for fig and host wasp phylogenies are provided in Wang, Peng, et al. (2019) at https://doi.org/10.1111/nph.16176.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wang, Ai-Ying, Yan-Qiong Peng, James M. Cook, Da-Rong Yang, Da-Yong Zhang, and Wan-Jin Liao. 2023. "Host Insect Specificity and Interspecific Competition Drive Parasitoid Diversification in a Plant–Insect Community." *Ecology* e4062. https://doi.org/10.1002/ecy.4062