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LETTER

Convergent structure of multitrophic communities over three continents

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Astract

Ecological theory predicts that communities using the same resources should have similar structure, but evolutionary constraints on colonisation and niche shifts may hamper such convergence. Multitrophic communities of wasps exploiting fig fruits, which first evolved about 75MYA, do not show long-term 'inheritance' of taxonomic (lineage) composition or species diversity. However, communities on three continents have converged ecologically in the presence and relative abundance of five insect guilds that we define. Some taxa fill the same niches in each community (phylogenetic niche conservatism). However, we show that overall convergence in ecological community structure depends also on a combination of niche shifts by resident lineages and local colonisations of figs by other insect lineages. Our study explores new ground, and develops new heuristic tools, in combining ecology and phylogeny to address patterns in the complex multitrophic communities of insect on plants, which comprise a large part of terrestrial biodiversity.

Keywords

Community assembly, evolution, *Ficus*, phylogenetics, wasp.

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INTRODUCTION

A fundamental question in ecology is how often a given resource base supports communities with similar structure (in terms of lineage identity, trophic level relative abundance and guild proportionality). If ecological rules determine how resources can be divided between species, then competition should produce similar communities in different places (Diamond & Cody 1975), although it can be difficult to derive and test appropriate alternative models (Connor & Simberloff 1979; Hubbell 2001). However, communities may not converge due to historical (evolutionary) constraints (Ricklefs & Schluter 1993; Emerson & Gillespie 2008). Alternatively, a vacant niche can be filled through colonisation by a pre-adapted species, or through a niche shift by resident species (Gillespie 2004). This filling of niche space can ultimately lead to convergence in structure across communities (Losos *et al.* 2003). However, neither event may occur because of constraints to colonisation and phylogenetic niche conservatism of resident species (Wiens and Graham, 2005).

Community structure therefore depends on both ecology and evolutionary history (Ricklefs & Schluter 1993; Emerson & Gillespie 2008) and considering these together has led to novel insights about, e.g. the assembly of plant (Silvertown *et al.* 2006) and lizard (Losos *et al.* 2003) communities in which phylogenetic niche conservatism appears to play a surprisingly limited role. Most such studies have focused on species at one trophic level, and mostly on plants or vertebrates, yet a large fraction of all biodiversity resides in multitrophic communities of insect herbivores and their parasitoids (Price 2002). These provide opportunities to compare ecological structure across trophic levels, e.g. by asking if ratios of herbivore to parasitoid species are convergent across communities (Compton & Hawkins 1992), and what host traits lead to similarity in parasite communities (Bailey *et al.* 2009). However, they also require new heuristic approaches and metrics to summarise ecological patterns across multiple trophic levels in a phylogenetic context (Bailey *et al.* 2009).

In this study, we develop metrics to compare the ecological structure of multitrophic insect communities using the same resources in Africa, Australia and America. We focus on the wasp communities associated with fig (*Ficus*) fruits, which include both herbivore (including fig-pollinators) and parasitoid species (Cook & Rasplus 2003; Herre *et al.* 2008). Each community is clearly bounded, because the wasps are specific to one *Ficus* species, and depends on the same resources packaged in fig fruits. Since none of the insect species are shared across continents, we first develop a statistical approach to cluster diverse species into guilds that use particular resources. Some previous work has outlined that such guilds exist (e.g. West *et al.* 1996; Cook & Rasplus 2003), or analysed more local variation in simpler trophic groupings (Compton & Hawkins 1992; Kerdelhué *et al.* 2000), but we use detailed behavioural and ecological data to allow broad geographic comparisons with high resolution. Our clustering approach also allows us to calculate 'ecological distances' between species to use in combination with genetic distances, opening up new analyses.

Community studies often focus on species richness. This emphasises coexistence of species competing for similar resources and we follow this approach for species within guilds. However, considering species diversity alone is less informative than also considering abundance, especially in multitrophic communities (Bailey *et al.*

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2009). Consider a simple example–community (1) has one herbivore and one parasitoid inflicting 20% mortality; (2) has one herbivore and one parasitoid inflicting 40% mortality; and (3) has one herbivore and two parasitoids, each inflicting 20% mortality. Based on species counts, communities 1 and 2 are more similar, but considering relative abundance of herbivore and parasitoid guilds, communities 2 and 3 are more similar, and both comparisons are valuable.

Figs and fig-pollinating wasps have co-radiated for about 75MY (Cruaud *et al.* 2012) to produce about 750 fig/pollinator symbioses, each of which supports a community of non-pollinating insects in its fruits. Given the reliance of many community members on pollination, and the common resource base of figs, we might predict similar ecological community structure across *Ficus* species (both in terms of trophic species richness and relative abundance). But how might evolutionary history influence the ecological similarity of communities? The 'inheritance' hypothesis predicts that communities retain (inherit) similar phylogenetic and ecological structure through long-term cospeciation and niche conservatism. In this case, the same clades would occupy the same trophic level across communities and communities would have equal phylogenetic diversity. There is some evidence for co-diversification and consistent species richness in one group of African fig wasp communities (Jousselin *et al.* 2008), but this has not been explored at a global scale across continents.

Without community inheritance, ecological similarity of communities across continents may be limited, because barriers to colonisation leave some niches empty. Some fig traits, such as latex and the unusual fig fruits, constrain colonisation and probably contribute strongly to all fig wasps being host-specific to one (or rarely 2 or 3 closely related) *Ficus* species (Cook & Segar 2010). The 'constraint' hypothesis therefore predicts that both phylogenetic and ecological community structure diverge across continents.

A third 'convergence' hypothesis predicts that communities reach similar ecological structure through different phylogenetic structures. It predicts that empty niches are filled through a combination of colonisation by pre-adapted species and/or niche shifts by resident lineages. This 'colonisation vs. radiation' approach has proved informative with small assemblages of spiders (Gillespie 2004) and lizards (Losos *et al.* 2003) on islands. Here, we extend it in a novel way to diverse communities across multiple trophic levels on host plant 'islands'.

