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Network structure and taxonomic composition of tritrophic communities of Fagaceae, cynipid gallwasps and parasitoids in Sichuan, China

中国四川的壳斗科、瘿蜂、和寄生蜂之三級营养生物群落的结构和组成

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Abstract

1. A key question in insect community ecology is whether parasitoid assemblages are structured by the food plants of their herbivore hosts.

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2. Tritrophic communities centred on oak-feeding cynipid gallwasps are one of the best-studied tritrophic insect communities. Previous work suggests that host plant identity is a much stronger predictor of oak–cynipid interactions than of cynipid–parasitoid interactions. However, these relationships have not been formally quantified.
3. We reason that the potential for 'bottom-up' effects should increase with host plant phylogenetic diversity. We, therefore, generated quantified interaction network data for previously unstudied tritrophic cynipid communities in Sichuan, China, where, in addition to *Quercus*, cynipid host plants include *Castanea*, *Castanopsis* and *Lithocarpus*. We characterise these communities taxonomically and compare the extent to which host plant taxonomy predicts plant–herbivore and plant–parasitoid associations.
4. We sampled 42,620 cynipid galls of 176 morphotypes from 23 host plant species, yielding over 4500 specimens of 64 parasitoid morphospecies. Many parasitoids were identifiable to chalcidoid taxa present in other Holarctic oak cynipid communities, with the addition of *Cynipencyrtus* (Cynipencyrtidae). As elsewhere, Sichuan parasitoid assemblages were dominated by generalists.
5. Gallwasp–plant interaction networks were significantly more modular than parasitoid–plant association networks. Gallwasps were significantly more specialised to host plants (i.e. had higher mean d' values) than parasitoids. Parasitoid assemblages nevertheless showed significant plant-associated beta diversity, with a dominant turnover component.
6. We summarise parallels between our study and other Fagaceae-associated cynipid communities and discuss our findings in light of the processes thought to structure tritrophic interactions centred on endophytic insect herbivores.

KEYWORDS
Braconidae, Castanea, Castanopsis, Chalcidoidea, Cynipidae, Fagaceae, foodweb, interaction network, Lithocarpus, Quercus

INTRODUCTION

Tritrophic communities of plants, insect herbivores and associated parasitoids together comprise more than 50% of all described species (Novotny et al., 2010; Smith et al., 2008). Understanding the processes that structure these communities remains a major challenge in ecology (Terborgh, 2015; Vidal & Murphy, 2018). One key question is the extent to which the host plant associations of insect herbivores structure higher associated trophic levels of natural enemies (Janz, 2011; Pearse & Hipp, 2009; Prauchner & De Souza Mendonça, 2024; Wan et al., 2020). Are higher trophic levels structured by 'bottom-up' projection of the same processes that shape herbivore communities across host plants? Or are enemy–herbivore associations substantially determined by processes that are independent of plant identity (Janz, 2011; Luz et al., 2021; Prauchner & De Souza Mendonça, 2024; Singer & Stireman, 2005)?

One approach to revealing bottom-up plant effects in insect communities is through the analysis of trophic interaction networks (Kuzmanich et al., 2023; Maldonado-López et al., 2022; Müller et al., 1999; Paniagua et al., 2009; Prauchner & De Souza Mendonça, 2024; Van Veen et al., 2008). If strong bottom-up effects of plants exist, we expect both herbivore–plant and enemy–plant bipartite networks to show high specialisation at the individual taxon and whole network levels. In terms of network parameters, relative to null expectations, we would expect significantly high values of d' (which measures individual taxon specialisation) and significantly high H_2' and low connectance (both of which capture network-level specialisation) (Blüthgen et al., 2006; Memmott et al., 1994). Relative to null predictions, we also expect plant-specialised networks to show high modularity (Dormann et al., 2009; Vázquez et al., 2007), with module composition strongly structured by plant taxonomy or phylogeny (De Araújo & Maia, 2021; Nielsen & Bascompte, 2007; Oliveira et al., 2020). Such patterns would indicate that plant species support locally differentiated communities and we would further expect both herbivores and enemies to show strong plant-associated beta diversity (Rott & Godfray, 2000; Schönrogge & Crawley, 2000; Whitham et al., 2012), with a dominant signal of turnover between host plant species (Baselga, 2017). The extent to which plant–herbivore and plant–enemy networks show concordant patterns will reflect the extent to which plants structure trophic niches in these two trophic levels, either directly or (for enemies) also indirectly through herbivore–plant associations (Araújo et al., 2019; De Araújo & Maia, 2021; Müller et al., 1999; Oliveira et al., 2020; Prauchner & De Souza Mendonça, 2024).

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Here we explore these predictions using bipartite interaction networks for a tritrophic community comprising Fagaceae host plants, cynipid gallwasp herbivores and parasitoid natural enemies. Several properties of gall communities make them convenient model systems for the study of bottom-up effects (Cook & Rasplus, 2003; Craig & Itami, 2021; Nelson et al., 2014). First, galling insects are abundant and species-rich in many plant communities, with an estimated 21,000–211,000 species (Espírito-Santo & Fernandes, 2007). Second, most gall inducers induce diagnostic gall morphologies, allowing the use of gall morphotype-based classification in the absence of Linnaean taxonomy and facilitating research in highly biodiverse areas with a substantial taxonomic impediment (Blanche, 2000; Butterill & Novotny, 2015; Coelho et al., 2017; Cuevas-Reyes et al., 2007; de Araújo et al., 2021; Oliveira et al., 2020). Third, insect galls often support characteristic communities of other inhabitants, including herbivorous inquilines and parasitoids, for which host plant effects can be quantified (De Araújo & Maia, 2021; Paniagua et al., 2009; Stone & Schönrogge, 2003). Because the communities associated with a particular gall-inducer guild (such as cynipids on oaks or fig-wasps on *Ficus*) are largely ecologically closed (Askew et al., 2013; Cook & Rasplus, 2003), they can meaningfully be considered in ecological isolation. Finally, galls are easy to sample quantitatively, facilitating the generation of quantified interaction networks and associated metrics (De Araújo & Maia, 2021; Maldonado-López et al., 2022; Prauchner & De Souza Mendonça, 2024; Schönrogge & Crawley, 2000).

Gallwasps (Hymenoptera; Cynipidae; Cynipini) on Fagaceae host plants are one of the best-studied tritrophic galling systems. Across the Holarctic, these communities have a characteristic structure and taxonomic composition (Abe et al., 2007; Askew et al., 2013; Csóka et al., 2005; Ward, Bagley, et al., 2022). As for most galling insects (Butterill & Novotny, 2015; Csóka et al., 2017; Scheffer et al., 2017), cynipid gallwasps are host plant specialists: with the exception of two clades with host-alternating lifecycles, all Cynipini only gall sets of closely related Fagaceae species (Lobato-Vila et al., 2022; Stone et al., 2009; Ward, Bagley, et al., 2022). Across their global distribution, Cynipini galls are attacked by rich assemblages of parasitoids dominated by the chalcidoid families Eulophidae, Eupelmidae, Eurytomidae, Megastigmidae, Ormyridae, Pteromalidae and Torymidae (Abe et al., 2007; Askew et al., 2013; Bird et al., 2013; Eliason & Potter, 2001; Fernandes et al., 1999; Forbes et al., 2016; Janšta et al., 2018; Joseph et al., 2011; Maldonado-López et al., 2022; Ward, Busbee, et al., 2022; Washburn & Cornell, 1981; Weinersmith et al., 2020). The extent to which these parasitoid assemblages are structured by Cynipini–plant associations remains little studied. Plant taxonomy is a significant predictor of parasitoid assemblage composition in Western Palaearctic oak cynipid galls (Bailey et al., 2009), but these communities are nevertheless dominated by generalist parasitoids that attack multiple host gall types on phylogenetically divergent host oaks (Askew et al., 2013). In contrast, host plant identity structures at least some cynipid–parasitoid interactions in Nearctic oak gall communities (Sheikh et al., 2022; Zhang, Mullin, et al., 2022). However, no formal comparison of the extent to which host plant identity structures tree–cynipid and cynipid–parasitoid interactions has yet been made for any cynipid community.

We reason that the greatest potential for plant trait-structured niche space, and hence for detecting bottom-up effects on gallwasps and parasitoids, should exist where Cynipini induce galls on the greatest richness and phylogenetic diversity of host Fagaceae (Basset et al., 2012; Ødegaard et al., 2005; Staab et al., 2016; Wang et al., 2020; Zhang et al., 2016). This exists in Southwestern China and Southeast Asia, where Fagaceae lineages known to host cynipids include around 150 oak species in four sections across both subgenera of *Quercus* (sections *Cerris*, *Ilex* and *Cyclobalanopsis* in subgenus *Cerris*, and section *Quercus* in subgenus *Quercus*), as well as *Castanea* Mill. (4 species), *Castanopsis* (D. Don) (146 species) Spach and *Lithocarpus* Blume (341 species) (Lobato-Vila et al., 2022; WFO, 2023). In comparison, native Cynipini in the Western Palaearctic are associated only with oaks (ca. 32 species in sections *Cerris* and *Ilex* in subgenus *Cerris* and sections *Ponticae* and *Quercus* in subgenus *Quercus*), while Nearctic Cynipini are mainly associated with *Quercus* (ca. 285 species in sections *Lobatae*, *Protobalanus*, *Ponticae*, *Quercus* and *Virentes* in subgenus *Quercus*) and species-poor radiations of *Chrysolepis* Hjelmq. (2 species) and *Notholithocarpus* Manos, Cannon & S.H.Oh (1 species) (Buffington & Morita, 2009; Nicholls, Melika, et al., 2018a; Nicholls, Melika, et al., 2018b; WFO, 2023).

While southwestern China offers very high host plant lineage diversity, associated cynipid faunas are substantially undersampled or completely unknown (Lobato-Vila et al., 2022; Pénzes et al., 2018). Even less is known about associated parasitoids. Almost all parasitoid studies in China and Southeast Asia have focused on a single global pest species—the Oriental Chestnut gallwasp *Dryocosmus kuriphilus* Yasumatsu, 1951 (Abe et al., 2007; Aebi et al., 2006). Available (and assumed very incomplete) data show that the same chalcid parasitoid families recorded from Cynipini galls in the Western Palaearctic and Nearctic are also present in China and Southeast Asia (Abe et al., 2007; Narendran et al., 2007; Ren, 2009; Xiao et al., 2016, 2021; Yang, 2008), with the addition of *Cynipencyrtus* (Cynipencyrtidae: Abe et al., 2007; Singh, 2008; Tatchikawa, 1978; Yasumatsu & Kamijo, 1979; Zhang et al., 2006). It remains unknown whether this global centre of Fagaceae phylogenetic diversity supports additional cynipid-associated parasitoid lineages absent from previously studied communities.

Here we provide the first quantitative analysis of any cynipid community in China or Southeast Asia. We provide a first taxonomic overview of the associated parasitoid assemblages and use interaction networks to explore the structure of bipartite interactions between each of the three trophic levels. Given the high specificity of gallwasp–plant associations elsewhere, we predict that gallwasp–plant networks will show significant plant specialisation and network modularity, with module composition structured by plant taxonomy and significant between-plant turnover in species composition. The dominance of generalist parasitoids in other gallwasp communities leads us to predict that, relative to gallwasp–plant networks, parasitoid–plant networks will be less specialised, with higher connectance, lower network-level (H_2') and taxon-level (d') specialisation and lower modularity, with modules less strongly structured by host plant taxonomy (Nielsen & Bascompte, 2007; Oliveira et al., 2020). We also expect the taxonomic composition of parasitoids on plants to show lower overall beta diversity, with generalists contributing to a relatively greater signature of nestedness to turnover than observed in gallwasp–plant interactions.

