Habitat and fig characteristics influence the bird assemblage and network properties of fig trees from Xishuangbanna, South-West China

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Abstract: To understand how fruit tree characteristics and microhabitats shape the assemblage of birds on fig trees and the pattern of fig–bird interactions, we observed and recorded, over 96 d and 816 h, the frugivorous birds visiting 32 individual trees belonging to 14 species of *Ficus* that were distributed across four different sites. A total of 30 bird species were recorded as eating figs, comprising 66.7% of the total number of frugivorous bird species recorded at the four sites. Small passerine birds such as bulbuls were the dominant frugivores for fig species. The number of bird species visiting different fig trees was significantly influenced by the crop size and canopy volume. Fruit colour and fruit size did not significantly influence the number of bird species, whereas habitats appeared to influence the composition of visiting birds. The fig–frugivorous bird interaction was asymmetrically structured, and the degree of nestedness appeared to be influenced by the forest type and degree of disturbance: the degree of nestedness in non-limestone forest tended to be higher than limestone forest; forest with less disturbance tend to be more nested compared with the open forest with high disturbance.

Key Words: canopy width, crop size, *Ficus*, fig-eating birds, fruit colour, fruit size, nested subset analysis, tree height

INTRODUCTION

With about 800 species distributed worldwide in the tropics and subtropics, *Ficus* (Moraceae) is one of the largest genera of woody plants (Berg 1989, Janzen 1979). Fruits of figs have been recognized as important 'keystone' food resources, as they provide large and sustained amounts of food to many frugivorous animals in tropical forests (Kannan & James 1999, Kinnaird *et al.* 1996, Kissling *et al.* 2007, Lambert & Marshall 1991, Leighton & Leighton 1983, Terborgh 1986). The fruit characteristics of figs, a soft pulp and numerous tiny seeds, make it suitable for consumption by many birds and other animals (Janzen 1979, McKey 1975, Shanahan *et al.* 2001). A comprehensive review indicated that animals known to eat figs include over 10% of the world's bird species (18% of genera) and over 6% of the world's mammals (14% of genera) (Shanahan *et al.* 2001).

Fig species vary greatly in their morphology, such as the fruit traits (size and colour, etc.), ways of fruit display,

crop size, canopy height, and other characteristics. These differences may affect the assemblage of frugivores on different figs. For example, fruits spanning a wide range of size classes, which ripen synchronously and remain green (greenish) when ripe, are often dispersed by bats, and thus recognized as 'bat' figs. In contrast, fruits of 'bird' figs have small fruit that ripen asynchronously and turn red when ripe. The fruit size of figs in the New World was found to be correlated with the body size of the bats that dispersed the seeds (Kalko *et al.* 1996). Vertical stratification of figs significantly influenced the assemblage of fig eaters in lowland tropical forests in South-East Asia (Shanahan & Compton 2001). Many other works aiming at recording frugivores feeding on fig trees in tropical Asia have also demonstrated a wide range of animals consuming figs (Kinnaird & O'Brien 2005, Poonswad *et al.* 1998). However, to our knowledge, systematic studies to understand how fig fruit characteristics influence the assemblage of frugivorous animals are still lacking (except Shanahan & Compton 2001).

Forest habitats may also affect avian community structure (Gil-Tena *et al.* 2007, Mitchell *et al.* 2006). Those differences, in turn, will influence the frugivore

composition in each fruiting tree that is located in different habitats. For example, the degree of human disturbance, such as fragmentation of the forest (Brawn *et al.* 2001), may affect the community structure of birds and thus may be reflected by the frugivores visiting fruiting plants.

Studies of plant–animal networks, especially for mutualistic interactions, have grown extraordinarily in the last few years (see Bascompte & Jordano 2007 for a review). A specific type of asymmetrical specialization, termed nestedness, is often used to describe the interaction network (Bascompte *et al.* 2003). Nested networks are characterized by: (1) generalists that all interact with each other, forming a core of interacting species; (2) specialists that commonly interact only with generalists; and (3) the absence of specialists that interact only with other specialists (Guimarães *et al.* 2006). Recent work has led to the conclusion that mutualistic networks, in comparison with other interactions such as antagonistic networks, are much more nested (Bascompte & Jordano 2007, Jordano *et al.* 2003). Several mechanisms have been proposed to explain nested patterns in species assemblages, including differences in extinction probabilities, differences in colonization abilities, nested structure of habitats or niche space and passive sampling (Cutler 1994, Lomolino 1996, Worthen 1996). Research is needed to understand how the nestedness of mutualistic networks changes in time and space, and how it changes in response to forest disturbance (Bascompte & Jordano 2007, Guimarães *et al.* 2006, Martínez-Morales 2005, Meyer & Kalko 2008).