MATERIALS AND METHODS

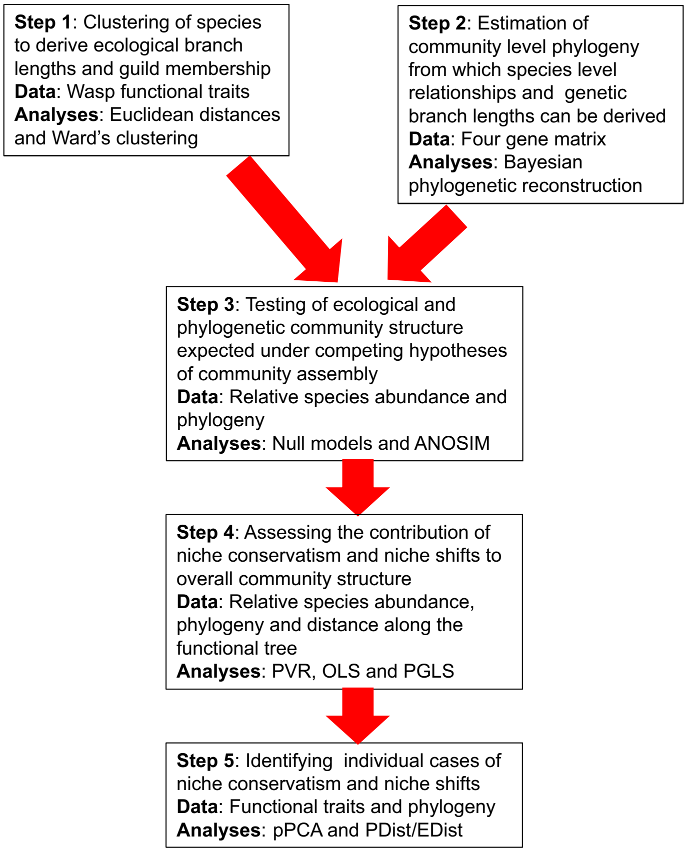
Overview of methods

To test our competing hypotheses, we developed a stepwise framework (see Fig. 1 and below) to measure both the ecological and phylogenetic similarity of communities. Our approach was designed to test predictions under each hypothesis of community assembly and then assess the contributions of phylogenetic conservatism and niche convergence to observed community structure:

(1) We clustered species into functional guilds and estimated 'ecological distances' between species.

(2) We estimated a molecular phylogeny and genetic distances between species.

(3) We compared the structure of our observed communities with null simulations under our 'inheritance', 'convergence' and 'constraint' hypotheses, in terms of both species and individuals per guild. We also used null models to compare the ecological and phylogenetic diversity of each community and tested for phylogenetic niche conservatism.



Step 1: Clustering of species to derive ecological branch lengths and guild membership
Data: Wasp functional traits
Analyses: Euclidean distances and Ward's clustering

Step 2: Estimation of community level phylogeny from which species level relationships and genetic branch lengths can be derived
Data: Four gene matrix
Analyses: Bayesian phylogenetic reconstruction

Step 3: Testing of ecological and phylogenetic community structure expected under competing hypotheses of community assembly
Data: Relative species abundance and phylogeny
Analyses: Null models and ANOSIM

Step 4: Assessing the contribution of niche conservatism and niche shifts to overall community structure
Data: Relative species abundance, phylogeny and distance along the functional tree
Analyses: PVR, OLS and PGLS

Step 5: Identifying individual cases of niche conservatism and niche shifts
Data: Functional traits and phylogeny
Analyses: pPCA and PDist/EDist

Figure 1 A flow diagram summarising our stepwise analytical framework.

(4) We measured the overall contribution of niche conservatism and niche shifts to community structure.

(5) Finally, after summarising overall community patterns in steps 3 and 4, we then identified specific cases of niche conservatism and convergence across communities responsible for the general patterns, using a novel index and contemporary methods.

Selection and sampling of insect communities

Fig trees form the large (> 750 species) pantropical genus *Ficus,* which comprises six subgenera and 19 infra-generic sections. We selected three fig species from different continent-endemic radiations: *F. obliqua* G. Forst. (section *Malvanthera*, Australia), *F. burtt-davyi* Hutch. (*Galoglychia*, Africa) and *F. citrifolia* Mill. (*Americana*, South America). Their last common ancestor existed ca. 50 Ma, while *Galoglychia* and *Americana* diverged around 40 Ma (Rønsted *et al.* 2005). However, they are ecologically similar and each can grow as either a free-standing tree or as a strangler/lithophyte in forest or open habitats. Each *Ficus* species hosts one or more pollinating wasps (family Agaonidae), whose larvae gall fig flowers, and up to 30 species of non-pollinating fig wasps (NPFWs), which fill a range of niches (see below). These NPFWs belong to diverse chalcid (and occasionally braconid) wasp taxa, some restricted to figs, and others associated with multiple host plants but with fig-specific radiations. Wasps of all groups are highly host plant specific.

We collected and dissected crops (collections from single trees) of intact figs as detailed by Segar & Cook (2012). We sampled 149 *F. obliqua* syconia from 18 crops (1–19 syconia per crop) in Australia; 1014 *F. burtt-davyi* syconia from 146 crops (1–10 syconia) in southern Africa; and 685 *F. citrifolia* syconia from 34 crops (20–25 syconia) in Brazil. The syconia of *F. burtt-davyi* (6–15 mm diameter) and *F. obliqua* (4–11 mm) are similar in size and those of *F. citrifolia* (10–20 mm) slightly larger.

Defining wasp guilds and ecological distances

Fig wasp communities comprise herbivores (including pollinators) that gall fig flowers and wall tissue and parasites that exploit these galls. The parasites include true parasitoids that feed directly on gallers, and 'lethal inquilines' that kill them and usurp their galls (Cook & Segar 2010). In addition, some species may be hyperparasitoids, but there is only evidence for this in one genus (Compton *et al.* 2009), which is usually rare (Segar & Cook 2012). For tractability, we refer to herbivores as either pollinators or gallers, and to all members of higher trophic levels (parasitoids, inquilines, hyperparasitoids) as parasitoids. Finer resolution of our parasitoid category would be more informative, but exact larval habit is difficult to determine and known for very few species. Furthermore, since each parasitoid displaces one herbivore, there is a degree of ecological equivalence.