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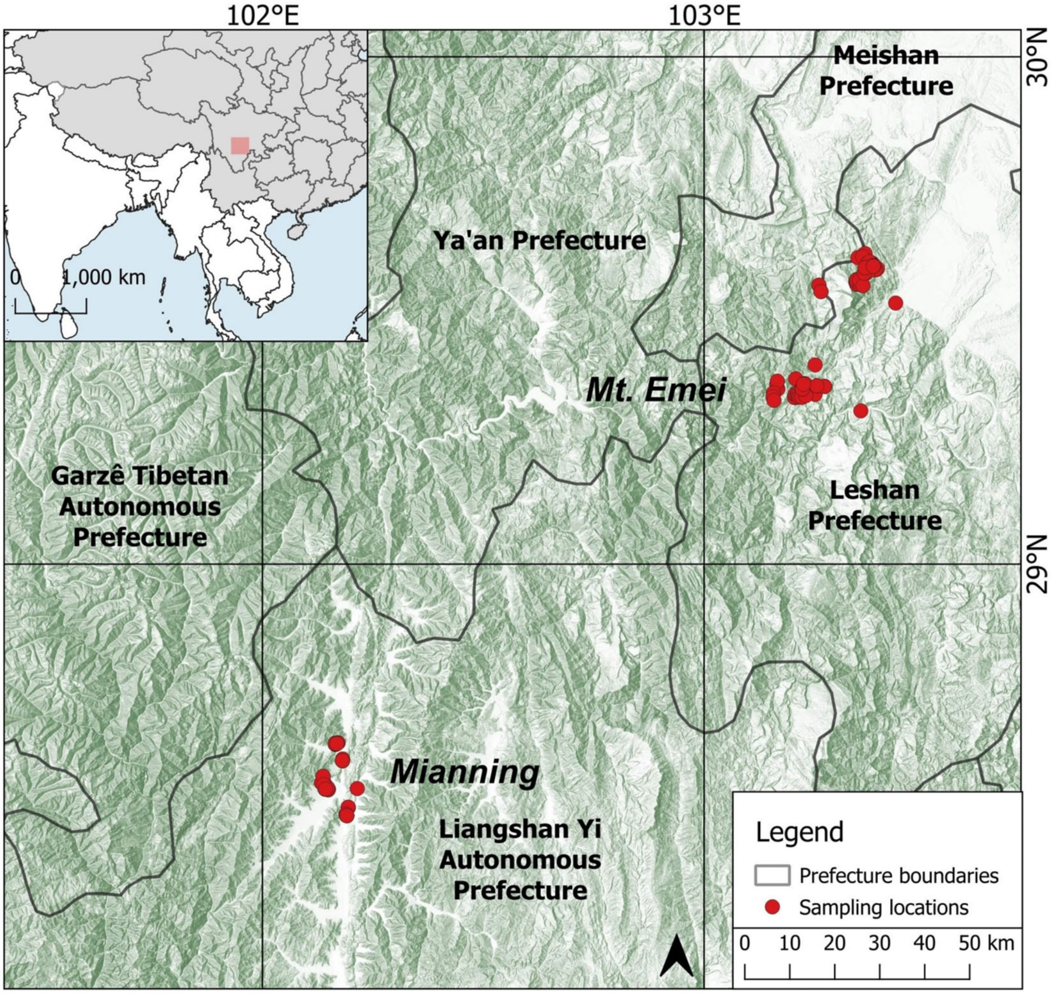

FIGURE 1 Site locations for Emeishan (Mount Emei) and Mianning in Sichuan Province, China. Red circles indicate individual sample sites at each of Emeishan and Mianning. The filled red square on the inset map shows the location of the map area within Sichuan Province, China.

MATERIALS AND METHODS

Study area and Fagaceae taxon sampling

Galls were collected between November 2017 and June 2022 from two sites 132 km apart in Western Sichuan: Emeishan (29.35681 N, 103.2268 E for Emeishan Botanical Gardens) and Mianning County in Liangshan Yi Autonomous Prefecture (28.6094 N, 102.181111 E for Huian Pingba). At each site, we sampled from multiple locations separated by distances ranging from 100 m to 35 kilometres (full sample location and sampling effort metadata are provided in Appendix S1). Because we suspect that parasitoids and gallwasps can disperse over these distances, we choose to amalgamate our data at our site scale. However, we do not know the spatial scales of the processes structuring the networks under study, and we do not regard our sites as formally independent in the statistical sense. The study sites lie within a global biodiversity hotspot in the eastern outliers of the Hengduan mountains, at the eastern rim of the Tibetan Plateau (Figure 1; Xing & Ree, 2017; Wan et al., 2021). Sampling locations ranged in altitude from 552 to 2288 m at Emeishan and from 1713 to 2056 m in Mianning. We sampled multiple individuals of 20 Fagaceae species at Emeishan (2 *Castanea*, 3 *Castanopsis*, 5 *Lithocarpus* and 10 *Quercus* (2 in section *Cerris*, 5 *Cyclobalanopsis*, 1 *Ilex*, 2 *Quercus*)) and 6 species at Mianning (1 *Castanea*, 1 *Lithocarpus*, 4 *Quercus* (1 in section *Cerris*, 1 *Cyclobalanopsis*, 1 *Ilex*, 1 *Quercus*)), with six species present at both sites (Table 1). Full Bipartite trophic association datasets are available from the Edinburgh Data Share repository (https://doi.org/10.7488/ds/7756).

Cynipid gall collection and rearing

For each tree on each sampling date, we collected all galls from 10 branches, defined as 4 years of growth (based on tracking ring scars back along the main shoot from its tip) by a main shoot and all associated side shoots. For the sampled tree species, this corresponds approximately to the most recent 1 m of shoot growth. All galls were reared in mesh-covered containers at external ambient temperatures

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TABLE 1 Summary of sampling effort, gall collections and reared parasitoid specimens by tree taxon and site.

	Emeishan								Mianning								Both sites combined			
	No. of trees								No. of trees											
Host tree taxon	Spr	Aut	G	GT	GT_{est}	P	PT	PT_{est}	Spr	Aut	G	GT	GT_{est}	P	PT	PT_{est}	GT	GT_{est}	PT	PT_{est}
Castanea	–	–	–	**1**	**1.00 (0.00)**	–	**13**	**13.0 (0)**	–	–	–	**1**	**1.00 (0.00)**	–	**20**	**25.0 (5.52)**	**1**	**1.00 (0.00)**	**24**	**31.5 (8.13)**
C. henryi Rehder and Wilson	16	52	212	1	–	3	2	–	0	0	0	0	–	0	0	–	1	–	2	–
C. molissima Blume	216	45	6426	1	–	660	13	–	241	0	4082	1	–	643	20	–	1	–	24	–
Castanopsis	–	–	–	**20**	**23.3 (4.11)**	–	**13**	**16.8 (4.19)**	–	–	–	**0**	**NA**	–	**0**	**NA**	**20**	**23.2 (4.11)**	**13**	**16.8 (4.19)**
C. carlesii (Hemsl.) Hayata	14	64	167	9	–	0	0	–	0	0	0	0	–	0	0	–	9	–	0	–
C. fargesii Franch.	1	7	7	5	–	1	1	–	0	0	0	0	–	0	0	–	5	–	1	–
C. platyacantha Rehder and Wilson	18	105	424	13	–	46	13	–	0	0	0	0	–	0	0	–	13	–	13	–
Lithocarpus	–	–	–	**14**	**14.3 (0.92)**	–	**12**	**14 (2.86)**	–	–	–	**5**	**5.00 (0.00)**	–	**12**	**14.0 (2.86)**	**18**	**18.3 (0.73)**	**19**	**26.5 (8.12)**
L. cleistocarpus Rehder and Wilson	41	49	578	11	–	569	10	–	0	0	0	00	–	00	0	–	11	–	10	–
L. dealbatus Rehder	0	0	0	0	–	0	0	–	56	11	462	5	–	131	12	–	5	–	12	–
L. hancei Rehder	1	5	87	6	–	0	0	–	0	0	0	0	–	0	0	–	6	–	0	–
L. litseifolius Chun	0	1	1	1	–	0	0	–	0	0	0	0	–	0	0	–	1	–	0	–
L. megalophyllus Rehder and Wilson	3	9	50	7	–	9	4	–	0	0	0	0	–	0	0	–	7	–	4	–
L. oblanceolatus Huang and Chang	0	2	2	1	–	0	0	–	0	0	0	0	–	0	0	–	1	–	0	–
Quercus section *Cerris*	–	–	–	**34**	**37.0 (4.16)**	–	**19**	**24.0 (5.52)**	–	–	–	**18**	**18.0 (0.24)**	–	**33**	**40.0 (6.64)**	**36**	**36.3 (0.92)**	**39**	**42.0 (3.18)**
Q. acutissima Carruth.	16	37	3504	29	–	91	18	–	0	0	0	0	–	288	17	–	30	–	27	–
Q. variabilis Blume	5	26	664	23	–	18	8	–	61	21	3926	18	–	365	28	–	27	–	30	–
Quercus section *Cyclobalanopsis*	–	–	–	**57**	**61.2 (4.34)**	–	**24**	**52.0 (21.4)**	–	–	–	**16**	**16.2 (0.62)**	–	**17**	**18.5 (2.22)**	**70**	**74.0 (3.89)**	**28**	**42.0 (13.2)**
Q. gambleana A. Camus	3	3	20	4	–	2	1	–	0	0	0	0	–	0	0	–	4	–	1	–
Q. schottkyana Rehder and Wilson	0	0	0	0	–	0	0	–	38	6	1425	16	–	248	17	–	16	–	17	–
Q. ciliaris Huang and Chang	7	29	2173	25	–	317	20	–	0	0	0	0	–	0	0	–	25	–	20	–
Q. hypargyrea (Seemen)	0	15	90	6	–	0	0	–	0	0	0	0	–	0	0	–	6	–	0	–

(Continues)

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TABLE 1 (Continued)

	Emeishan								Mianning								Both sites combined			
	No. of trees								No. of trees											
Host tree taxon	Spr	Aut	G	GT	GT_{est}	P	PT	PT_{est}	Spr	Aut	G	GT	GT_{est}	P	PT	PT_{est}	GT	GT_{est}	PT	PT_{est}
Q. myrsinaefolia Blume	10	30	5538	24	–	169	14	–	0	0	0	0	–	0	0	–	25	–	14	–
Q. oxyodon Miq.	24	55	1564	30	–	64	12	–	0	0	0	0	–	0	0	–	30	–	12	–
Quercus section Ilex	–	–	–	**0**	NA	–	**0**	NA	–	–	–	**7**	7.00 (0.46)	–	**22**	37.0 (12.8)	**7**	7.00 (0.46)	**22**	37.0 (12.8)
Q. monimotricha Hand.-Mazz.	1	0	0	0	–	0	0	–	77	38	981	7	–	160	22	–	7	–	22	–
Quercus section Quercus	–	–	–	**24**	24.3 (0.73)	–	**22**	24.5 (3.15)	–	–	–	**5**	5.00 (0.00)	–	**14**	21.0 (7.08)	**27**	27.3 (0.73)	**27**	32.6 (5.34)
Q. aliena Blume	0	0	0	0	–	0	0	–	17	12	558	5	–	82	13	–	4	–	13	–
Q. fabri Hance	69	119	9645	24	–	697	22	–	0	0	0	0	–	4	2	–	26	–	22	–
Q.s serrata Murray	1	1	34	2	–	0	0	–	0	0	0	0	–	0	0	–	2	–	0	–
Total per locality	**446**	**654**	**31,186**	**147**	**161.5** (9.45)	**2646**	**46**	**51.3** (5.37)	**490**	**88**	**11,434**	**52**	**52.9** (1.39)	**1921**	**54**	**80.0** (20.0)	**175**	**186.4** (6.96)	**64**	**94.3** (22.7)

Note: Includes: the numbers of trees sampled (no. of trees) during spring (Spr = March–June) and autumn (Aut = July–December) field seasons; the number of individual galls reared (G); the number of distinct cynipid gall morphotypes (GT) and the Chao estimate for gall morphotype richness (GT_{est}); the number of parasitoid specimens reared (P); the number of associated parasitoid morphospecies (PT) and the Chao estimate for parasitoid species richness (PT_{est}). Chao estimates are followed by their standard errors in parentheses. Table values in bold font show summed totals for each oak section or non-oak genus. Note GT for Emei (147) is 3 less than the sum of the individual Fagaceae taxon totals (150) because three gall morphotypes were found either on two sections within *Quercus* or on both *Quercus* and another Fagaceae genus (see Appendix S4 for a discussion of these cases).

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at Emeishan Botanical Gardens. Total rearing effort was 42,620 galls from 1678 trees (Table 1). Rearings were checked every 2 weeks, and emerged insects were photographed individually using a Leica EZ4W photomicroscope with built-in camera before preservation as physical vouchers in 99% ethanol.

Defining taxonomic units

Host plants

Host plants were identified using morphological characters as applied in Chinese floras (Fu & Hong, 1999; Wu & Raven, 1999). Our taxonomy follows the World Flora Online (WFO, 2023).

Cynipid gall inducers

A subset of sampled galls could be linked to named cynipid species based on existing literature (Lobato-Vila et al., 2022). We sorted all other galls into distinct morphotypes and identified cynipid-induced galls by dissection and identification of cynipid larvae, pupae or adults. For transparency and repeatability, we provide digital vouchers for all gall morphotypes in Appendix S2. Almost all Cynipini have a lifecycle involving alternation between a spring sexual generation and an autumn asexual generation (Stone et al., 2002), each of which induces a distinctive gall morphology (Stone et al., 2002). Cynipid species for which we sampled both generations are thus likely to be represented by two gall morphotypes in our data. Similar gall morphotype-based approaches have been used elsewhere in studies on cynipids (Cuevas-Reyes et al., 2007; Cuevas-Reyes, Quesada, Hanson, et al., 2004; Cuevas-Reyes, Quesada, Siebe, & Oyama, 2004; Maldonado-López et al., 2022; Pérez-López et al., 2016) and other gall inducers (Blanche, 2000; Butterill & Novotny, 2015; Coelho et al., 2017; De Araújo et al., 2013; de Araújo et al., 2021; Kuzmanich et al., 2023; Oliveira et al., 2020).