In this study, we conducted a systematic survey of the interaction between figs and frugivorous birds, one of the typical mutualistic interactions in most tropical areas. We developed the following hypotheses: (1) The morphological differences between *Ficus* species, such as fruit size, fruit colour, tree height, crop size and canopy size, will influence the composition of the frugivore assemblage attracted. (2) Different microhabitats may also shape frugivorous bird assemblages of fig trees. (3) The fig and frugivorous bird network may differ among the different habitats.

METHODS

Study sites

The study was conducted from May 2004 to January 2006 in Menglun, Xishuangbanna, Yunnan province, China (21°55′N, 101°15′E, 550–600 m asl). Climate in the study site is tropical monsoon, characterized by a distinct rainy season (May–October), with peak precipitation occurring in July–September, followed by a cool-dry season (November–January) and a hot-dry season (February–April).

We selected four different sites representing the different microhabitats in this area. The study sites are 2–9 km apart (Figure 1). (1) Arboretum in Xishuangbanna Tropical Botanical Garden (XTBG arboretum). Different fig species have been planted in the arboretum. Fig trees in the arboretum are often in an open space and the arboretum is disturbed by tourist activities. (2) Seasonal rain forest in Xishuangbanna Tropical Botanical Garden (XTBG forest). This is a piece of fragmented forest located on the eastern part of the XTBG with an area of 100 ha. The original forest was seasonal tropical rain forest. It was severely logged during the 1970s and thereafter was strictly protected. Occasional visitors walk along trails inside the forest. (3) Limestone tropical rain forest (Limestone forest). This is an isolated piece of primary forest with an area of about 300 ha belonging to the national natural reserve. The forest type is tropical seasonal moist forest located on limestone (Zhu 2006). Human activities are forbidden inside the forest. (4) Menglun Natural Reserve (ML primary forest). This is a continuous forest belonging to the national natural reserve with an area of about 3000 ha. The forest type is tropical seasonal rain forest (Cao *et al.* 1996) and is strictly protected against human activities.

Observation of frugivorous bird species in fig trees

We investigated fig-eating birds in 32 fruiting fig trees belonging to 14 species located in four different habitats (Table 1). These four habitats represented a varied degree of fragmentation and human disturbance in the same area ($< 100 \, km^2$) in Xishuangbanna, Yunnan province of China (Figure 1).

We used the focal observation technique for recording bird species that visited each selected fig tree and took an area of $2 \times 2 \, m^2$ in tree canopy for quantitatively recording the visiting frequencies of birds. During observations, we recorded fig-eating bird species, number of individuals, feeding behaviour and number of fruits consumed. Fig-eating birds were observed with the aid of 8×50 binoculars, and identified based on the bird field guide (MacKinnon & Phillipps 2000). Three days of observation per fig tree were conducted. For each observation day, six time periods were selected for observation: 7h00–8h30, 9h00–10h30, 11h00–12h30, 13h00–14h30, 15h00–16h30 and 17h00–18h00. We then calculated the number of bird species and number of individuals of each bird species at each fig tree. A total of 96 days and 816 h of observations were conducted for the 32 individual trees.