Since no species are shared between communities, we need to compare communities according to the ecological roles of their members. We also required a measure of pairwise ecological distance comparable to pairwise genetic distance. We therefore define guilds of ecologically similar species, using several traits (see below and Kerdelhué *et al.* 2000). The data were taken from the literature for *F. citrifolia* and *F. burtt-davyi* (Compton 1993; Compton *et al.* 1994; Elias *et al.* 2008), and from our new observations for *F. obliqua*:

Timing of oviposition (day)
This indicates when (measured in time) a species lays its eggs. We divided mean total fig development time by the mean day of attack.

Fig developmental stage
This indicates into which of three fig morphological development stages (pre-pollination, early and late interfloral stages) wasps lay eggs.

Gall size
Small galls form in flowers and large galls in either flowers or fig wall tissue. Large galls can exploit a different resource and their inhabitants are much larger (2–10 times) than those of small galls.

Pollinator or non-pollinator
Whether the species is a pollinator wasp.

Internal/external oviposition
This describes whether the wasp species enters the fig to lay eggs or does so through the wall from the outside.

Correlation with pollinators
This indicates whether the number of wasps of a given species is correlated positively or negatively with number of pollinator wasps in a fig. We used a multiple regression with the response variable '(sqrt) pollinator number' and numbers of each wasp species as explanatory variables. We also controlled for differences between crops. The slopes for all *Eurytoma* species and *Idarnes carme* sp 15 were large with high leverage, but derived from very few observations. They were therefore set to zero, which may enhance clustering of species with non-zero slopes of a similar sign, but seems preferable to including extreme values based on very limited evidence, given that rare species should have little impact on pollinator numbers.

Correlation with seeds
This was analysed as above, but with seeds as the response variable.

Prevalence
This estimates the proportion of all figs in which a species was found and describes its distribution across figs and crops.

We gathered trait data for all wasp species from *F. obliqua* and all but one from *F. burtt-davyi* (two *Sycoryctes* species share ecological data). However, the diverse *F. citrifolia* community included some extremely rare species. In such cases, data were collected at the species group level, e.g. we used the same oviposition data for all *Idarnes carme* group wasps.

We analysed traits by generating Euclidian distances to obtain 'ecological' branch lengths in R v2.10.1 (R Development Core Team 2009), and clustered species with Ward's hierarchical method. We used k-means analysis to determine the guilds, and assessed support for each using approximately unbiased (AU) *P*-values (based on bootstrap resampling). Nodes resampled with > 95% frequency are considered strongly supported.

Molecular procedures and phylogeny estimation

We constructed phylogenies using two mtDNA fragments: cytochrome b (cyt-*b*) and cytochrome oxidase 1 (COI), and two nuclear ones: the D1–D3 regions of the ribosomal gene 28S (28S) and the F2 copy of elongation factor 1-alpha (EF-1α) (further details can be found in the Supporting Information). Sequence data were either collected from newly processed individuals (21 species) or obtained from previous studies. For a few species, we could not obtain all sequences, so used data from close congeners (c.f. Novotny *et al.* 2010), i.e. species that attack closely related figs in the same *Ficus* section (Table S1). We prefer this approach to having missing data because (1) a more complete character matrix yields a better phylogeny, (2) the replacements are closer to the named species than to other species in the analysis and (3) congeneric wasp species attacking figs in the same section are generally very close relatives.

Comparing phylogenetic and ecological structure

Guild comparison across communities
Both the 'inheritance' and 'convergence' hypotheses predict similar proportions of individuals in each guild across continents. However, the 'inheritance' hypothesis also predicts similarity in lineage composition and species richness within guilds, because of long-term cospeciation between figs and wasp communities (e.g. Jousselin *et al.* 2008). If even partial co-speciation is the main mode of diversification (as

opposed to ecological speciation or host shifts) we would expect species groups of wasps to retain the same richness on each host after each speciation event (Lopez-Vaamonde *et al.* 2001; Jousselin *et al.* 2008). Different relative abundances across guilds would support the 'constraint' hypothesis. We tested the hypothesis that communities had similar numbers of both species and individuals within each guild using two null modelling approaches.

First, we tested for similarity across communities in (1) species number within each guild and (2) the proportion of all individual wasps in the community found within each guild (relative abundance). We simulated 50 000 (Fayle & Manica 2010) communities using sequential swap models (burnin 50 000), which constrain both row and column frequencies (Gotelli & Entsminger 2003). Column frequencies denote species richness of each community and rows represent species occurrence frequency, which here must always be one species per row.

We also used a slightly less constrained model ('R2'–Wright *et al.* 1998). This maintains species occurrence frequencies but allows column frequencies to vary slightly (in proportion to observed frequencies). Consequently, species can colonise any pseudo-community independently of each other until each community reaches a similar number of species to the observed community. This model may have more power than the first, as comparison with overly structured null models can mask real patterns (Moore & Swihart 2007). For both models, we used the observed variance in column sum totals across communities as our nestedness statistic. Our null hypothesis was that the variance across columns in the real communities was not less than that found in 95% of null communities.

We also made one more set of comparisons focusing on small wasps (pollinators, small galllers, small parasitoids) vs. large wasps (large gallers, large parasitoids), since these function as largely separate community modules (Compton 1993b). This allowed us to investigate how the communities were structured at different scales, from individuals within a guild to community modules. Finally, we used ANOSIM to compare the proportion of all individuals that occupied each guild across communities. We permuted communities at the syconium level 1000 times and compared them using Bray Curtis matrices.

Phylogenetic and ecological diversity

The 'constraint' hypothesis predicts differences in ecological, and the 'convergence' hypothesis differences in phylogenetic, diversity. Phylogenetic diversity is quantified using genetic distances between species, so we derive a similar index for ecological distances from our trait clustering analysis. Our approach is similar, although independently derived, to the functional diversity methods of Petchey & Gaston (2002). However, here we use functional diversity in a novel manner and context to directly contrast ecological and phylogenetic diversity of multitrophic insect communities. For each community, we calculated the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) (Webb *et al.* 2002) to assess community diversity across (1) the molecular phylogeny and (2) a neighbour-joining tree built from the ecological Euclidean distances.