Because morphotyping may lump morphologically similar galls induced by different cynipid species, or split morphologically different developmental stages of a single gall type (Plantard & Hochberg, 1998; Stone et al., 2007), we used DNA barcoding to explore the validity of our morphotype-based gall taxonomy. Assuming that DNA barcodes recover gallwasp species boundaries (Nicholls et al., 2012), we expect that Cynipini from different gall morphotypes developing at the same time of year will have different barcode sequences. We also expect that sometimes inducers sequenced from very different morphotypes in spring and autumn will have very similar or identical barcode sequences, consistent with their being two generations of the same biological species (Stone et al., 2007).

We sequenced 658 base pairs of the Folmer barcode region of the mitochondrial cytochrome c oxidase 1 (COI) gene for 148 cynipid gall inducer specimens (31 adults, 14 pupae and 103 larvae) from 35 gall types (6 named taxa for method validation and 29 undescribed morphotypes; Table S3). We extracted total genomic DNA from a single leg of adults or a portion of the body for pupae or larvae using a Chelex extraction protocol (Nicholls et al., 2010) or the Qiagen Blood and Tissue Kit following the manufacturer's protocol. Polymerase chain reaction (PCR) amplification used primers LCO2198/HCO1490 (Folmer et al., 1994) and PCR conditions in Bozsó et al. (2015). For 141 specimens, amplicons were Sanger sequenced as described in Fang et al. (2020). For seven specimens that proved impossible to sequence directly, we generated barcode sequences by cloning. PCR products for these specimens were purified using the Trelief DNA gel extraction kit, inserted into a pClone 007 Vector using the pClone 007 Simple Vector kit and used to transform Trelief TM 5α chemically competent cells (Tsingke Biotechnology Co., Ltd, Beijing, China). Positive clones were miniprepped in *Escherichia coli* using 2× YT medium and confirmed using M13F/M13R primers with T5 colony PCR mix and the following PCR conditions: 98°C for 3 min then 30 cycles of 98°C for 10 s, 53°C for 10 s, 72°C for 10 s, ending with 72°C for 5 min. All sequences were checked by eye in Sequencher 5.4.6. (Gene Codes Corporation, n.d.) and confirmed as coding DNA to exclude pseudogenes (Porter & Hajibabaei, 2021). Sequences were deposited in Genbank with accession numbers listed in Table S3 and in Barcode of Life Data Systems (BOLD; Ratnasingham et al., 2007), project name TRICO.

Sequences were allocated to molecular operational taxonomic units (OTUs) using the *Cluster Sequences* analytical tool in BOLD with default parameters. We constructed a neighbour-joining phylogeny using uncorrected P distances in the BOLD tool *Taxon ID Tree*. To simplify visualisation, we included a single copy of each haplotype per gall morphotype, resulting in 56 sequences. We checked for potential matches between novel sequences and published sequences for previously reported taxa using the BOLD tool *ID Engine* (Ratnasingham et al., 2007), using the full BOLD COI database with the similarity filter parameter set to a minimum 98% (Hebert et al., 2003) and other parameters at default settings. In particular, we used published sequences for *D. kuriphilus* (DQ286810, JF411594, JF411595, JF411598, KF308606, MH8011331 and MH119939) and *Dryocosmus zhuili* Liu & Zhu, 2015 (JF411596 and JF411597) to confirm identities of 34 individuals sampled from 32 galls on *Castanea mollissima* (the typical host of *D. kuriphilus*) and 7 individuals sampled from 7 galls on *Castanea henryi* (the typical host of *D. zhuili*).

Parasitoids

We sorted all parasitoids to family, genus (where possible) and morphospecies based on morphological traits (Table S2). We excluded from our analyses occasional parasitoid taxa (such as large ichneumonids) that are very unlikely to be directly associated with cynipid galls and more likely to be associated with opportunistic occupants of emerged galls. For transparency and to allow replication, we provide a diagnostic key and digital vouchers for all parasitoid morphospecies in Appendix S3. Criteria for pairing of males and females, and for exclusion of some specimens from analyses, are detailed in Appendix S4.4. Two *Torymus* species (*Torymus sinensis* and *Torymus geranii*) were

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identified using adult morphological characters (Vere Graham & Gijswijt, 1998; Yasumatsu & Kamijo, 1979).

Individual cynipid and parasitoid specimens with unique project codes are deposited at the Emeishan Biological Resources Research Station, Sichuan Provincial Academy of Natural Resources Sciences, Emeishan Wannian Parking Lot, Leishan, Sichuan Province 614201, China.

Analyses of taxon richness

We estimated the asymptotic richness of gall morphotypes and parasitoid morphospecies using the bias-corrected Chao estimator (Chiu et al., 2014; O'hara, 2005) calculated with the *estimateR*() function of the *Vegan* R package (Oksanen et al., 2022). Values are given ±1 standard error. The estimator was applied to counts of gall or parasitoid taxa associated with a particular host plant taxon and treated the host plant taxon as a single site. Separate estimates were made for each sampling locality and for both localities combined.

Analyses of bipartite interaction networks

We analysed bipartite interaction matrices for gall morphotypes on host plants, parasitoid morphospecies on host plants and parasitoid morphospecies in gall morphotypes. To allow comparison across trophic levels, we included only those gall morphotypes from which parasitoids had emerged. While the gallwasp–plant interactions comprise a true trophic network, the hosts of the parasitoids are unknown and could be the gall inducer, inquiline cynipids or other parasitoids (Askew et al., 2013; Csóka et al., 2005; Ward, Busbee, et al., 2022). The parasitoid–gall interactions thus comprise an association network (Schönrogge & Crawley, 2000). For simplicity, we use the term link to refer to all bipartite species associations. Given the observed between-site differences in the species composition for each of the tree, gall inducer and parasitoid trophic levels, we analysed matrices for each site individually to exclude potential impacts of spatial beta diversity on network structure and associated metrics (Galiana et al., 2019; Soininen et al., 2007). Unless otherwise specified, network analyses were carried out using the *Bipartite* R package v.2.18 (Dormann et al., 2009).

Modularity

We identified network modules using the *metaComputeModules* function ($n = 500$) in *Bipartite* with default parameters including the Beckett (2016) algorithm and reported the associated modularity likelihood (equivalent to Q in Newman, 2006). Modules can be identified for either incidence data (binary presence–absence, unweighted networks) or frequency data (count-based, weighted networks). Incidence data incorporate no information on interaction strength (Berlow et al., 2005) and thus cannot discriminate between alternative scenarios in which a species in one trophic level associates with two alternative members of another trophic level at relative rates of 99:1 and 50:50. In contrast, frequency data allow detection of cross-species variation in interaction strength. By not discriminating between weak and strong links (Berlow et al., 2005), a presence/absence approach may oversimplify network patterns. For our data, results for weighted (count-based) and unweighted (incidence) interaction matrices were very similar and here we present data for the weighted matrices. We assessed the significance of observed modularity relative to values for 500 randomised networks created using the r2d and VazNull models using *z*-scores, following Vázquez et al. (2007), Blüthgen et al. (2006) and Dormann et al. (2009). Positive *z*-scores indicate values higher than null predictions, while negative *z*-scores indicate values lower than null predictions.

Taxon network roles

The roles of individual taxa in network structure can be described using indices that capture their contributions to links within and between network modules. We follow Guimerà and Amaral (2005), Guimerà et al. (2005), Olesen et al. (2007) and Dormann and Strauss (2014) in using the standardised connection or participation coefficient, c, as an index of between-module connectivity (P in Guimerà et al., 2005), and relative within-community degree, z, as an index of within-module connectivity. Both are based on the degree (=number of links) of a particular type for a focal taxon and are not weighted by each link's frequency. c (defined as 1 − sqr(degree within module/total degree)) quantifies the extent to which links involving a focal taxon are distributed between (high *c*) versus within (low *c*) modules. z is defined as the number of links involving an individual species standardised by the average within-module number of links per species, divided by the standard deviation (Dormann & Strauss, 2014; Guimerà et al., 2005; Olesen et al., 2007). A high value of z indicates a 'hub' taxon, which is well connected to other taxa in the same module in comparison to other module members. Here we apply a simplified version of the roles for taxa with particular combinations of c and z values proposed by Guimerà and Amaral (2005) and Guimerà et al. (2005). Taxa that have high values of both z and c (i.e. hub taxa in one module that are also well connected to other modules) are termed connector hubs. Taxa that only have high z values are termed local hubs. Taxa that have high c but low z (termed 'kinless' by Guimerà and Amaral (2005)) are not strongly associated with a particular module, and we refer to them as module connectors. Taxa with low values for both c and z interact mainly with a small subset of taxa in a single module and we refer to these as local nodes. Highly generalist species are expected to be either connector hubs or module connectors, while we expect specialists to be local nodes. To define threshold values of c and z for this classification, we follow a suggestion by Dormann et al. (2009) and Dormann and Strauss (2014) and calculate network-specific critical values using the 95% quantiles for c and z values extracted from 500 iterations of the r2d null model. Critical values for each network and dataset are shown in Table S4. Following Guimerà

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and Amaral (2005) and Guimerà et al. (2005), our figures use these thresholds to divide cz-space into four zones (connector hubs, local hubs, module connectors and local nodes) above and below the 95% quantiles along c and z axes.

Specialisation of species in gall inducer and parasitoid guilds

We used the d' index to compare the relative specialisation of gallwasp–plant and parasitoid–plant associations. The d' index measures how strongly a species' observed interaction richness deviates from a random sampling of available partners (Blüthgen et al., 2006) and varies between 0 (no specialisation) and 1 (perfect specialist). In contrast to presence/absence measures, d' accounts for how likely an observed link is, so that for instance, an apparently specialist parasitoid that only attacks a very common host would have a lower value of d' than a parasitoid attacking a single rare host. Our prediction is that the intimate manipulation of plant gene expression involved in gall induction will result in higher host plant specialisation, and hence higher mean d', in gall inducers as a guild than in parasitoids. We compared mean d' values between gall morphotypes and parasitoids in relation to host tree species using a Wilcoxon rank sum test with continuity correction in R.

Connectance and network-level specialisation (H_2')

Network connectance is a measure of the proportion of all possible links that are realised (Memmott et al., 1994) and can be seen as a network-wide measure of specialisation using binary presence/absence data: networks dominated by specialised interactions are characterised by low connectance. We also calculated H_2', which is a network scale measure of specialisation that incorporates link frequency information (Blüthgen et al., 2006). Both were calculated in *Bipartite*. We used *z*-scores to assess the significance of observed values relative to values for 500 randomised networks created using the r2d and VazNull null models. Significance was assessed for both connectance and H_2' for the r2d null model, but only for H_2' in the VazNull model since connectance is a retained property of this model (Blüthgen et al., 2006; Dormann et al., 2009; Vázquez et al., 2007).

Beta diversity of plant associations

Beta diversity captures the extent to which component communities contain different sets of species. It can be measured in terms of Sørensen dissimilarity for presence/absence data and Bray–Curtis dissimilarity for abundance data (Chao et al., 2012; Chao & Chiu, 2016; Jost, 2007). We used Baselga's (2010) method of partitioning beta diversity into two components, representing nestedness (the extent to which species in component communities tend to be subsets of each other) and turnover (the extent to which component communities involve non-overlapping sets of species). The R package *betapart* (v. 1.6) allows estimation of 'nested' (NES) and 'turnover' (SIM) components for Sørensen dissimilarity in presence/absence data, and of analogous 'balanced' (BAL) and 'gradient' (GRA) components for Bray–Curtis dissimilarity in abundance data (Baselga, 2010, 2017; Baselga & Orme, 2012). We compared the nestedness and turnover components using both incidence and abundance data for gall morphotype and parasitoid morphospecies associations with host trees. Our expectation is that if cynipid gall inducers are more host tree specific than parasitoids, then gall–tree networks should show greater turnover and lower nestedness components than corresponding parasitoid–tree networks. We used the functions beta.sample and beta.sample.abund to estimate gall and parasitoid dissimilarities (and their beta diversity components) among sampled tree species 1000 times for each site dataset, and for each of presence/absence and abundance data. We report the means ±95% confidence intervals (CI) together with the 95% CI of the difference of the mean between gall types and parasitoid communities. In addition, we report the proportion of sub-sampled values (equivalent to a *p* value) for which nestedness (GRA and NES) is significantly larger for galls, and for which turnover (BAL & SIM) is significantly larger for parasitoid communities, as described in the betapart manual (Baselga & Orme, 2012).

RESULTS

Gallwasp community richness and DNA barcode validation of gall morphotypes

Over both sites, 42,620 galls yielded 176 cynipid gall morphotypes. Only 11 were identifiable to described species, for 10 of which we provide first records for Western China (see Appendix S4.1 for further details). The remaining 165 morphotypes are not associated with any described cynipid species we know (see Figure 2 for examples). Gall assemblages were substantially different between our two sites: we recorded 147 gall morphotypes at Emeishan and 52 gall morphotypes at Mianning (Table 1 and Table S1), of which only 23 (13%) were shared between sites. Observed values of gall morphotype richness were ≥90% of Chao estimates (Table 1), implying relatively complete sampling of cynipid gall morphotypes at each site.