Survey of bird species at the four study sites

To understand the bird community in the four study sites, we conducted line transects and fixed-radius counts
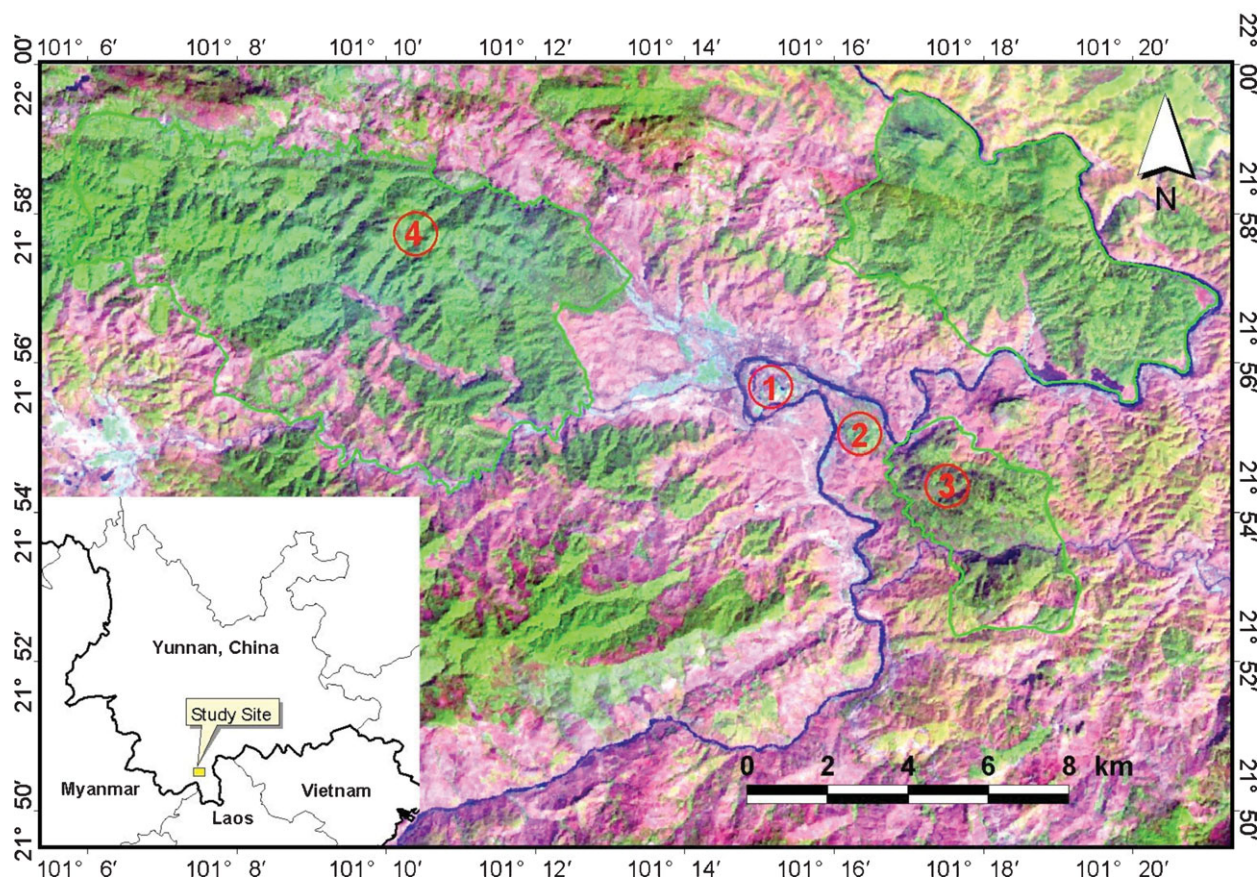
Figure 1. Map showing the location of the four study sites and the degree of fragmentation. The pink areas represent rubber plantations and the green natural forest. Site 1: XTBG arboretum; Site 2: XTBG forest; Site 3: limestone forest; Site 4: ML primary forest.

between March 2004 and February 2005. The surveys were conducted in three different seasons: dry and hot season (February–April), rainy season (June–October) and cool and dry season (November–January). The transects were about 1500 m long and were divided into 30 plots at intervals of 50 m. It took about 6 min for observation in each plot at a radius of 25 m. Records included the numbers and species of all birds seen. Time

Table 1. Morphology of 14 *Ficus* species and distribution of 32 observed fig individuals at the four different sites. Nomenclature follows Zhou & Gilbert (2003). Fruit brightness was calculated by the area under the curve of the reflectance curve. See text for the description for each site. Site 1: XTBG arboretum; Site 2: XTBG forest; Site 3: limestone forest; Site 4: ML primary forest.

Species	Code number	Tree height (m)	Fruit colour	Fruit brightness	Seed diameter (mm)	Fruit diameter (mm)	Individuals in each site				
							Site 1	Site 2	Site 3	Site 4	Total
F. altissima	F 3	>30	Red	775.9	0.93	20.0	1	0	0	1	2
F. benjamina	F 1	20–30	Black	445.3	0.97	22.6	1	0	1	1	3
F. concinna	F 6	20–30	Black	356.8	0.65	7.2	3	0	0	2	5
F. curtipes	F 7	10–20	Black	592.4	1.26	18.5	1	0	1	0	2
F. cyrtophylla	F 11	< 10	Red	400.2	0.73	12.2	1	1	1	0	3
F. drupacea	F 8	20–30	Red	856.0	1.24	29.9	0	0	0	1	1
F. hispida	F 13	<10	Yellow	1245.7	0.75	26.9	0	1	0	0	1
F. kurzii	F 9	10–20	Pink	1161.8	0.82	11.3	1	0	0	0	1
F. langkokensis	F 10	<10	Red	1092.8	0.89	7.5	0	1	0	0	1
F. maclellandi	F 14	20–30	Red	364.8	1.04	11.4	0	0	0	1	1
F. religiosa	F 5	20–30	Black	375.9	1.10	10.9	3	0	0	0	3
F. subulata	F 12	20–30	Red	495.9	0.75	11.9	0	2	0	0	2
F. tinctoria	F 2	10–20	Red	462.6	0.85	10.9	2	1	0	1	3
F. virens	F 4	>30	Black	468.6	0.83	9.8	1	0	0	2	3
Total							14	8	3	9	34

during the day was 6h30 to 18h30, divided into four periods: 6h30–9h30, 9h30–12h30, 12h30–15h30 and 15h30–18h30. Each study site was observed for 4 d (48 h) per season, so a total of 576 h of observation were made over three seasons. Fig-eating birds were observed with the aid of 8×50 binoculars, Birds in field were identified based on two bird field guides (Lekagul & Round 1991, MacKinnon & Phillipps 2000).