We compared our results to standardised effect sizes generated under null models of tip label randomisation (999 runs). This allowed us to compare phylogenetic with ecological structure across communities and test for differences from null expectations. We also tested for phylogenetic signal in guild membership and log(relative species abundance) with unstandardised independent contrasts tests (Blomberg *et al.* 2003) and the same randomisation. Phylogenetic signal in either would suggest that phylogenetic conservatism plays a role in community structure.

As our phylogeny contains only 35 species, it may be difficult to detect non-random patterns, especially in our smallest (seven species) community. Consequently, we tested the power of null models to correctly accept or reject the hypothesis of random signal. Using a seven species community on a 35 species tree, we simulated 1250 seven species communities, with or without phylogenetic signal, and tested the performance of MPD and MNTD indices.

Ecology and phylogeny as predictors of relative abundance

The tests above can reject the 'constraint' hypothesis, but further analyses are needed to discriminate between the other two hypotheses. We used two complementary approaches to determine the overall influence of niche shifts and phylogenetic niche conservatism on community structure.

We tested the explanatory power of ecological role (guild membership) and phylogeny as predictors of log(relative species abundance) (a measure of community structure). If ecological role is non-significant after controlling for phylogeny then we can reject 'convergence' and accept the 'inheritance' hypothesis. However, if relative species abundance still depends on ecological role, then 'convergence' is suggested.

First, we carried out phylogenetic eigenvector regression (PVR) (Diniz-Filho *et al.* 1998), which can quantity the relative contributions of ecological role and phylogeny. We decomposed the ecological distance matrix into 34 eigenvectors using principle co-ordinate analysis (PCoA) and selected the eigenvector(s) explaining most variation in log(relative species abundance) according to Moran's index. We then decomposed the phylogenetic distance matrix and performed PVR with the ecological eigenvector(s) as explanatory variables(s). This revealed how much variance in log(relative species abundance) was explained by (1) ecology alone, (2) ecology and phylogeny and (3) phylogeny alone. To explore further, we used PGLS to model log(relative species abundance) for each species against the ecological eigenvector(s), using Pagel's lambda correlation structure. Finally, we compared OLS and PGLS model fit with a likelihood ratio test (Rezende *et al.* 2009).

Detecting niche convergence and adaptive radiation

The last stage of analysis aims to attribute global trends revealed above to specific cases of phylogenetic conservatism and ecological convergence within our communities. We used phylogenetic principle components analysis (pPCA) to detect 'global' (positive, deep phylogenetic inertia) and 'local' (negative, ecological convergence) phylogenetic autocorrelation in traits (Jombart *et al.* 2010). We conducted pPCA using all quantitative ecological traits including the principle ecological eigenvector. Traits were centred to a mean of zero and scaled to unit variance and Abouheif's (1999) measure of phylogenetic proximity was used to define the phylogenetic weights. PGLS, PVR and pPCA were conducted using an ultrametric phylogenetic tree (see Supporting Information).

In a complementary analysis, we divided the proportion of phylogenetic (pPDist) distance by the proportion of ecological (pEDist) distance occupied by each pairwise comparison to derive a novel index. We considered cases in the 95th quantile of the distribution to reflect PDist ≫ EDist and therefore potential cases of ecological convergence.

RESULTS

Community structure

We recorded 35 wasp species across the three communities associated with these partially independent *Ficus* radiations. There was little taxonomic overlap at the subfamily level and only Agaoninae (pollinators) occurred in all three communities. Species richness differed considerably with seven in the African, 10 in the Australian and 18 in the American communities.

Our clustering analyses identified five guilds (Fig. 2): (1) parasitoids of large gallers, (2) parasitoids of small gallers, (3) pollinators, (4) large gallers and (5) small gallers. Most guilds (13/15 combinations) occur in all three communities and only the large galler and large parasitoid niches are ever vacant (in Africa) (with one guild being reliant on the other). However, the number of species per guild differs considerably (Table 1, Fig. 3). In contrast, at the individual level, similar proportions of insects fall into a given guild (Table 1, Fig. 3). Overall, we see strong ecological similarity across communities in terms of guild abundance, which reflects quantitative links between trophic levels, despite differences in numbers of species. Importantly, while species richnesses per guild differed among communities, relative abundances at the guild level were broadly similar.

The Australian and African communities differ significantly in proportion for only one guild (Fig. 3). The African community had no large wasps (unknown on *F. burtt-davyi,* although found on other section *Galoglychia Ficus* species) and the Australian community also had few of these. The American community differs more, but, even then, the significant differences have small effect sizes. The main difference observed is higher parasitism in the American community (but see Discussion). The overall similarity in ecological structure is supported further by MPD and MNTD 'ecological diversity' indices that do not differ significantly from null expectations across communities (MPD: 1.196, 1.863 and 1.386, MNTD: 0.559, 0.544 and 0.480 for Africa, Australia and America).

Phylogeny

We recovered a well-resolved phylogeny with good support for many nodes (Fig. 4). The Phylogenetic MPD and MNTD indices were similar for Australian and American but lower for the African, the only community to show significant phylogenetic clustering ($\mathrm{MPD}_{\mathrm{obs}} = 0.280$, $\mathrm{MPD}_{\mathrm{rand.mean}} = 0.495$, $P = 0.001$; $\mathrm{MNTD}_{\mathrm{obs}} = 0.199$, $\mathrm{MNTD}_{\mathrm{rand.mean}} = 0.328$, $P = 0.007$). This shows that communities differ in phylogenetic diversity. Power tests showed that MPD/MNTD indices performed adequately, detecting true positive