DNA barcoding results supported the inference that each morphotype is induced by a single gallwasp species and generation. The 148 COI sequences were clustered into 34 OTUs (Table S3 and Figure S1), of which 29 contained sequences for a single gall morphotype. For further information on the DNA barcoding results, see Appendix S4.2. Three OTUs contained sequences from different spring and autumn gall morphotypes (Figure S1), which we interpret as alternating generations in the life cycle of a single gallwasp species. Assuming that each gall type is induced by a single generation of a single species, our sampling of 100 undescribed autumn (asexual generation) gall types and 55 undescribed spring (sexual generation) gall types implies a minimum of 100 undescribed Cynipini at Emeishan and Mianning combined.

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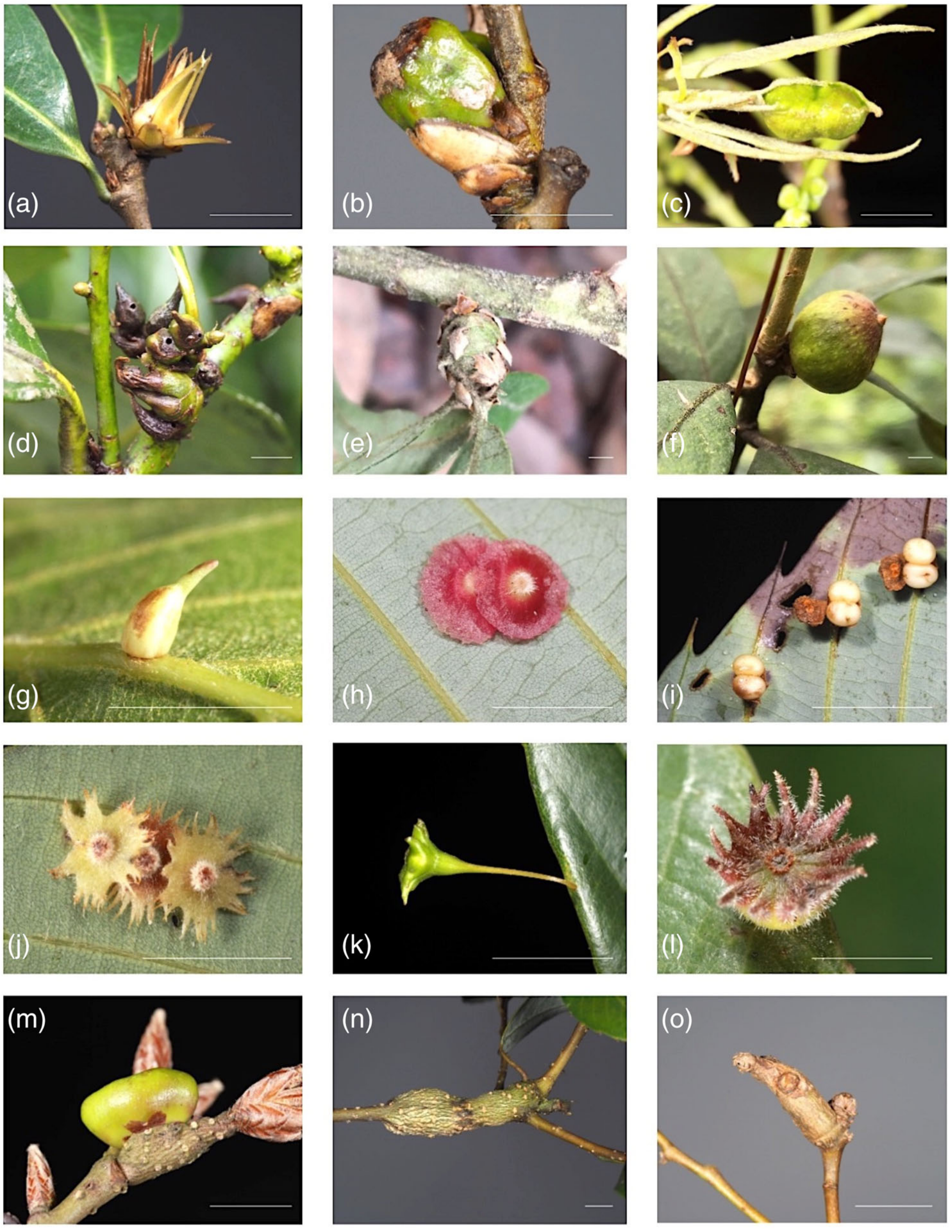

FIGURE 2 Examples of undescribed cynipid galls on Sichuan Fagaceae at Emeishan and Mianning. Oak sections for *Quercus* species are abbreviated to C = *Cerris*, Cy = *Cyclobalanopsis* and Q = *Quercus*. Gall morphotype numbers are used throughout figures and supplementary information. The scale bar in each image is 5 mm. (a) 16 on bud of *Castanopsis carlesii*. (b) 63 on bud of *Castanopsis platyacantha*. (c) 116 on young leaves/shoots of *Castanopsis carlesii*. (d) 38 on leaf petiole of *Lithocarpus cleistocarpus*. (e) 304 on bud of *Lithocarpus dealbatus*. (f) 306 on bud of *Lithocarpus dealbatus*. (g) 86 on leaf of *Q. acutissima* (C). (h) 57 on leaf of *Q. oxyodon* (Cy). (i) 59 on leaf of *Q. oxyodon*. (j) 71 on leaf of *Q. oxyodon*. (k) 242 on leaf of *Q. hypargyrea* (Cy). (l) 160 on leaf of *Q. myrsinaefolia* (Cy). (m) 181 on shoot of *Q. ciliaris* (Cy). (n) 54B on stem of *Q. ciliaris*. (o) 22 on acorn peduncle of *Q. fabri* (q).

Across host plant lineages (here defined as sections within *Quercus* or distinct non-oak genera), estimated gall morphotype richness for both sites combined (Table 1) was highest for the oak sections *Cyclobalanopsis* (75.0 ± 3.89) and *Cerris* (36.3 ± 0.92) and lowest for *Castanea* (1 ± 0). The only cynipid species reared from over 10,500 galls and 500 tree sampling events for *C. mollissima* and 212 galls from 68 tree sampling events for *C. henryi* (Table 1) was *D. kuriphilus*, confirmed by DNA barcoding (Appendix S4). The highest observed gall morphotype richness on an individual tree species at a single site was 30 on *Quercus oxyodon* (section *Cyclobalanopsis*) at Emeishan.

Parasitoid community richness and composition

Eighty of the 176 gall morphotypes (59 at Emeishan, 30 at Mianning) produced parasitoids, resulting in a total of 4567 specimens of

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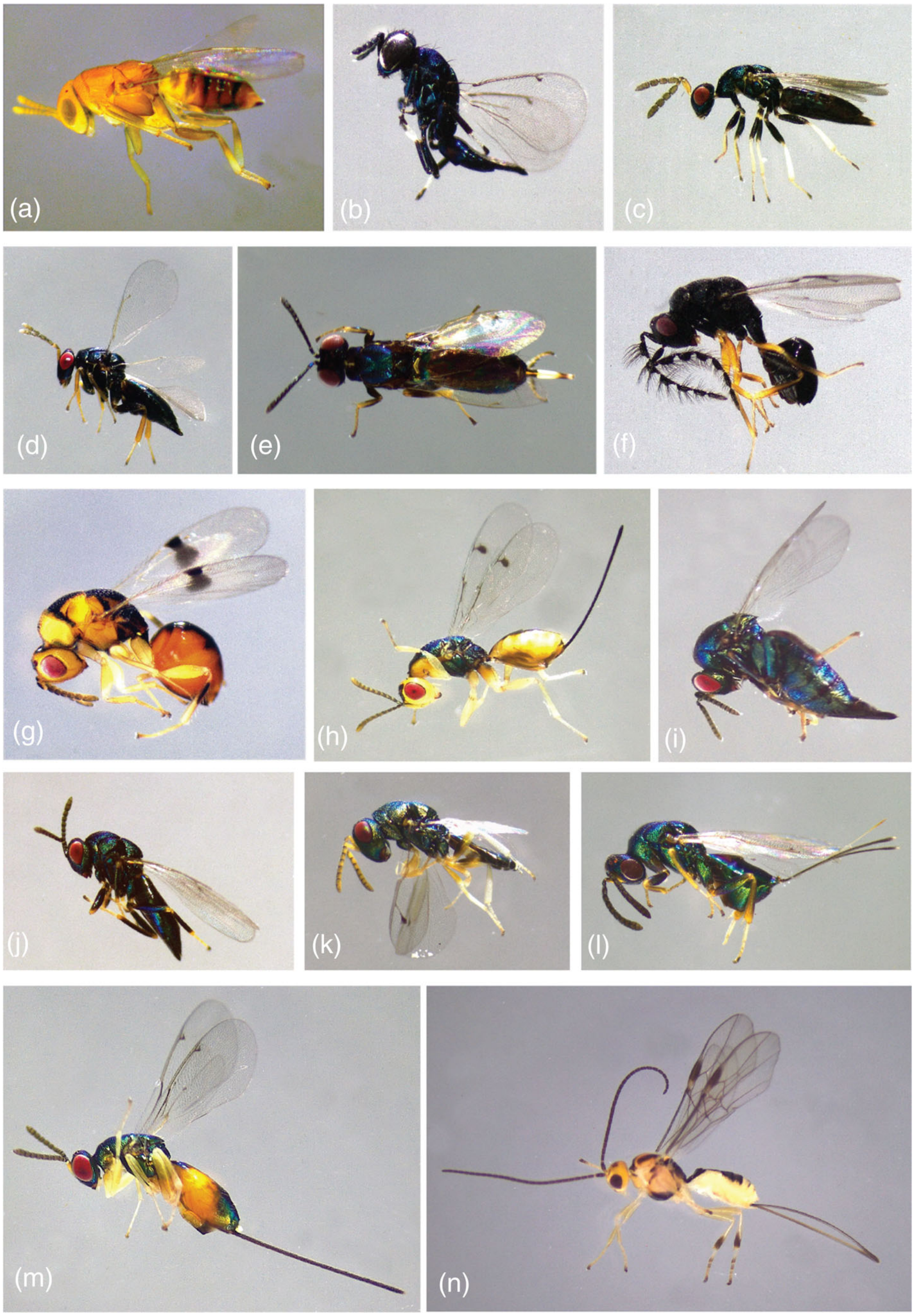

FIGURE 3 Family and subfamily taxonomic diversity of parasitoids associated with cynipid galls on Fagaceae at Emeishan and Mianning. All families and subfamilies are represented. (a) *Cynipencyrtus* 1 (Cynipencyrtidae). (b) Eulophidae 12. (c) Eulophidae 5. (d) Eulophidae 1. (e) *Eupelmus* 1 (Eupelmidae). (f) *Eurytoma* 1 (Eurytomidae). (g) *Sycophila* 3 (Eurytomidae). (h) *Bootanomyia* 1 (Megastigmidae). (i) *Ormyrus* 4 (Ormyridae). (j) Pteromalidae 4. (k) Pteromalidae 6. (l) *Torymus* 1 cf. *sinensis* (Torymidae). (m) *Torymus* 2 cf. *geranii* (Torymidae). (n) *Bracon* 1 (Braconidae). Further taxonomic information on morphospecies is provided in Table S2.

64 parasitoid morphospecies (Table 1 and Table S1) of which 36 were shared between sites. For Emeishan, the observed richness was 90% of the Chao estimate (51.3 ± 5.4), suggesting reasonably thorough sampling. For Mianning, the observed richness was only 67.5% of the Chao estimate (80 ± 20), implying substantial unsampled parasitoid richness. Over both sites, parasitoid morphospecies richness was highest for the oak sections *Cerris* (39), *Cyclobalanopsis* (28) and *Quercus* (27) (Table 1). Across gall morphotypes, highest parasitoid richness was recorded for the asexual generation galls of *Latuspina abemakiphila* (25), *D. kuriphilus* (24) and *Heocynips furvoaurantius* (17).