Fig species and fruit characteristics

We took the most common fig species in our study area for this study. *Ficus* species were identified by reference (Zhou & Gilbert 2003) and voucher specimens were deposited in the Herbarium of the Xishuangbanna Tropical Botanical Garden (HITBC). We collected 20–30 ripe fruits of each fig species and measured fruit size with vernier callipers (0.1 mm in accuracy). Ripe fruits were collected and both the brightness and colour of fruit were determined. The reflectance values were determined by using an Ocean Optics S2000 spectrometer (OOIIrrad2 software ver. 2.05.00 PR 12) with a Xenon strobe light source using standard techniques. We calculated the area under the reflectance curve from 400 to 700 nm as a measure of overall reflectance for the brightness (we followed Borgia & Keagy 2006). Tree height was calculated by using a clinometer. The canopy width was measured and averaged by cross directions. Crop size was estimated as fruit production per branch × canopy volume. Fruit production per branch was calculated by counting fruits on ten 1-m branches; canopy volume was estimated as canopy height × canopy width × canopy length.

Statistical analysis

The species diversity of frugivorous birds in each site was described using Shannon's index (H'), maximum diversity (H_{max}) and evenness (J), and the similarity of the bird community between each pair of sites was estimated using Sørensen's index (Cs) (Southwood 1978).

A nested ANOVA was adapted to analyse if significant differences of visiting birds, indicated by the total number of bird individuals (Nb), number of bird species (Ns) and bird diversity index (H'), existed among different sites. Simple and multiple regressions were used to examine whether fruit traits (size, colour and brightness) and tree characteristics (canopy volume and crop size) were related to visiting frugivorous birds.

To understand the properties of the fig–bird network, we first followed Bascompte *et al.* (2003) for the calculation of T value. T is the matrix temperature, a measure of matrix disorder with values ranging from $0°$ (perfectly nested) to $100°$ (perfectly non-nested). The T value was calculated by using the software Nestedness Calculator (The nestedness temperature calculator: a visual basic program, including 294 presence–absence matrices. AICS Research, Inc., University Park, NM, USA). We understand the T value for each community may be influenced by species richness in the networks. To compare nestedness among different study sites, we tested this hypothesis using the following algorithm to compare pairs of networks in which L is the larger network and l is the smaller network. (1) Assuming that the probability of a plant species being removed is equal for all plant species, randomly remove plant species of L until $F_L = F_l$; (2) record the nestedness of the rarefied L network; (3) repeat 1000 times; (4) calculate the probability P that a rarefied L shows a degree of nestedness equal to or more extreme than l.

Secondly, we used a FORTRAN program (Nestedness – a FORTRAN program for calculating ecological matrix temperatures. www.uni.torun.pl/∼ulrichw) to evaluate the properties of the interaction. The program gave the results for the matrix temperature, the observed matrix temperature and the simulated temperatures according to the predefined null model and the standard deviation. The program also calculated the respective lower and upper 95% confidence limits.

RESULTS

Frugivorous bird species at four study sites

A total of 45 species of frugivorous bird was recorded at the four study sites. The ML primary forest had the highest species number (35 spp.), followed by the XTBG forest (31 spp.), the XTBG arboretum (27 spp.), and the limestone forest (22 spp.). The Shannon diversity index (H') showed a similar pattern to species number (Table 2). The XTBG arboretum and the XTBG forest sites achieved the highest similarity ($Cs = 0.85$) between their frugivore assemblages, while the XTBG arboretum and the ML primary forest sites had the lowest ($Cs = 0.55$) (Table 3).

The most abundant frugivorous birds in the area were the red-whiskered bulbul (*Pycnonotus jocosus*) (46.1%), Japanese white-eye (*Zosterops japonicus*) (12.7%),

Table 2. Species diversity indices of frugivorous birds in different habitats. See text for description of the different sites.

Sites	Shannon's index (H')	Maximum diversity (H_{max})	Evenness (J)
XTBG arboretum	0.54	1.43	0.38
XTBG forest	0.83	1.49	0.56
Limestone forest	0.54	1.34	0.40
ML primary forest	0.99	1.54	0.64

Table 3. Similarity of frugivorous bird species in four sites calculated by Sørensen's similarity index (*Cs*). See text for description of different sites.

	XTBG arboretum	XTBG forest	Limestone forest	ML Natural reserve
XTBG arboretum		0.85	0.69	0.55
XTBG forest			0.74	0.72
Limestone forest				0.70

sooty-headed bulbul (*Pycnonotus aurigaster*) (8.3%) and puff-throated bulbul (*Criniger pallidus*) (5.8%). However, the most abundant bird species differed amongst sites, except that red-whiskered bulbul was always common across the four sites. Puff-throated bulbul (*Criniger pallidus*) was abundant at both the XTBG forest (12.8%) and ML primary forest sites (16.1%); black-crested bulbul (*Pycnonotus melanicterus*) was rather abundant at the limestone forest site (11.6%) and Japanese white-eye (*Zosterops japonicus*) was dominant at the XTBG arboretum site (19.6%) (Appendix 1).