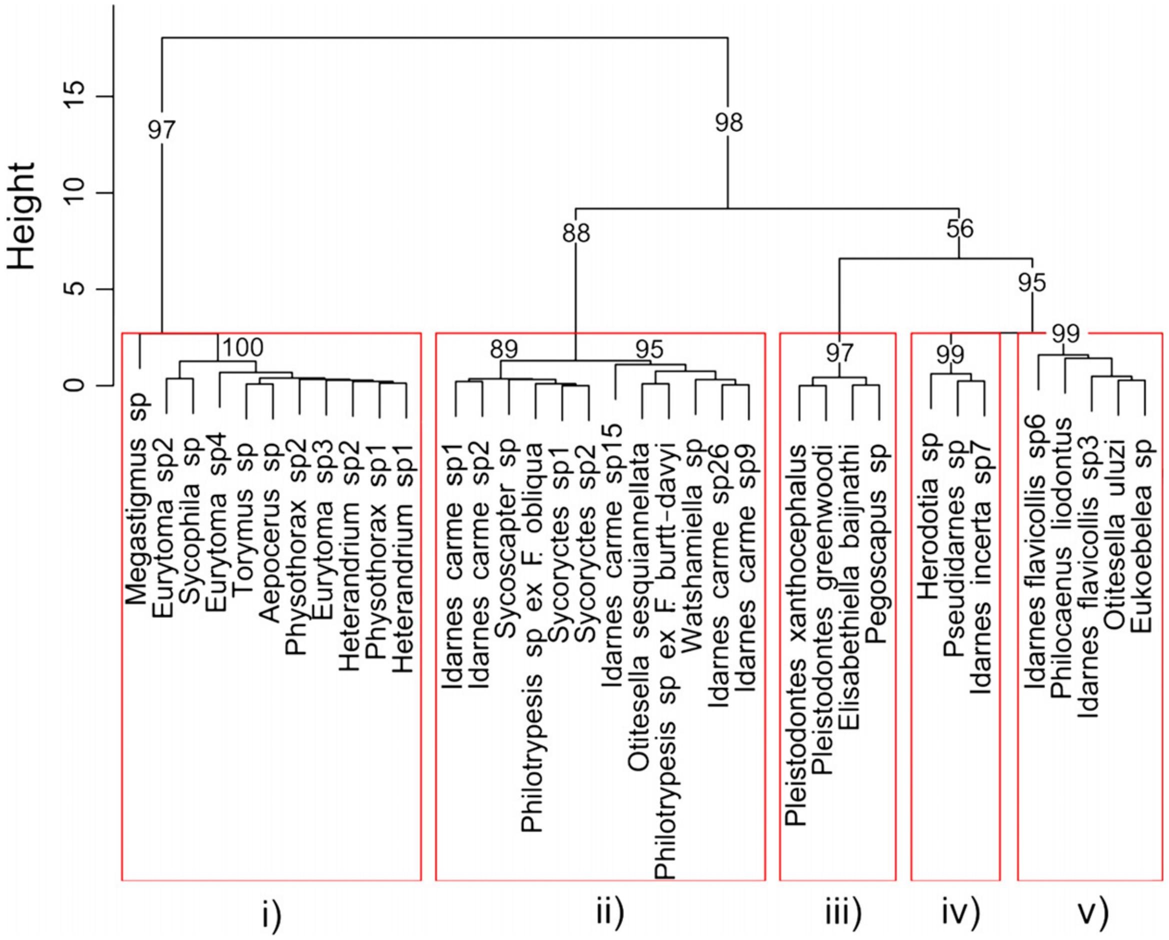


Figure 2 Guilds identified by k-means clustering analysis of ecological variables. Approximately unbiased *P*-values are shown as percentages on major nodes. Values over 95% represent strong support. Five guilds are denoted by red rectangles, from left to right: (1) large parasitoids, (2) small parasitoids, (3) pollinators, (4) large gallers and (5) non-pollinating small gallers. See text for further details.

Table 1 Testing for differences in relative guild abundance across the three wasp communities using null models. Results for a) 'swap' and b) 'R2' models. The statistic is the observed variance across column sums in the real communities, while the median value of the null distribution is also given for comparison. Our null hypothesis was that the variance across columns in the real communities was not less than that found in 95% of the null communities

Test	Statistic	Median (a)	*P* (a)	Median (b)	*P* (b)
Species number	32.333	30.333	0.563	70.333	0.229
Pollinator relative abundance	0.010	0.142	0.171	0.680	0.038*
Parasitoid relative abundance	0.001	0.010	0.111	0.022	0.043*
Small galler relative abundance	0.001	0.002	0.133	0.003	0.045*
Pollinator and parasitoid relative abundance	0.006	0.309	0.021*	0.523	0.008*
Pollinator and small galler relative abundance	0.004	0.293	0.041*	0.470	0.021*
Small wasp relative abundance	0.001	0.302	0.006*	0.432	0.002*
Large galler relative abundance	0.000	0.000	0.335	0.000	0.161
Large galler parasitoid relative abundance	0.001	0.001	0.891	0.001	0.259
Large wasp relative abundance	0.002	0.001	0.775	0.001	0.261

Asterisks represent higher similarity than expected by chance.

signal in 82%/97% of cases and rejecting random signal in 95% of cases (both MPD and MNTD). Although communities differ in phylogenetic diversity, there is clearly still a role for niche conservatism because guild (K = 1.38, PIC_{obs} = 3.93, $PIC_{rand.mean}$ = 12.117, $P = 0.001$) and relative abundance (K = 0.90, PIC_{obs} = 8.977, $PIC_{rand.mean}$ = 17.654, $P = 0.001$) show significant phylogenetic signal.

The contribution of ecology and phylogeny

Separate OLS regression analyses showed that the principle ecological eigenvector explained 26% variance ($t_{1,33} = 3.444$, $P = 0.00158$), while the principle phylogenetic eigenvector explained 47% of variance ($t_{1,33} = 5.44$, $P < 0.001$) in log(species relative abundance). Variance partitioning of the phylogenetic eigenvector regression showed that ecology alone explained 8% ($t_{2,32} = 2.416$, $P = 0.0216$) and phylogeny alone explained 29% ($t_{2,32} = 4.560$, $P < 0.001$) of the variance. A further 18% variance was shared between ecology and phylogeny and 45% remained unexplained. Meanwhile, in the PGLS regression analysis, ecology still explained 12% of variance, after controlling for phylogeny ($t_{2,32} = 2.142$, $P = 0.0397$, Lambda = 0.758). Model comparison revealed that there was a significant difference in the explanatory power (PGLS > OLS > 0) (ΔAIC = 5.0, Likelihood ratio = 6.975, $P = 0.0083$).