All of the families and many of the genera present in Western Palaearctic and Nearctic oak gall communities were also present in Sichuan (Figure 3): Eulophidae (17 morphospecies, including putative *Aprostocetus* (1), *Baryscapus* (2), *Chrysonotomyia* (1), *Chrysocharis* (1), *Cirrospilus* (1), *Pediobius* (1)), Eupelmidae (7, including 3 *Eupelmus*), Eurytomidae (3 *Eurytoma*, 3 *Sycophila*), Megastigmidae (7 *Bootanomyia*),

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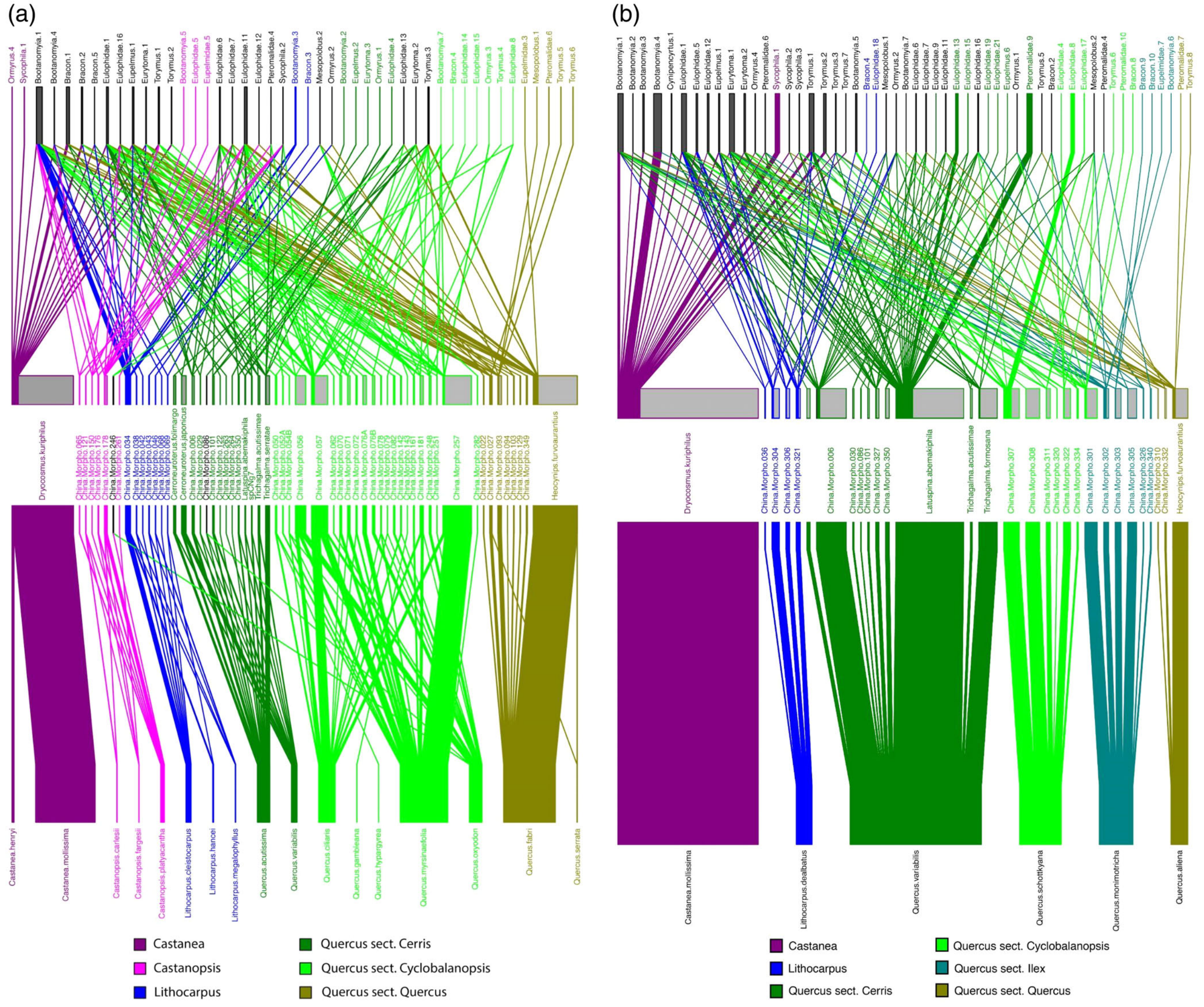

FIGURE 4 Tripartite interaction network for (a) Emeishan and (b) Mianning. Trophic levels (from bottom to top) are plants, gall inducers and parasitoids. Bars, links and taxon names are coloured by the plant taxon hosting the interaction. Bars and taxon names for gall inducers and parasitoids associated with multiple plant taxa black. The width of the bars in the plant and gall inducer trophic levels is scaled by the number of galls sampled. The width of the bar above the gall inducer taxon names is divided between those attacked by parasitoids (coloured) and those not attacked, and so is an indication of gall attack rate. The width of the bars in the parasitoid trophic level indicates their contribution to the total number of parasitoid-attacked galls.

Ormyridae (4 *Ormyrus*), Pteromalidae (6, including 2 *Mesopolobus* and 1 putative *Cecidostiba*) and Torymidae (8 *Torymus*, including *Torymus* 1 putatively identified as the biocontrol agent *T. sinensis* Kamijo, and *Torymus* 2 = *T. geranii* (Walker)). Novel elements absent from the Western Palearctic and Nearctic include eight morphospecies of *Bracon* (Ichneumonoidea: Braconidae), *Cynipencyrtus flavus* (Chalcidoidea: Cynipencyrtidae) and *Chrysonotomyia* (Eulophidae) (see Appendix S4 for more information on parasitoid community composition).

Parasitoid morphospecies varied substantially in abundance (Table S2). The top 10 ranked parasitoids at each of Emeishan and Mianning contributed 81.6% and 71% of specimens, respectively, and at both sites included *Bootanomyia* 1, Eulophidae 1 and *Torymus* 1 (putative *T. sinensis*; see Appendix S4.5 for a more detailed summary). The most abundant parasitoids all attacked multiple host galls on multiple plant lineages, paralleling patterns in the Western Palaearctic (see below). At the other end of the abundance spectrum, 23 morphospecies were represented by fewer than 10 specimens across both sites, including 14 represented by a single specimen.

The structure of gallwasp–plant interaction networks

Tripartite interaction networks for Emeishan and Mianning are shown in Figure 4. With only three exceptions, all at Emei, all gall

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TABLE 2 Modularity, connectance and H_2' measures of network specialisation for gallwasp–plant, parasitoid–plant and gallwasp–parasitoid networks at each site.

	Modularity			Connectance		H_2'		
	Observed value (Q)	*z* (R2d)	*z* (VazNull)	Observed value	*z* (R2d)	Observed value	*z* (R2d)	*z* (VazNull)
Emeishan								
Gallwasp–plant	0.738	474.5***	28.9***	0.103	−58.7***	0.874	2222.4***	25.0***
Parasitoid–plant	0.510	97.6***	62.8***	0.231	−22.0***	0.516	196.8***	56.2***
Gallwasp–parasitoid	0.551	113.2***	53.4***	0.071	−30.6***	0.541	165.4***	42.2***
Mianning								
Gallwasp–plant	0.720	318.3***	2.4*	0.167	−58.1***	1.0	1943.5***	2.1*
Parasitoid–plant	0.530	86.1***	43.7***	0.364	−23.1***	0.644	187.1***	33.3***
Gallwasp–parasitoid	0.568	87.6***	47.5***	0.109	−30.1***	0.624	147.5***	38.3***

Note: For each measure, we provide observed values and *z*-scores for comparison with null model predictions generated for 500 replicate webs using the r2d and VazNull models. Positive *z*-scores indicate values higher than null predictions, while negative *z*-scores indicate values lower than null predictions. Significance levels are indicated as *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

morphotypes were specialists on a single Fagaceae lineage, that is, reared from species in a single oak section or non-oak genus (Figure 4a,b; see Appendix S4.3 for further information on the exceptions). This means that at Emei, 147 gall morphotypes contributed to a total of 150 interactions at the level of oak sections or non-oak genera (Table 1). This host specificity resulted in very low connectance, very high network-level specialisation (H_2') and high modularity in comparison to expectations of both null models (Table 2). At Emeishan, 103 gallwasp–plant links were partitioned into 6 modules (Figure 5a), which contained 90% ($n = 93$) of observed links. Links for 50 of 59 gallwasp taxa were entirely within-module. A similar pattern was observed at Mianning, where 6 modules contained all 30 gallwasp–plant links (Figure 6a). Both gallwasp–plant networks were strongly structured by plant taxonomy: all modules only involved tree species in either a single oak section or single non-oak genus of Fagaceae.

Locations of taxa in a c-z ordination are shown for Emeishan in Figure 7 and Mianning in Figure 8. Because links for most galls and host plants at both sites were entirely within-module, $c = 0$ for these taxa and no module connector or connector hub taxa were identified for this pair of trophic levels (Figures 7a,b and 8a,b). Note that because the denominator for z is the standard deviation of links of a focal species to others within a module, it is not defined for modules containing a single taxon in either trophic level (Figure 6a), which means that z values cannot be estimated for the Mianning gallwasp–plant network (Figure 8a). In the herbivore trophic level, the asexual generation gall of *H. furvoaurantius* was identified as a local (i.e. within-module) hub in the Emeishan network (Figure 7b), with three additional local hub taxa in the Emeishan network (China-Morpho.050, China-Morpho.034 and China-Morpho.027).

The structure of parasitoid–plant interaction networks

In strong contrast to cynipid–plant interactions, many parasitoid morphospecies were associated with multiple plant lineages (Table S2). Of 39 taxa represented by >10 specimens over both sites, all but 6 were associated with tree species in more than one oak section or non-oak genus (Figures 4, 5b and 6b; Figure S3b). *Bootanomyia* 1 and *Torymus* 1 (putative *T. sinensis*) attacked hosts on *Castanea*, *Castanopsis*, *Lithocarpus* and all four oak sections. Six other parasitoids attacked galls on six plant lineages comprising non oak Fagaceae and multiple oak sections (*Bracon* 2, *Eurytoma* 1, *Eulophidae* 16, *Sycophila* 2 and *Torymus* 3). In contrast, very few parasitoid taxa were host–plant specialists. Only four parasitoid taxa with $n > 20$ over both sites were associated with a single tree lineage: *Sycophila* 1 ($n = 164$, *C. mollissima*), Pteromalidae 9 ($n = 157$, *Quercus* section *Cerris*), Eulophidae 8 ($n = 114$, *Quercus* section *Cyclobalanopsis*) and *Ormyrus* 3 ($n = 30$, *Quercus myrsinaefolia*, section *Cyclobalanopsis*).

Parasitoids at both sites showed significantly non-random plant associations, with significantly lower connectance and greater network-level specialisation (H_2') and modularity than null model expectations (Table 2). However, the proportion of links placed within modules was much lower than for the corresponding gallwasp–plant networks. At Emeishan, 138 parasitoid–plant links were partitioned into six modules (Figure 5b), although 77 links (56%) involving 25 of 46 parasitoid morphospecies were not placed in any module. Similarly, at Mianning 118 parasitoid–plant links were partitioned into five modules (Figure 6b), of which 62 (52.5%) across 31 of 54 parasitoid morphospecies were not placed in any module. At both sites, parasitoid–plant links were far less structured by plant taxonomy than gallwasp–plant links: at Emeishan and Mianning, four of six modules and three of five modules, respectively, included tree species from multiple oak sections and/or Fagaceae genera.

In the Emeishan network, the plant trophic level (Figure 7c) contained one local hub (*Quercus variabilis*) and five module connectors, that is, associated with parasitoids from multiple modules (*Quercus acutissima*, *Quercus aliena*, *Quercus myrsinaefolia*, *Quercus schottkyana* and *Lithocarpus cleistocarpus*). The parasitoid trophic level (Figure 7d) contained one connector hub (Eulophidae 16), two local hubs (Eulophidae 6 and Eulophidae 11) and four module connectors (*Bootanomyia* 1, *Bootanomyia* 4, *Bracon* 1 and *Bracon* 2). At Mianning, the

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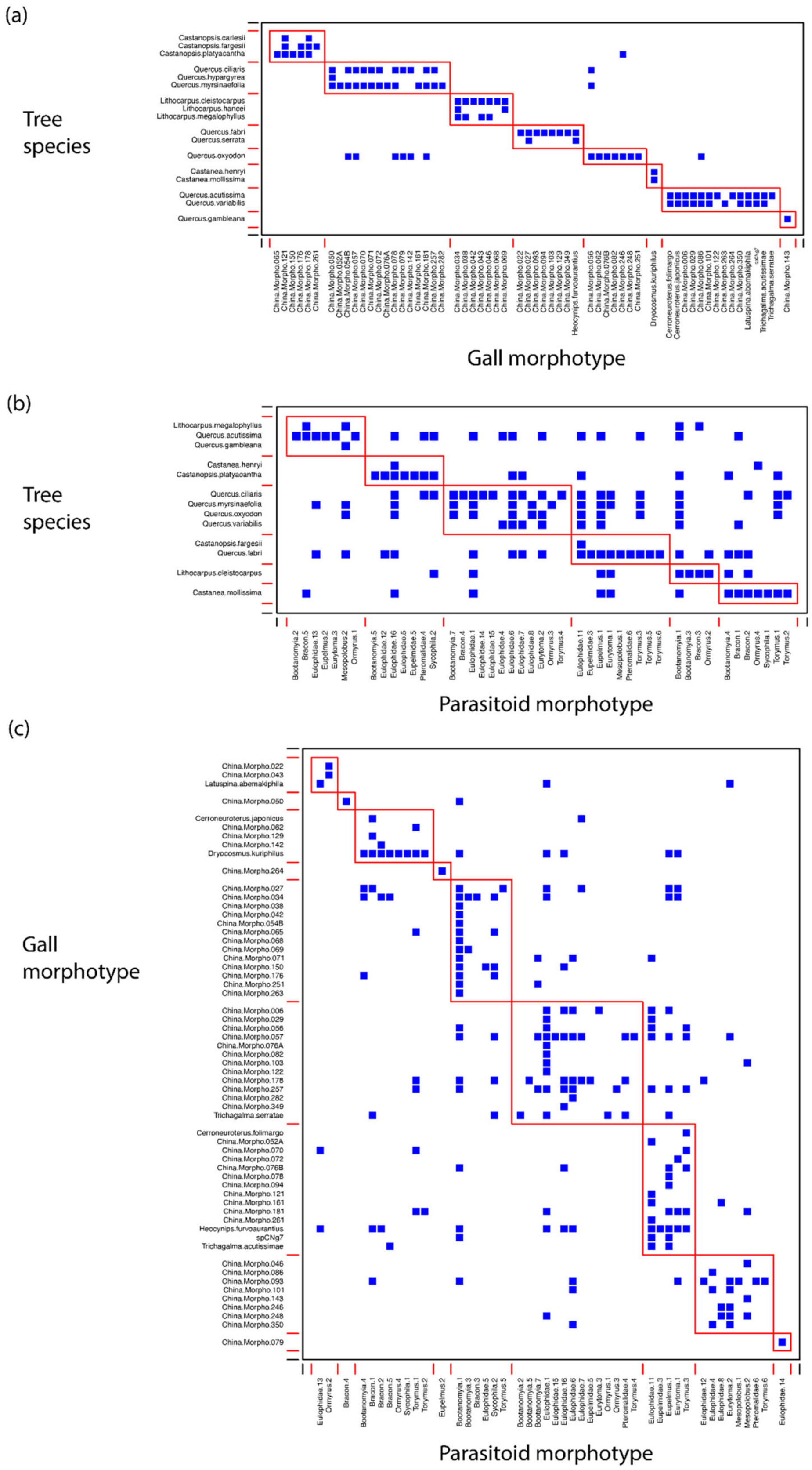