Frugivorous birds visiting fig trees

A total of 30 species belong to 10 families of fig-eating birds was recorded visiting the 32 fig trees of 14 species in the four microhabitats. Fig-eating birds were composed of bulbuls (10 spp., 33.3%), barbets (6 spp., 20.0%), flowerpeckers (4 spp., 13.3%), white-eyes (2 spp., 6.7%), starlings (2 spp., 6.7%), leafbirds (2 spp., 6.7%), bluebirds (1 sp., 3.3%) and orioles (1 sp., 3.3%), and some opportunistic frugivorous birds such as sunbirds (1 sp., 3.3%) and warblers (1 sp., 3.3%) (Appendix 1).

Among the fig species, *Ficus benjamina*, *F. tinctoria* and *F. altissima* had the highest diversity of visiting bird species, a total of 15 bird species for each. Some other fig species, such as *F. cyrtophylla*, *F. subulata* and *F. maclellandi*, had relatively few bird species visitors.

Across the four sites, red-whiskered bulbul (*Pycnonotus jocosus*), blue-throated barbet (*Megalaima asiatica*), sooty-headed bulbul (*Pycnonotus aurigaster*) and puff-throated bulbul (*Criniger pallidus*) were the bird species that visited the most different fig species. White-headed bulbul (*Hypsipetes thompsoni*) and brown-breasted bulbul (*Pycnonotus xanthorrhous*) were the bird species that visited the fewest fig species.

Frugivorous birds visiting most fig species often were the species with highest abundances in the habitat. For example, the most abundant bird species at the XTBG arboretum were red-whiskered bulbul (53%) and Japanese white-eye (19.6%). Both of these were the frugivorous species that visited the most fig trees. Similar tendencies occurred for puff-throated bulbul (16.1%), red-
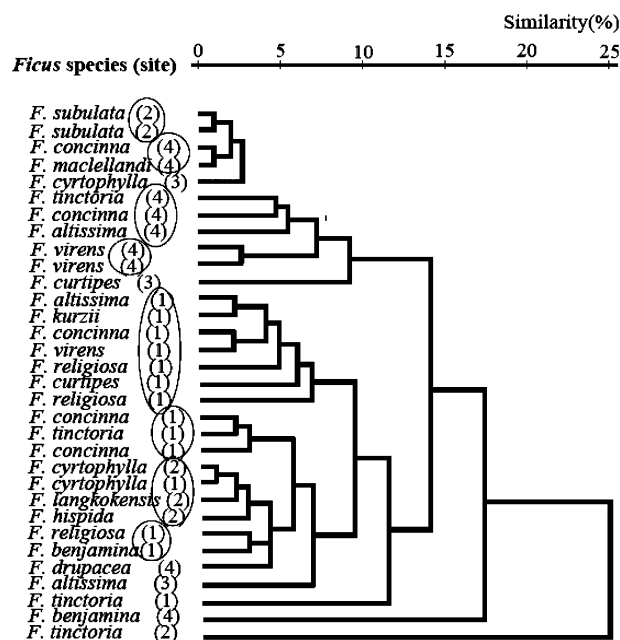

Figure 2. Dendrogram showed the similarity of visiting bird assemblages using cluster analysis (SPSS version 11.5). Numbers of individuals of different birds were calculated. The similarity of visiting bird assemblages to fig plants at the same site generally appeared to be higher than that at different sites, as indicated by the rings around groups of sites.

whiskered bulbul (14.2%) and grey-eyed bulbul (13.9%) in the ML primary forest (Appendix 1).

Habitat, season and characteristics of fig trees that influence dispersers

The total number of birds visiting each fruiting tree (*Nb*) was significantly correlated to the total number of species visiting (*Ns*) (Pearson correlation, $r = 0.448$, $P = 0.01$), but not to the Shannon Index of bird diversity (*H'*) ($r = 0.168$, $P = 0.359$). *Ns* was significantly correlated to Shannon index *H'* ($r = 0.843$, $P < 0.0001$).

The nested ANOVA test indicated that habitat did not have a significant influence on the total number of visiting birds ($F_{3, 22} = 1.79$, $P = 0.248$), total bird species ($F_{3, 22} = 0.611$, $P = 0.6323$) and bird diversity index ($F_{3, 22} = 0.486$, $P = 0.704$). Cluster analysis indicated that habitat may influence the composition of bird species on a fig tree. Different fig species located at the same site received a similar assemblage of birds compared with the same fig species located at a different site (Figure 2).