The results above reveal both phylogenetic and ecological elements to species abundance. The pPCA found global structures (deep phylogeny) to be dominant (positive component eigenvalues: 1.271, 0.283 and 0.191), but also revealed local structure (close relatives with different PC signs) (Fig 5). We identified 31 pair-wise comparisons in the 95th quantile, which represented potential cases of extreme ecological convergence (Table S2). Underlying research data are accessible through EMBL/Genbank (see Table S1), the University of Reading Repository (http://centaur.reading.ac.uk/) or by contacting the authors.

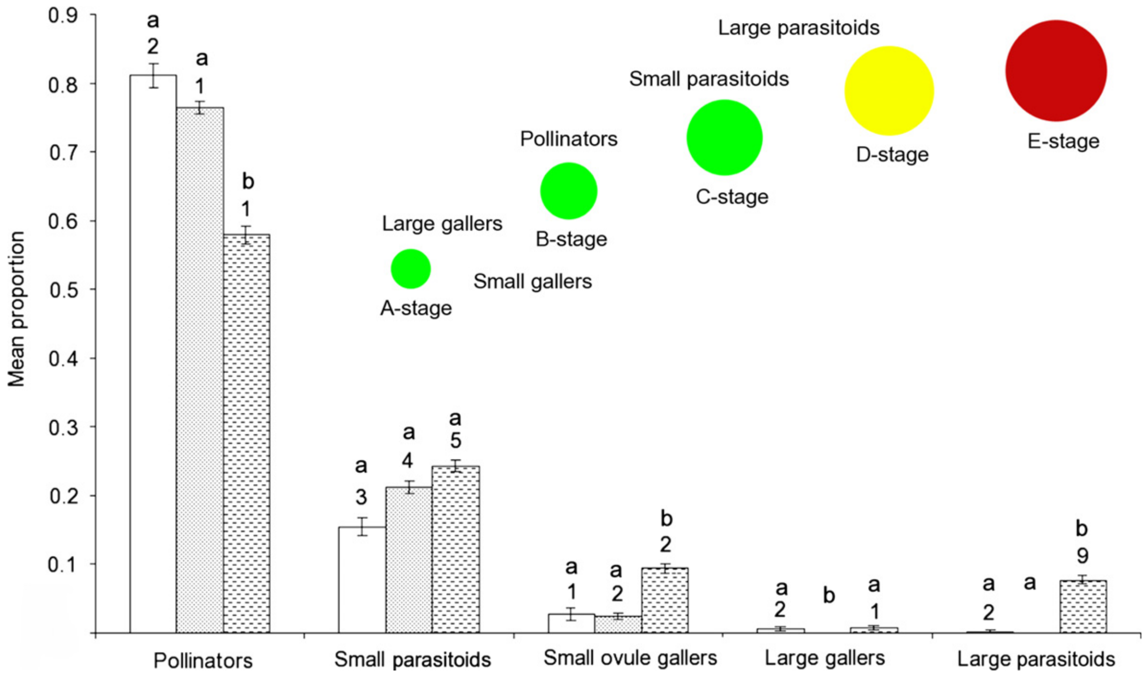


Figure 3 The ecological structure of three fig wasp communities in terms of the proportion of all insects (relative abundance) belonging to each of five guilds (see Fig. 1.). The few syconia that did not contain pollinators (but did not abort due to the presence of galls) were excluded so that all potential trophic links could occur in each comparison. White bars show the Australian community (*F. obliqua*), dotted bars show the African community (*F. burtt-davyi*) and dashed bars the American community (*F. citrifolia*). Numbers above bars show species diversity in that guild and community. Error bars represent 1 SEM of the total mean and letters denote significant differences as detected by ANOSIM. Inset: the generalised developmental profile of a monoecious *Ficus* species with stages according to Galil & Eisikowitch (1968). The typical time of attack is given for each guild, colours match those of *F. obliqua* figs throughout their development and are purely to aid visualisation.