FIGURE 5 Network modules for Emeishan, for (a) galls on trees, (b) parasitoids on trees and (c) parasitoids on galls. Red boxes circumscribe the links that comprise each module. A summary plot for both sites combined is provided in Figure S2. Note that the set of plant species in (b) excludes species in (a) for which sampled gall types only yielded parasitoids when developing on other host plants.

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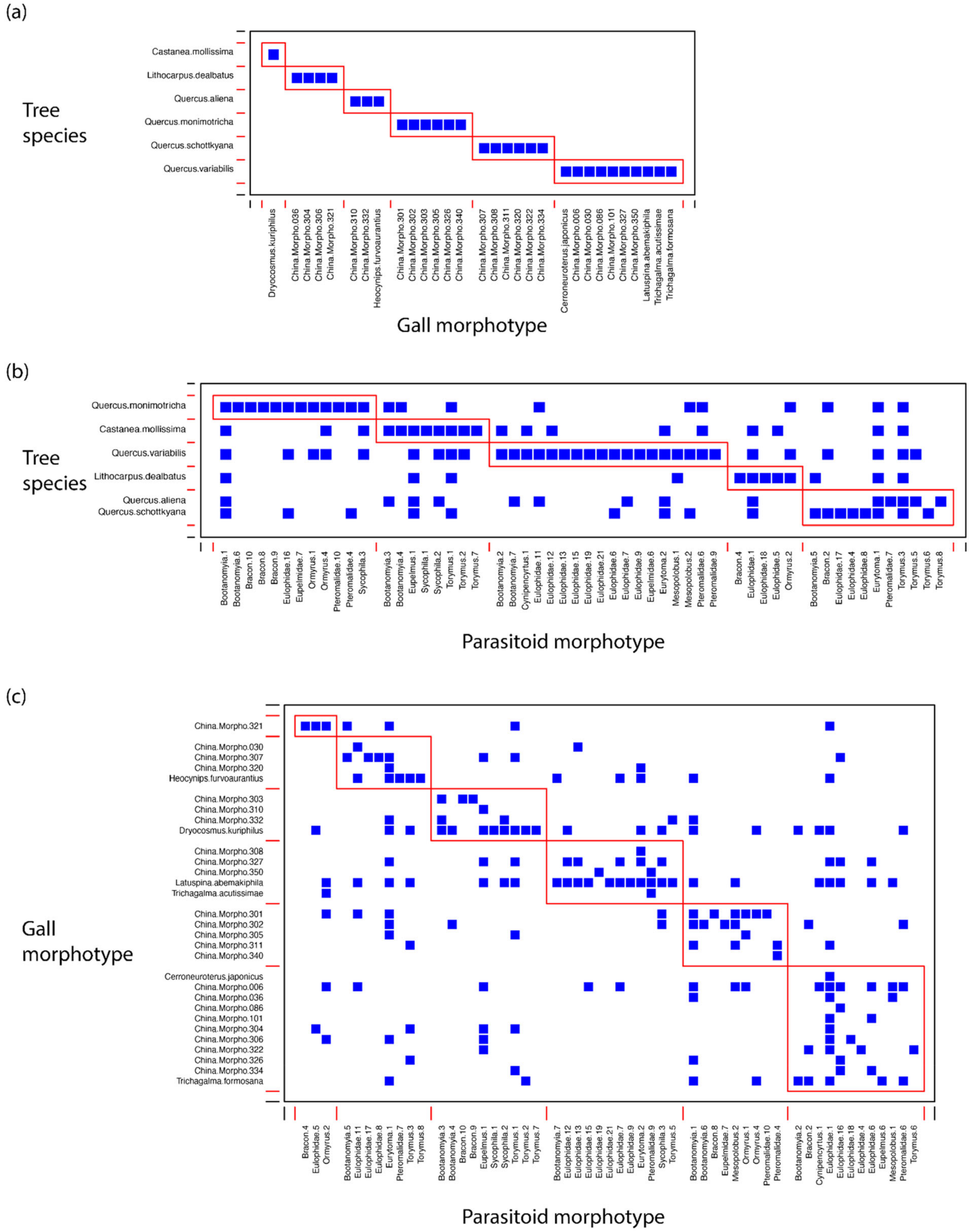

FIGURE 6 Network modules for Mianning, for (a) galls on trees, (b) parasitoids on trees and (c) parasitoids on galls. Red boxes circumscribe the links that comprise each module.

plant trophic level (Figure 8c) contained one module connector (*Q. aliena*), while the parasitoid trophic level (Figure 8d) contained two connector hubs (*Eurytoma* 1 and *Torymus* 3) and two module connectors (*Bootanomyia* 1 and *Torymus* 1). At both sites, the parasitoid module connectors and connector hubs were all abundant and generalist taxa (see below).

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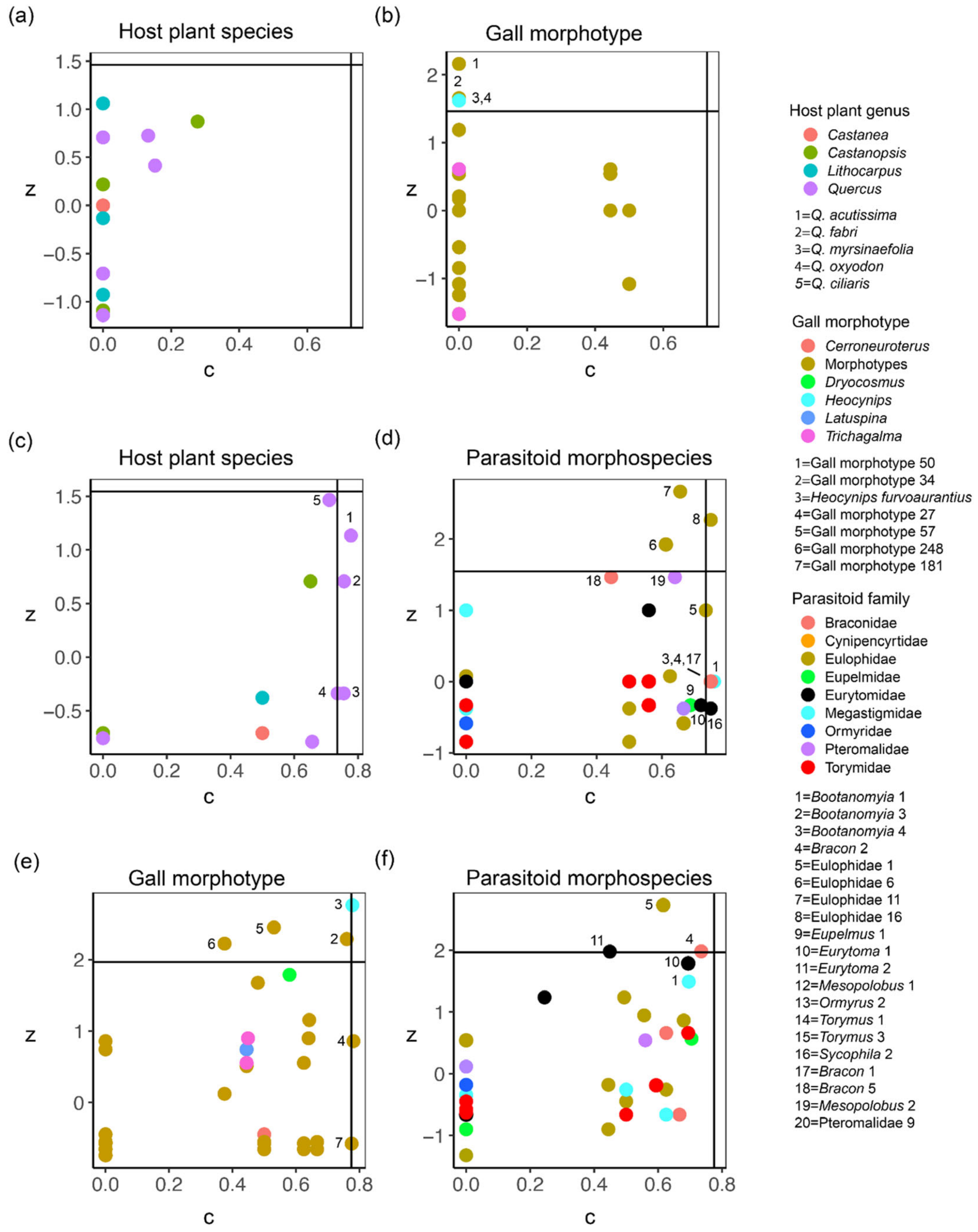

FIGURE 7 Localisation of taxa in ordinations by c (participation coefficient, a measure of between-module connectedness) and z (relative within-community degree, a measure of within-module connectedness) for each trophic level in three bipartite networks for the Emeishan site dataset: (a,b) cynipid galls on Fagaceae; (c,d) parasitoids on Fagaceae; (e,f) parasitoids on cynipid galls. In each plot, the horizontal and vertical solid lines represent the 95% quantile for r2d null model simulations for the same network and represent the threshold value above which z and c, respectively, are considered significant. Numbers by points identify taxa significant for c, z or both. Note that because the denominator for z is the standard deviation of links of a focal species to others within a module, it is not defined for species that create their 'own' module. Some taxa present in Figure 5 are thus absent from Figure 7.

The structure of parasitoid–gall interaction networks

Parasitoid–gall interactions were dominated by generalists (Table S2). Average host gall type richness over both sites was 5.4 ± 0.8 ($n = 64$, range 1–32). Of 39 taxa represented by >10 specimens over both sites, all but 4 were reared from multiple host gall types and 12 parasitoid taxa were reared from 10 or more host gall types. The five taxa with the widest host gall range were *Bootanomyia* 1 (32 gall morphotypes), Eulophidae 1 (27), *Eupelmus* 1 (21), *Eurytoma* 1 (18) and Eulophidae 11 (16). *Torymus* 1 (putative *T. sinensis*) was reared from five