Among the characteristics tested, both crop size (Pearson correlation, $r = 0.443$, $P < 0.05$) and canopy volume ($r = 0.418$, $P < 0.05$) were significantly correlated to *H'* value. Other characteristics did not show a significant correlation to visiting bird species.
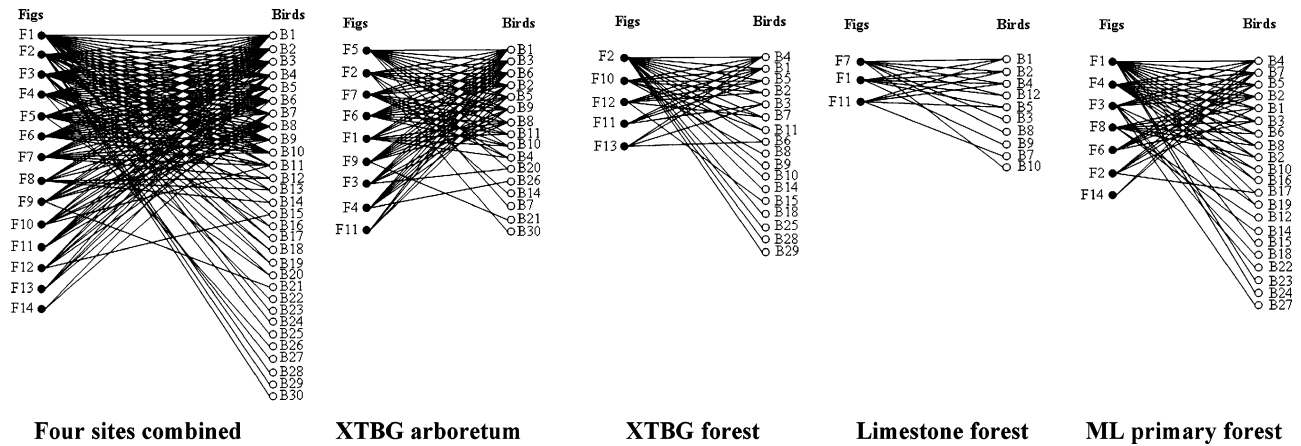
Figure 3. The networks among figs and fig-eating birds at four study sites. *Ficus* and bird species in the figure are indicated by codes explained in Table 1 and Appendix 1 respectively.

Fig–frugivorous bird network

The interaction networks in the four sites and the four sites combined are presented in Figure 3. Combining the four sites together, fig and frugivorous bird interactions showed a significant nestedness (Table 4). Different sites showed a different nestedness structure. High nestedness occurred in the ML primary forest and the XTBG forest (Table 4). The limestone forest had the lowest nestedness. While controlling for network size among the four sites, the ML primary forest and the XTBG forest showed a similar degree of nestedness, but these two sites showed significantly stronger asymmetries than the other two sites. The limestone forest had the least asymmetry compared with the other sites (data not shown).

The overall interaction of fig–birds across the four sites estimated using the FORTRAN program had a nestedness temperature (T) of 10.6, which was significantly lower ($P < 0.05$) than the mean T of 1000 randomly generated matrices (T = 27.1, SD = 2.68) (Table 4). For the different sites, only the T value of the ML primary forest and XTBG forest sites were significantly lower than the randomly generated matrices, while the other two sites did not differ significantly between the T value and the mean of 1000 randomly generated matrices (Table 4).

DISCUSSION

Which species eat figs?

In this study, fig species attracted a total of 30 species of bird, comprising 66.7% of the total recorded frugivorous bird species in this area. Small passerine birds such as bulbuls were the dominant frugivores of fig trees.

Fig fruits, with soft pulp and numerous tiny seeds, are suitable for consumption by most birds and other animals, thus playing a role as important 'keystone' food resources to many frugivorous animals in tropical forests. Forty years ago, Janzen (1979) raised the question: 'who eats figs?' to which he answered 'everybody'. Bulbuls were the prevalent birds visiting fig fruits in the marginal tropical area. Previous studies in tropical Asia also revealed that small passerines were the dominant frugivores of fig species. In India (Balasubramanian 1996) and the

Table 4. Summary of fig–bird interactions at the four sites. n_1: Number of fig species involved, n_2: Number of bird species involved, κ_1: Median number of interactions per fig species, κ_2: Median number of interactions per bird species. T_1: a measure of matrix temperature calculated with Nestedness Calculator.software T_2: temperature matrix measured using Nestedness program. Tem: the observed matrix temperature. SimT: the simulated temperatures according to the predefined null model. 95%CI represents the 95% confidence limits.

Sites	n_1	n_2	$\kappa_1 \pm$ SD	$\kappa_2 \pm$ SD	T_1 (°)	T_2 (°) Tem	SimT	95%CI	P
XTBG arboretum	9	16	8.0 ± 1.94	4.5 ± 3.16	50.0	19.4	21.0	14.7–26.5	> 0.05
XTBG forest	5	17	7.2 ± 4.55	1.9 ± 1.14	42.3	7.3	18.6	11.7–26.0	< 0.05
Limestone forest	3	10	6.0 ± 1.00	1.8 ± 0.92	60.0	19.1	16.2	6.0–27.8	> 0.05
ML primary forest	7	21	7.4 ± 4.04	2.9 ± 1.75	41.2	13.8	30.5	20.9–38.5	< 0.05
Four sites combined	14	30	9.6 ± 4.85	4.8 ± 4.25	32.6	10.6	27.1	22.1–32.2	< 0.05

Philippines (Heindl & Curio 1999), the most frequently observed frugivores were all passerine birds. These tendencies were also confirmed in the subtropical forests of Hong Kong (Corlett 1996, 1998) and Yakushima Island, Japan (Noma & Yumoto 1997).