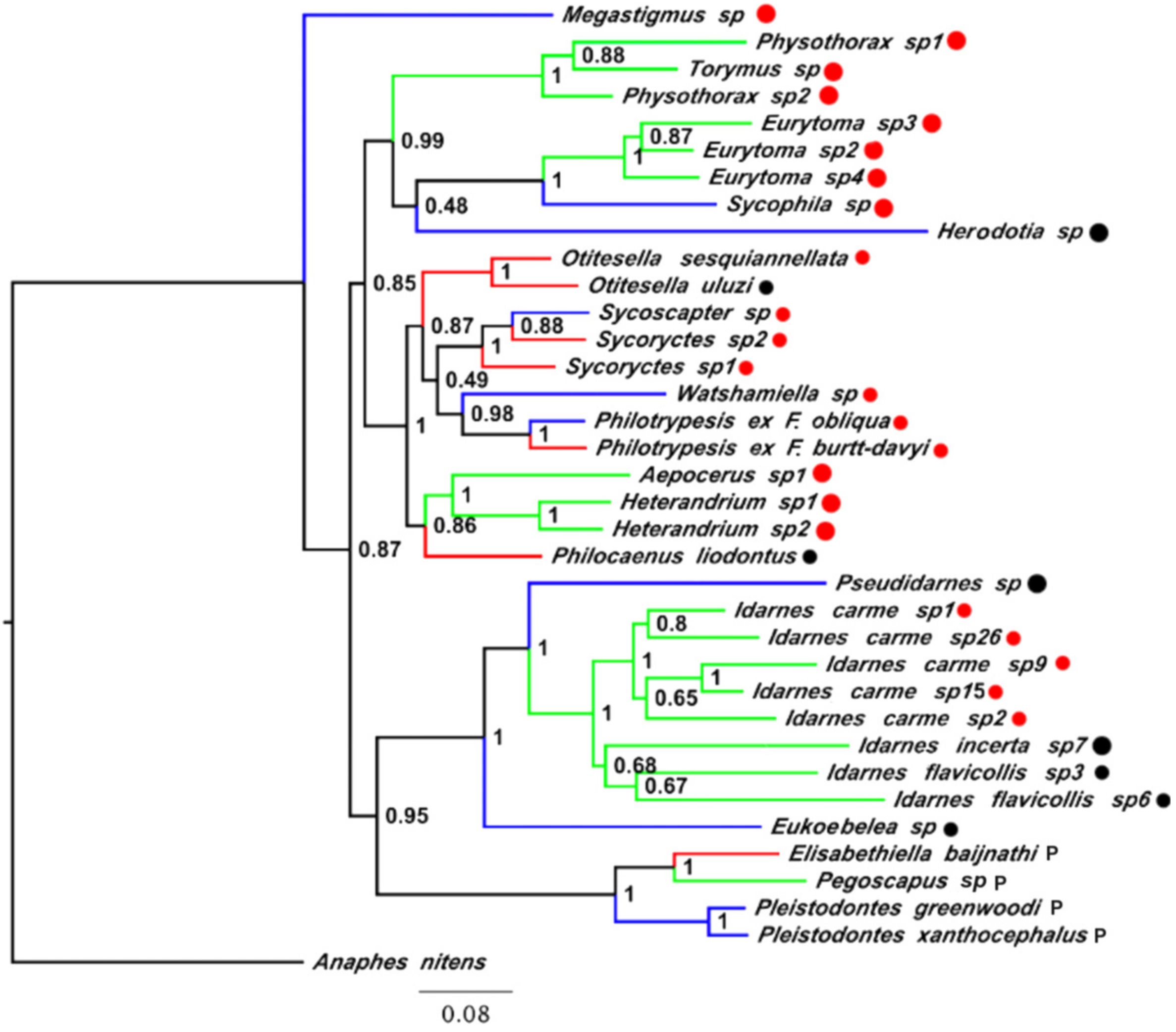


Figure 4 Bayesian consensus tree (of all compatible nodes) showing the relationship between all 35 fig wasp species sampled from the three *Ficus* species. Wasps from *F. obliqua* are coded by blue branches, wasps from *F. burtt-davyi* by red branches and wasps from *F. citrifolia* by green branches. Node labels represent posterior probabilities. Scale bar represents substitutions per site. Circles represent guild membership: large parasitoids (large red circles), large gallers (large black circles) small parasitoids (small red circles), small gallers (small black circles) and pollinators (P).

DISCUSSION

We compared three insect communities exploiting fig fruits on different continents. These communities have been evolving independently for at least 40 MY (Rønsted *et al.* 2005) and differ in taxonomic composition, providing an excellent opportunity to test for convergence in ecological community structure and explore the role of evolutionary history in generating or constraining such convergence (Herre *et al.* 2008). This integrated community phylogeny approach is increasingly common for species assemblages at a single trophic level (particularly plant communities, e.g. Cadotte *et al.* 2009). This approach has recently been used in local studies at higher trophic levels (Dinnage *et al.* 2012), but we extend it to infer community assembly processes in complex multitrophic insect communities across three continents.

We presented three hypotheses (inheritance, constraints and convergence) that predict different combinations of similarity in ecological and phylogenetic structure across communities. Communities could be similar in both respects due to 'inheritance', because community structure was established long ago and persistent co-diversification of insect lineages on figs has kept it essentially the same. Our results reject this possibility, because phylogenetic diversity differs considerably across the communities. For example, the community on *F. burtt-davyi* is phylogenetically clustered, because all NPFWs belong to the family Pteromalidae. In contrast, the other two communities are phylogentically diverse, including wasps from several higher taxa. In addition, species richness varies from 7 to 18 species, contradicting the 'inheritance' hypothesis.

A second, 'constraint', hypothesis emphasises that figs pose barriers to colonisation. If so, ecological structure will differ when some niches remain vacant in certain localities. This scenario is exemplified by one of the first comparisons of insect communities across continents–the herbivores of bracken fern (*Pteridium aquilinum* (L.) Kuhn) (Lawton *et al.* 1993). Some fig traits, such as latex, may severely constrain colonisation by insects. Further, fig wasps show numerous specific adaptations not just to fig trees, but to the particular morphological and chemical traits of the syconia of their only host *Ficus* species (Cook & Rasplus 2003). It is important to distinguish here