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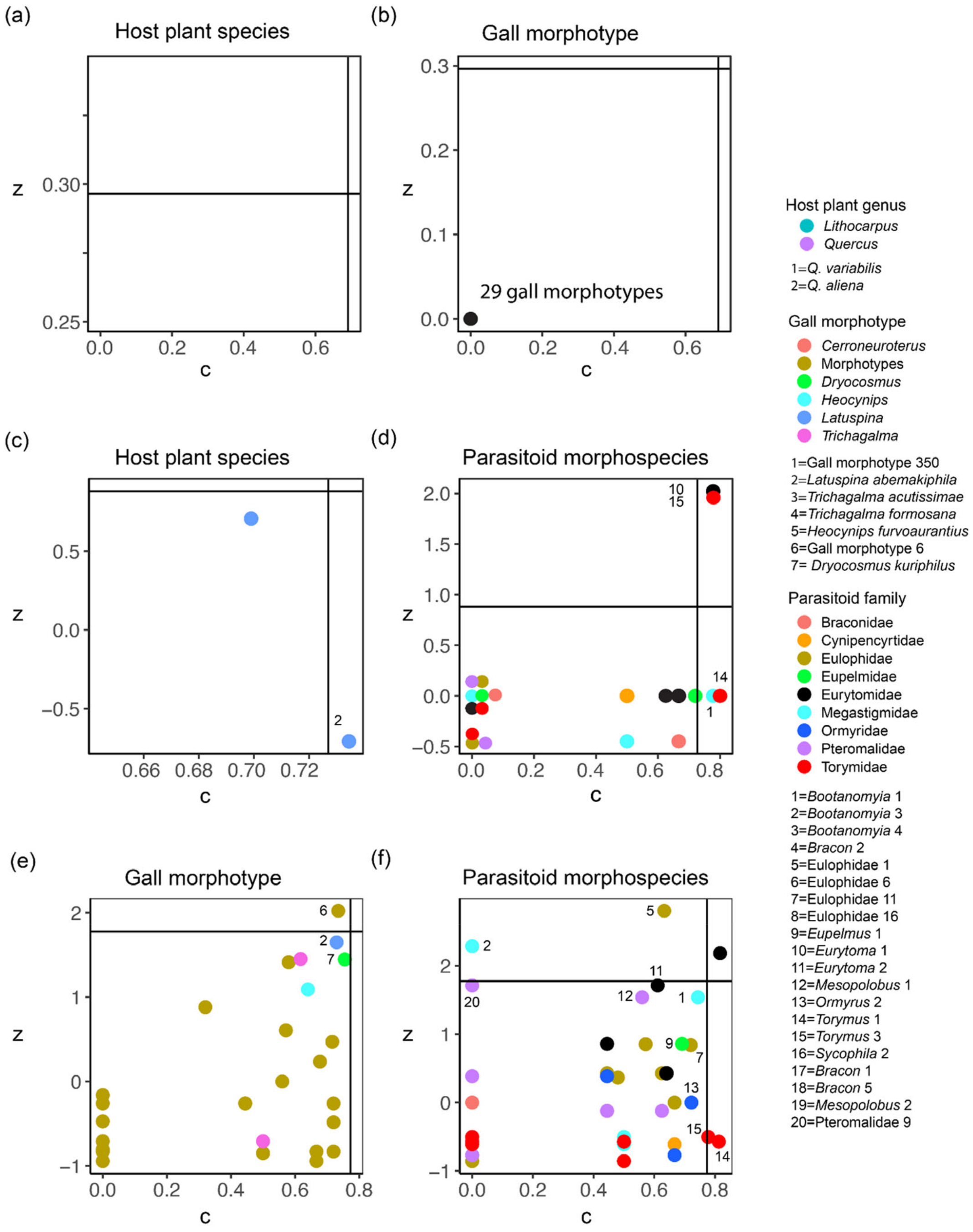

FIGURE 8 Localisation of taxa in ordinations by c (participation coefficient, a measure of between-module connectedness) and z (relative within-community degree, a measure of within-module connectedness) for each trophic level in three bipartite networks for the Mianning site dataset: (a,b) cynipid galls on Fagaceae; (c,d) parasitoids on Fagaceae; (e,f) parasitoids on cynipid galls. In each plot, the horizontal and vertical solid lines represent the 95% quantile for r2d null model simulations for the same network and represent the threshold value above which z and c, respectively, are considered significant. Numbers by points identify taxa significant for c, z or both. Note that because the denominator for z is the standard deviation of links of a focal species to others within a module, it is not defined for species that create their 'own' module. Some taxa present in Figure 6 are thus absent from Figure 8.

host galls on three plant lineages at Emei (*D. kuriphilus* on *Castanea* and four other gall types on *Castanopsis* and *Quercus* section *Cyclobalanopsis*; Figures 4 and 5) and from eight host galls on five plant lineages at Mianning (*D. kuriphilus* on *Castanea* and seven other gall types on *Lithocarpus*, and *Quercus* sections *Cerris*, *Ilex* and *Quercus*; Figures 4 and 6).

At the other end of the spectrum, 24 parasitoid taxa were reared from a single gall type. Fourteen of these were identified from a single specimen. Genuine host gall specialists—identified as parasitoids with substantive sampling that were reared from a single gall type—were very rare in our dataset. Only two parasitoids with $n > 20$ over both sites were reared from a single host gall: *Sycophila* 1 ($n = 164$ from

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galls of *D. kuriphilus* at Emeishan and Mianning) and *Ormyrus* 3 ($n = 30$ from China-Morpho.257 on *Q. myrsinaefolia* at Emeishan). Three further parasitoids with $10 \le n \le 20$ were reared from a single host gall: *Eupelmus* 2 (from China-Morpho.264 on *Q. acutissima* at Emeishan), Eulophidae.17 (from China-Morpho.307 on *Q. schottkyana* at Mianning) and Eulophidae.18 (from China-Morpho.306 on *Lithocarpus dealbatus* at Mianning).

Despite wide overlap in host gall ranges for many parasitoids, parasitoid–gall interactions at both sites showed significantly low connectance, high network-level specialisation (H_2') and high modularity relative to null model expectations (Table 2). At Emeishan, 193 parasitoid–gall links were partitioned into seven modules (Figure 5c), of which 80 (41.5%) were not placed in any module. Similarly, at Mianning 177 parasitoid–gall links were partitioned into six modules (Figure 6c), of which 87 (49%) were not placed in any module. Across both sites, all modules but one involved a taxonomically diverse assemblage of parasitoids. The exception, at Emeishan, was a module containing a single parasitoid (*Bracon* 4) associated with a single gall morphotype (China-Morpho.50) on section *Cyclobalanopsis*.

In the Emeishan network, the gallwasp trophic level (Figure 7e) contained one connector hub (*H. furvoaurantius*) and three local hubs (China-Morpho.248, China-Morpho.057 and China-Morpho.034), while the parasitoid trophic level (Figure 7f) contained three local hubs (*Bracon* 1, Eulophidae 1 and *Eurytoma* 2). At Mianning, the gallwasp trophic level (Figure 8e) contained one local hub (China-Morpho.006), while the parasitoid trophic level (Figure 8f) contained one connector hub (*Eurytoma* 1), two local hubs (*Bootanomyia* 3 and Eulophidae 1) and two module connectors (*Torymus* 1 and *Torymus* 3). At both sites, the parasitoid module connectors and connector hubs were all abundant and generalist taxa.

Relative specialisation of gallwasp–plant and parasitoid–plant associations

Gallwasp–plant networks had lower connectance and higher network-level specialisation (h_2) and modularity than parasitoid–plant networks (Table 2). Gallwasp–plant interactions were significantly more specialised at the species level (i.e. had higher mean d' values) than parasitoid–plant associations at both sites (Emeishan: gallwasps 0.47 ± 0.03, parasitoids 0.33 ± 0.02; $W = 880$, $p = 0.002$. Mianning: gallwasps 0.49 ± 0.04, parasitoids 0.24 ± 0.02; $W = 260$, $p < 0.001$). The d' frequency distributions for gall morphotypes and parasitoid morphospecies are shown in Figure S3.

Tree taxon-associated beta diversity for galls and parasitoids

At both sites, gall morphotypes and parasitoid morphospecies both showed high and significant beta diversity among tree taxa, for both abundance and presence/absence data (i.e. 95% confidence limits for all means excluded zero; Table 3). For both sites and data types, the turnover component of beta diversity was significantly higher than the nestedness component for both galls and parasitoids (Table 3; range of best estimates for turnover: 0.67–0.93; range for nestedness: 0.05–0.16). As predicted, for both data types at both sites, the turnover component of beta diversity for galls was significantly higher (and the nestedness component significantly lower) than for parasitoids (Table 3).

DISCUSSION

This study quantified association network structures between plants and each of cynipid gallwasp herbivores and their associated parasitoids, using data from previously unstudied communities centred on Fagaceae in Sichuan. Both gallwasp–plant and parasitoid–plant networks were significantly structured by host plant taxon, but gallwasps considerably more so. We first consider limitations of our taxonomic approach and place the Sichuan communities in a broader context of Cynipini communities worldwide. We then discuss observed network patterns and consider possible underlying causes for contrasts between gallwasp–plant and parasitoid–plant interactions.

Sensitivity of inferred network structures to taxonomic uncertainty

Because our taxonomic approach used morphotype OTUs whose correspondence to biological species is unknown, it is important to consider how sensitive our network inferences might be to classification errors (Pringle & Hutchinson, 2020). DNA barcoding validated the status of almost all gall morphotypes for which inducer DNA was available, and all but three unsequenced gall morphotypes had the high levels of host plant specificity expected for Cynipini species (Cook et al., 2002; Lobato-Vila et al., 2022; Stone et al., 2009; Ward, Bagley, et al., 2022). This reinforces the strong correspondence between species and gall phenotypes established by previous work on cynipids (Bailey et al., 2009; Cuevas-Reyes et al., 2007; Cuevas-Reyes, Quesada, Hanson, et al., 2004; Cuevas-Reyes, Quesada, Siebe, & Oyama, 2004; Maldonado-López et al., 2022; Pérez-López et al., 2016) and other gall inducing insects (Blanche, 2000; Butterill & Novotny, 2015; Coelho et al., 2017; De Araújo et al., 2013; de Araújo et al., 2021; Kuzmanich et al., 2023; Oliveira et al., 2020). Further DNA barcoding is nevertheless required to validate the remaining morphotypes and to link the sexual and asexual generations of individual biological species.

We have less validation for our parasitoid morphospecies, for which the taxonomic impediment is most severe. DNA barcoding studies have detected cryptic biological species within many morphologically defined Linnean parasitoid species (Heraty et al., 2007; Hrček & Godfray, 2015; Smith et al., 2008) and this is a possibility for the parasitoid OTUs in our analysis. The dominant morphospecies in our sampling were generalists that attacked multiple gall morphotypes on multiple Fagaceae lineages. If our taxonomy has erroneously

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TABLE 3 Beta diversity of cynipid gall morphotypes and parasitoid morphospecies among tree taxa (oak sections and non-oak genera), and its nestedness and turnover components, for Emeishan and Mianning datasets.

	Abundance data			Presence/absence data		
	Beta diversity	**Nestedness (GRA)**	**Turnover (BAL)**	**Beta diversity**	**Nestedness (SNE)**	**Turnover (SIM)**
Emeishan						
Cynipid galls	0.984 ± 0.01	0.050 ± 0.002	0.934 ± 0.003	0.941 ± 0.001	0.054 ± 0.001	0.888 ± 0.002
Parasitoids	0.942 ± 0.001	0.164 ± 0.003	0.778 ± 0.003	0.832 ± 0.001	0.163 ± 0.001	0.670 ± 0.001
Difference		−**0.117 ± 0.004** *	**0.151 ± 0.005** *		−**0.111 ± 0.004** ***	**0.215 ± 0.005** ***
Mianning						
Cynipid galls	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
Parasitoids	0.897 ± 0.001	0.099 ± 0.001	0.797 ± 0.001	0.703 ± 0.001	0.112 ± 0.002	0.591 ± 0.002
Difference		−**0.10 ± 0.003** ***	**0.202 ± 0.001** ***		−**0.113 ± 0.003** ***	**0.406 ± 0.005** ***

Note: Values are means ± 95% confidence interval for 1000 replicates for abundance data (calculated using Bray–Curtis dissimilarity) and presence/absence (calculated using Sørensen dissimilarity; see Section 2). For each site, the difference row gives the mean (±95% confidence interval) and significance of the difference in nestedness and turnover components for galls minus parasitoids for each data type. Difference values in bold are significantly different from 0 at levels indicated by $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

lumped morphologically cryptic species with higher specificity to particular plant or host gall lineages, then we will have underestimated parasitoid species richness, parasitoid specialisation and network modularity and overestimated connectance and the turnover component of beta diversity relative to nestedness (Pringle & Hutchinson, 2020). Such errors would also increase false positive detection rates for module connector and connector hub taxa (Pringle & Hutchinson, 2020). More generally, higher levels of morphologically cryptic taxa for parasitoid morphospecies than for gall morphotypes could explain higher apparent specialisation of gallwasp–plant interactions. The extent to which these issues apply to parasitoid taxa associated with Cynipini galls remains unclear. DNA barcoding studies of generalist parasitoids in Western Palaearctic oak gall communities have shown them either to consist of a single generalist lineage or multiple lineages that are nevertheless still generalists (Fusu, 2017; Gil-Tapetado et al., 2022; Kaartinen et al., 2010; Nicholls et al., 2010; Nicholls, Schönrogge, et al., 2018). In contrast, some Nearctic parasitoids have been shown to comprise sets of cryptic specialist species (Sheikh et al., 2022; Zhang, Sheikh, et al., 2022). This diversity of outcomes underlines the need to confirm the status of apparently generalist parasitoid species in Sichuan and elsewhere.

Richness and composition of Sichuan cynipid communities

Our surveys revealed very high cynipid and parasitoid richness, almost all of which is undescribed. To put the cynipid richness in context, our estimate of 165 undescribed gallwasp generations in at least 100 undescribed Cynipini species almost doubles current estimates for the Eastern Palaearctic and Oriental regions combined (Lobato-Vila et al., 2022). Similarly, the Chao estimate for total parasitoid morphospecies richness (94) is close to the ca. 100 parasitoid species recorded from oak gallwasp hosts across the entire Western Palaearctic (Askew et al., 2013). This increase probably reflects the high regional endemic species richness of Western Sichuan (López-Pujol et al., 2011; Wan et al., 2021; Xing & Ree, 2017) and very limited previous study (Lobato-Vila et al., 2022). Comparison of observed richness and Chao estimates suggests that while our sampling of Cynipini alpha diversity was relatively complete, many parasitoid morphospecies remain to be discovered.