Fruit-eating birds influenced by characteristics of fruit trees

In this study, the crop size and canopy volume had a significant effect on the species diversity (H') of frugivorous birds. Similar patterns have been reported from other studies on figs. For example, Shanahan & Compton (2001) reported that crop size had a significant effect on the number of visiting animal species. Crop size has also been reported to influence visiting frugivores for other fleshy fruited plant species (Fleming 1981, Gryj & Dominguez 1996, Howe & DeSteven 1979, Howe & Vande Kerckhove 1979, Korine *et al.* 2000, Murray 1987).

Fig morphology, such as fruit size and fruit colour, did not have a significant effect on the bird assemblage. Fruit size has a critical impact on the birds visiting most fruiting plants, but is less important with figs, where most birds can peck pieces from fruits too large to swallow. Our field observation also indicated that birds may alter their feed behaviours in response to different fig fruits. For example, red-whiskered bulbul with a gape width of 9.4 mm swallow small figs such as *F. concinna* (6.4 mm) and *F. langkokensis* (7.5 mm), but it pecks at large figs such as *F. cyrtophylla* (12.0 mm), *F. curtipes* (18.4 mm) and *F. benjamina* (22.2 mm). Most small birds, such as Japanese white-eye with a gape width of 6.0 mm, feed on most *Ficus* spp. by pecking, while most large birds, such as great barbet with a gape width of 27.2 mm, feed on most *Ficus* spp. by swallowing.

Fruit colour of figs did not show a significant effect on the visits of fig-eating birds. This may be because the fig species in this study are mainly bird-dispersed species with red (50%) or black (35.7%) figs, with only a few bat-dispersed species, such as *F. hispida* with a yellow colour. Thus, the effect of colour was not statistically significant. Other studies have suggested that plants may use ultraviolet signals to attract birds (Willson & Whelan 1989), but the figs in this study did not reflect in the ultraviolet, which is indicated by the reflection measurement.

Differences in fig–bird interaction nestedness among sites

As a whole, fig–bird interactions in this study showed a nested pattern of asymmetrical specialization. Comparing with the degree of nestedness among sites, significant nestedness only occurred in the ML primary forest and the XTBG forest. The four sites comprised many different variables, and it is difficult to generate any generalized patterns. However, the results clearly indicate that the four sites differed in the nestedness of fig–bird interactions.

These results corroborate and extend the conclusions of recent studies that suggest that interactions among free-living species in species-rich communities show a nested pattern of asymmetrical specialization (Bascompte *et al.* 2003). Plant species richness in the non-limestone forests was significantly higher than the neighbouring limestone forest (Zhu *et al.* 2003). Bird species in limestone forest were also significantly fewer than in the non-limestone forest.

Several studies have explored the degree of forest fragmentation that influence the plant–animal interaction, and suggested that the size of forest fragment did shape the interacting nestedness of plants with bats and many groups of birds (Martínez-Morales 2005, Meyer & Kalko 2008). Although the bird similarity between the XTBG arboretum and XTBG forest sites was relatively high (Table 3), the nestedness differed significantly. The XTBG arboretum is an open area with more human activities and this may alter the structure of the mutualistic interactions.

Determining the mechanism behind this requires a more detailed study. Several species in the XTBG arboretum were much more dominant compared with the XTBG forest and the ML primary forest sites. For example, red-whiskered bulbul (*Pycnonotus jocosus*) represented 53.3% of total recorded birds during the observation period in the XTBG arboretum and only made up 8.8% and 14.2% in the XTBG forest and ML primary forest, respectively (Table 2). Similarly, Japanese white-eye (*Zosterops japonicus*) represented 19.6% of total recorded birds in the XTBG arboretum and only 5.1% and 3.5% in the XTBG forest and ML primary forest, respectively. The 'abundance asymmetry hypothesis' proposed by Vázquez *et al.* (2007) suggested that abundant species have frequent encounters with individuals of many other species, most of which are relatively rare and specialized, given the pervasive right-skewed distribution of abundance. Furthermore, because the frequency of interaction can be a good surrogate of interaction strength when there is high variation in interaction frequency (Vázquez *et al.* 2005); the relative abundance of a species in a community would also determine its ecological effect on another species. Thus, most pairwise interactions in interaction networks are expected to be asymmetric both in terms of degree (specialists interact with generalists) and strength (rare specialists have weak effects on abundant generalists, but experience strong effects from them).