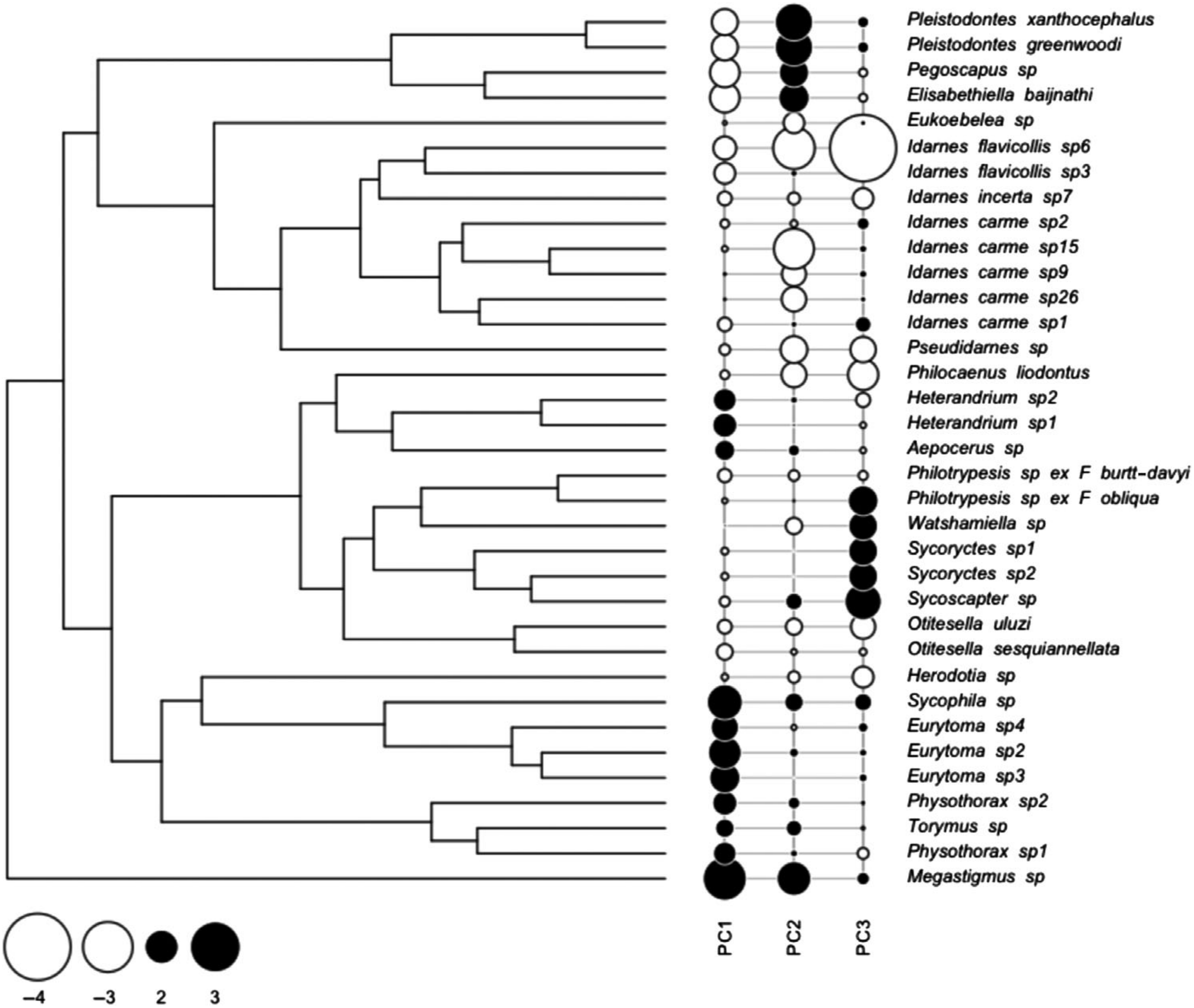


Figure 5 Phylogenetic principle components analysis of quantitative wasp trait data. The first three global principle components are shown. Positive principle component scores are represented by black circles and negatives scores by white circles. Circle size is proportional to absolute values.

between the fig/pollinator interaction and the wider multitrophic wasp community. Each community must have a pollinator species so we do not expect divergence in this respect. However, this does not prevent divergence in numbers of pollinator individuals or how many are parasitised, emphasising the importance of quantifying species abundance to study trophic links (Bailey *et al.* 2009). Moreover, mutualism persistence does not require the presence of any other wasp species, so similarity in wider community structure could be constrained by barriers to colonisation.

While figs present barriers to colonisation, we found similar ecological structure across continents. We show that, although communities differ in species richness, the proportion of individuals in each guild remains similar. We found only one herbivore guild and its associated parasitoid guild missing (in our African comparison), suggesting weak constraints on structure. Admittedly, wider sampling both within and between *Ficus* sections would better test the 'constraint' hypothesis. Arguably, the only substantial ecological difference between communities is more parasitoids, and especially large parasitoids, in the American community. However, large parasitoids are always rare and their numbers are easily inflated by the sporadic occurrence of occasional crops with unusually high abundance (Segar & Cook 2012).

Consequently, the overall pattern is one of similarity in ecological structure and difference in phylogenetic structure. This matches predictions of our 'convergence' hypothesis, but leaves open how this has arisen. We used community phylogeny to explore further and showed that phylogenetic niche conservatism still plays an important role–many species belong to lineages that consistently fill the same niches (e.g. pollinators and eurytomid parasitoids). However, communities only converge overall because some lineages have radiated locally to fill different niches, while some niches have been colonised on one continent by taxa that are absent from another. Our novel application of community phylogeny allowed us to test our global hypotheses and then identify specific cases underlying the observed patterns, providing detailed understanding of how convergence arose.

Adaptive radiation is crucial in driving the convergence and the genus *Idarnes* illustrates this best (Elias *et al.* 2012). *Idarnes* (subfamily Sycophaginae) has undergone local radiation in America to fill three niches: large galler, small galler, and small parasitoid. However, the large galler guild is dominated globally by wasps from other families, especially Epichrysomallinae. Similarly, the small parasitoid guild in Africa and Australia is filled largely by wasps from the subfamily Sycoryctinae, not Sycophaginae.

In other cases, distantly related wasp lineages have colonised the same niches in different communities. For example, the small galler niche is occupied by the sycophagine genus *Eukoebelea* in Australia but the phylogenetically distant *Otitesella uluzi* van Noort and *Philocaenus liodontus* Wiebes in Africa. Similarly, wasps from Eurytomidae and Otitesellinae occupy the large parasitoid guild in America, whilst representatives of Torymidae and Eurytomidae do so in Australia.

Overall, a combination of niche stasis, adaptive radiation and colonisation is responsible for community ecological convergence. The > 750 fig species worldwide show considerable phenotypic variation and host hundreds of 'replicate' wasp communities. However, few whole communities have been studied with good understanding of the ecological roles of species (Cook & Rasplus 2003). Indeed, most studies have focused either on establishing what species are present and where (e.g. Compton & Hawkins 1992), or the impacts of common wasp taxa on the mutualism (West *et al.* 1996; Pereira *et al.* 2000; Segar & Cook 2012).

Previous work has shown that species richness is correlated with host plant geographic range for African wasp communities (Compton & Hawkins 1992), and that monoecious figs host more wasp species than dioecious figs (Kerdelhué & Rasplus 1996). However, these studies focused on species presence (not abundance) and did not test for equivalence of ecological guild structure. Our study shows that communities can differ considerably in species richness (7, 10 and 18 species), but have similar ecological structure. It will be interesting to test if this holds across fig species with highly divergent fruit sizes, and for the same community at the centre and edge of the host plant range.

More generally, we build on recent successes in combining community ecology with phylogeny by extending the approach to multitrophic communities of insects on plants. These comprise much of all terrestrial species diversity and many systems are amenable to study following our approach. The generality of our findings awaits tests in other systems, but we expect our results to be best matched by other enclosed communities with well-defined resource units. These include communities centred on insect-induced galls (Bailey *et al.* 2009) and other concealed herbivores, and perhaps also those in true fruits and flower heads of composites (Asteraceae).

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AUTHORSHIP

STS and JMC designed the study and all authors collected data. STS conducted the data analyses. STS and JMC wrote the manuscript and conducted revisions based on comments from SGC, RASP and referees.

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