The Sichuan parasitoid assemblages share many genera with Cynipini-associated communities across the Holarctic and neotropics (Askew et al., 2013; Sanchéz et al., 2013; Ward, Busbee, et al., 2022). Ten of the genera (*Aprostocetus*, *Bootanomyia*, *Cecidostiba*, *Eupelmus*, *Eurytoma*, *Mesopolobus*, *Ormyrus*, *Pediobius*, *Sycophila* and *Torymus*) are known from cynipid galls in Japan (Abe et al., 2007). Six (*Bootanomyia*, *Eupelmus*, *Eurytoma*, *Mesopolobus*, *Ormyrus* and *Sycophila*) have also been recorded from cynipid galls in China, though their host associations are poorly known (Abe et al., 2007; Xiao et al., 2016). Despite its importance as a biological control agent of the Oriental Chestnut gallwasp *D. kuriphilus*, ours is the first community-wide study to explore the host gall and plant range of *T. sinensis*. We reared *Torymus* 1 (putative *T. sinensis*) from galls on all of *Castanea*, *Castanopsis*, *Lithocarpus* and all four sampled sections of *Quercus*. Though the status of *Torymus* 1 as a single species and as *T. sinensis* remains to be confirmed, the suggestion that *T. sinensis* may not be a strict specialist of *D. kuriphilus* on *Castanea* has obvious relevance to risk assessments associated with ongoing release of this parasitoid (Ferracini et al., 2015, 2017; Gil-Tapetado et al., 2023; Quacchia et al., 2014). The taxonomic similarity of parasitoid assemblages in Cynipini communities around the world is striking and implies substantial roles for co-diversification, host tracking or both in community assembly (Bunnefeld et al., 2018; Janz, 2011). The presence of parasitoid taxa absent from Western Palaearctic oak cynipid communities, particularly braconids and *Cynipencyrtus*, also implies regional (as well as holarctic) community assembly processes. For a more detailed discussion of these Asia-specific parasitoid elements, see Appendix S4.6.

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Bottom-up effects in gallwasp and parasitoid associations

Sichuan gallwasp–plant interactions were highly specific, resulting in networks with high plant taxon-associated modularity, specialisation and turnover, but low connectance and nestedness. Similar patterns have been demonstrated for other plant–gall inducer networks (Araújo et al., 2019; Butterill & Novotny, 2015; De Araújo & Maia, 2021; Oliveira et al., 2020) and are perhaps to be expected given the metabolic intimacy of gall induction (Gatjens-Boniche, 2019; Giron et al., 2016; Hearn et al., 2019; Martinson et al., 2022). In contrast, parasitoid–plant networks were less specialised, but nevertheless showed significant plant-associated structure. Though modules in parasitoid–plant networks were not obviously structured by plant taxonomy, there was significant taxonomic turnover in parasitoid assemblages between plant taxa. This is consistent with previous findings of plant-associated structure for parasitoid assemblages attacking oak cynipids (Askew, 1961; Bailey et al., 2009) and other insect herbivores (Askew & Shaw, 1974; Forbes et al., 2009; Hawkins & Goeden, 1984; Ives & Godfray, 2006; Müller et al., 1999; Rott & Godfray, 2000; for an exception, see Toro-Delgado et al. (2022)).

Non-random parasitoid–plant associations could arise through between-plant variation in parasitoid search behaviour (e.g. parasitoids preferentially search some plants over others) or parasitoid performance (e.g. hosts on one plant are more abundant or of higher quality than those on another; Desneux et al., 2012; Kaplan et al., 2016; Xi et al., 2017). Askew (1980) has suggested that parasitoids attacking multiple host galls on the same oak species may have evolved responses to plant cues rather than gall-specific cues in response to high variation in the abundance of individual host gall types (Askew, 1980). This is equivalent to search strategies in other parasitoid guilds that first locate the host (micro)habitat and then locate the host (Frederickx et al., 2014; Segura et al., 2012). For most parasitoids, the specific cues used in host location are unknown, but chemical cues—particularly volatile organic compounds (VOCs)—often play key roles (Borges, 2018; Dicke & Baldwin, 2010; Graziosi & Rieske, 2013). Regardless of the nature of the cues, observed structure in parasitoid–plant networks could result from responses to particular plant taxa, or to plant-specific galls, or both (Prauchner & De Souza Mendonça, 2024; Van Oudenhove et al., 2017).

Many Sichuan parasitoids attack galls on multiple plant taxa, suggesting search behaviours that incorporate cues uncorrelated with plant taxonomy (Bailey et al., 2009; Pearse & Hipp, 2009). We hypothesise that host location behaviour in these taxa is likely to involve high rates of between-tree movement and response to shorter range cues (Peters, 2011) associated with gall location on the tree or gall morphology (Askew, 1961; Bailey et al., 2009; Luz et al., 2021; Prauchner & De Souza Mendonça, 2024; Stone & Schönrogge, 2003). Parasitoids can respond to visual cues associated with size, shape and colour (Graziosi & Rieske, 2013; Segura et al., 2007), all of which can be diagnostic of the gall inducer and gall developmental stage (Bailey et al., 2009; Hearn et al., 2019; Prauchner & De Souza Mendonça, 2024). Parasitoids could also respond to local volatile cues indicating the presence of a host gall, whether produced constitutively by gall tissues or as herbivore-induced plant volatiles (HIPVs) released as a plant-induced defensive response to oviposition or gall induction (Borges, 2018; Caselli et al., 2022; Van Oudenhove et al., 2017). We might expect selection to favour parasitoids that could detect such cues (Huang et al., 2022; Xiaoyi & Zhongqi, 2008), and also to favour gall induction mechanisms that minimise their production (Barônio & Oliveira, 2019; Tooker et al., 2008; Tooker & De Moraes, 2008). While very few studies have investigated these issues in cynipid galls, at least some parasitoids can detect cynipid gall-associated volatiles (Graziosi & Rieske, 2013; Tooker & Hanks, 2006) and cynipid gall induction alters VOC release from neighbouring non-gall plant tissues (Jiang et al., 2018; Tooker et al., 2002). It remains an open question whether the significant parasitoid–plant associations are due to direct use of plant cues (or direct plant taxon-induced selection) or indirect effects via non-random distribution of preferred gallwasp host taxa.

Dominant roles in network structure for generalist parasitoids

As in the Western Palaearctic, Sichuan parasitoid assemblages were dominated by taxa that attack multiple host gall morphotypes on multiple plant taxa (Askew, 1980; Askew et al., 2013; Bailey et al., 2009; Schönrogge & Crawley, 2000). Generalist parasitoids are present in some other gall-centred communities (Cuevas-Reyes et al., 2007; De Araújo & Maia, 2021), though this is not always the case (Paniagua et al., 2009). In Sichuan, generalist parasitoid morphospecies with many links outside modules contributed module connectors (high c, low z) and connector hubs (high c and z), while generalists associated with multiple plant and gall taxa in a single module contributed local hubs (Guimerà et al., 2005; Guimerà & Amaral, 2005). If network role is a fundamental biological property, we might expect a particular parasitoid taxon to fulfil the same network role across both of our sampling sites. This was true in the parasitoid–plant networks (Figures 6d and 7d) for *Bootanomyia* 1 (module connector) and in the parasitoid–gall networks (Figures 6f and 7f) for Eulophidae 1 (local hub). However, all other taxa exceeded c and z threshold values for specific network roles in one site only. This suggests that network-specific factors, such as the composition and relative abundances of species present at each trophic level, might influence the network roles attributable to individual species. Such variation could be artefactual (e.g. a result of between-network variation in statistical power to attribute network roles) or reflect variation in parasitoid realised niches. The latter could arise through between-site variation in available host gall diversity, parasitoid search behaviour, preferences or success on each host gall/plant. Such variation has previously been documented for generalist parasitoids, in which local host preferences can be imprinted (Emden et al., 2008) or learned rather than innate (Kalyanaraman et al., 2021; Segura et al., 2007). It will be interesting going forward to see if similar network roles can be identified in

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cynipid communities elsewhere, which typically have much lower plant taxon richness and perhaps less potential for plant-associated network structure.

AUTHOR CONTRIBUTIONS

Zhiqiang Fang: Funding acquisition; project administration; methodology; investigation; data curation; resources; conceptualization. **Chang-Ti Tang:** Investigation; writing – review and editing; methodology; data curation; formal analysis; project administration; conceptualization; supervision. **Frazer Sinclair:** Data curation; funding acquisition; writing – review and editing; writing – original draft; visualization; validation; formal analysis; project administration; supervision; conceptualization. **György Csóka:** Investigation. **Jack Hearn:** Investigation; funding acquisition. **Koorosh McCormack:** Investigation; validation. **George Melika:** Investigation; funding acquisition. **Katarzyna M. Mikolajczak:** Investigation. **James A. Nicholls:** Data curation; methodology; validation. **José-Luis Nieves-Aldrey:** Investigation; validation. **David G. Notton:** Investigation; validation; methodology. **Sara Radosevic:** Conceptualization; investigation; writing – original draft; formal analysis. **Richard I. Bailey:** Writing – review and editing; formal analysis; validation. **Alexander Reiss:** Investigation; writing – review and editing. **Yuanmeng M. Zhang:** Investigation; writing – review and editing; validation. **Ying Zhu:** Investigation; project administration; supervision. **Shengguo Fang:** Funding acquisition. **Karsten Schönrogge:** Conceptualization; funding acquisition; writing – original draft; validation; formal analysis; data curation; project administration; writing – review and editing; visualization. **Graham N. Stone:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Edinburgh DataShare repository at https://doi.org/10.7488/ds/7756.

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SUPPORTING INFORMATION

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

Appendix S1. Metadata for all sampling locations.

Appendix S2. Photographic guide to gall morphotypes sampled in this study, with summaries of biological and morphological traits.

Appendix S3. Morphological keys to parasitoid Hymenoptera reared from Sichuan Cynipini galls on Fagaceae and digital voucher habitus images of all parasitoid morphospecies.

Appendix S4. Biological appendix, containing additional information on sampled gallwasp and parasitoid taxa.

Table S1. List of gall morphotypes with summary of their host associations, seasonality, number of galls collected (#G), number of parasitoids emerged (#P), corresponding number of parasitoid morphotypes (#PT), number of inducers that were DNA barcoded and locations (E: Emeishan; M: Mianning) where the gall morphotypes were collected. The seasonality was scored following the criteria: (1) sexual generation, male reared; (2) spring, probable sexual generation; (3) asexual generation, females only; (4) autumn, probable asexual generation; and (5) generation unknown.

Table S2. List of parasitoid morphospecies, with a summary of their taxonomy, number of individuals emerged in Emeishan (#E) and Mianning (#M), number of host tree species (#HTS) and number of host gall morphotypes (#HGT). Generic identifications ending with a question mark are preliminary. Morphotype names ending with an asterisk (*) are known only from males.

Table S3. List of barcoded Cynipini gall inducers with details of their gall morphotype, seasonality (see Table S1 for scoring criteria), OTU membership following the BOLD clustering algorithm (see Figure S1), GenBank accession number, project specimen codes, sequence generation method and life stage for DNA extraction.

Table S4. Threshold values above which c (participation coefficient, a measure of between-module connectedness) and z (relative within-community degree, a measure of within-module connectedness) are considered significant in three types of bipartite network: cynipid galls on Fagaceae, parasitoids on Fagaceae and parasitoids on cynipid galls. Values are the mean and standard error (SE) of the 95% quantiles extracted from 500 iterations of the r2d null model (see Section 2). Taxa significant only for c are module connectors, taxa significant only for z are local hubs and taxa significant for both are connector hubs following Guimerà and Amaral (2005).

Figure S1. Neighbour-joining phylogenetic tree of Cynipid barcode sequences, using uncorrected P distances and with scale bar indicating substitution rate per site. Tip labels include details of GenBank accession numbers, specimen codes, gall morphotype and OTU membership following the BOLD clustering algorithm. Blue and black labels indicate specimens from spring (i.e. sexual) and autumn (i.e. asexual) generations, respectively. The numbers of sequenced specimens with identical haplotypes belonging to the same gall morphotype are indicated in parentheses. Details of all sequenced specimens are provided in Table S3.

Figure S2. Network modules for the combined sites dataset, for (a) galls on trees, (b) parasitoids on trees and (c) parasitoids on galls. Red boxes circumscribe the interactions that comprise each module.

Figure S3. Frequency distributions of the specialisation index d’ with respect to Sichuan Fagaceae for cynipid gall morphotypes (green) and associated parasitoid morphospecies (yellow). Frequencies are for d’ intervals of 0.1, for which the x-axis tick labels are the upper bound.

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