Understanding plant–animal interaction properties and the adaptations in response to environmental changes may shed light on proper strategy development

of biodiversity management. In a disturbed environment, most plants may still get service for seed dispersal while the asymmetrical interaction relationship with frugivorous animals may be altered, which may affect the long-term coevolutionary process between food plants and their dispersers.

ACKNOWLEDGEMENTS

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Appendix 1. Abundance of frugivorous birds (nomenclature follows MacKinnon & Phillipps 2000) at the four study sites. Diet: O = omnivorous, F = frugivorous, N = nectarivorous, and I = insectivorous birds. Birds' diet was determined based on MacKinnon & Phillipps (2000) and authors' observation. § indicates the bird species observed feeding on fig fruit in this study.

Species	Common name	Code number	Diet	Frequency (%)				
				XTBG arboretum	XTBG forest	Limestone forest	ML primary forest	Four sites combined
Chloropseidae								
Chloropsis aurifrons	Golden-fronted leafbird		O	0.0	0.0	0.4	0.6	0.1
Chloropsis cochinchinensis	Blue-winged leafbird §	B 16	O	0.0	0.0	0.0	2.2	0.3
Chloropsis hardwickii	Orange-bellied leafbird §	B 15	O	0.1	0.4	0.0	0.6	0.2
Columbidae								
Chalcophaps indica	Emerald dove		F	0.2	0.9	0.4	2.2	0.6
Treron apicauda	Pin-tailed pigeon		F	0.4	1.3	0.0	0.0	0.5
Treron curvirostra	Thick-billed pigeon		F	0.4	0.9	0.0	0.0	0.4
Treron sphenura	Wedge-tailed pigeon		F	0.6	1.5	0.0	0.0	0.6
Corvidae								
Cissa chinensis	Green magpie		O	0.0	0.2	0.0	0.3	0.1
Urocissa erythrorhyncha	Blue magpie		O	0.0	0.9	0.0	0.3	0.2
Dicaeidae								
Dicaeum agile	Thick-billed flowerpecker §	B 29	F	0.0	2.3	0.0	0.0	0.5
Dicaeum chrysorrheum	Yellow-vented flowerpecker §	B 8	F	0.1	1.9	0.7	1.3	0.7
Dicaeum concolor	Plain flowerpecker §	B 10	F	0.4	3.2	0.4	1.3	1.1
Dicaeum cruentatum	Scarlet-backed flowerpecker §	B 11	F	0.1	0.4	0.7	0.6	0.3
Dicaeum ignipectus	Buff-bellied flowerpecker		F	0.0	0.0	0.7	0.0	0.1
Eurylaimidae								
Psarisomus dalhousiae	Long-tailed broadbill		O	0.1	1.1	0.7	1.6	0.6
Irenidae								
Irena puella	Asian fairy-bluebird §	B 19	O	0.0	0.0	0.0	0.6	0.1
Megalaimidae								
Megalaima asiatica	Blue-throated barbet §	B 2	F	0.8	2.1	1.8	1.9	1.3
Megalaima australis	Blue-eared barbet §	B 13	F	0.0	0.0	0.0	1.6	0.2
Megalaima faiostricta	Green-eared barbet §	B 20	F	0.2	0.4	0.7	0.6	0.4
Megalaima haemacephala	Coppersmith barbet §	B 9	F	0.8	0.2	0.7	0.3	0.6
Megalaima henricii	Yellow-crowned barbet §	B 27	F	0.0	0.0	0.0	1.3	0.2
Megalaima virens	Great barbet §	B 12	F	0.0	0.2	0.4	0.3	0.1
Nectariniidae								
Aethopyga siparaja	Crimson sunbird §	B 30	N	1.2	1.1	1.1	1.0	1.1
Oriolidae								
Oriolus chinensis	Black-naped oriole		O	0.1	0.8	0.0	0.6	0.3
Oriolus traillii	Maroon oriole §	B 17	O	0.1	0.2	0.4	0.6	0.2
Psittacidae								
Psittacula finschii	Grey-headed parakeet		F	0.1	0.0	0.0	1.6	0.2
Pycnonotidae								
Criniger flaveolus	White-throated bulbul		F	0.0	0.0	0.0	0.6	0.1
Criniger pallidus	Puff-throated bulbul §	B 4	F	0.1	12.8	9.8	16.1	5.8
Hypsipetes flavala	Ashy bulbul		F	0.0	0.0	0.0	2.5	0.3
Hypsipetes madagascariensis	Black bulbul §	B 18	F	0.0	0.2	0.0	0.3	0.1
Hypsipetes propinquus	Grey-eyed bulbul §	B 7	F	0.0	0.9	3.5	13.9	2.3
Hypsipetes thompsoni	White-headed bulbul §	B 22	F	0.0	0.0	0.0	0.3	0.0
Pycnonotus atriceps	Black-headed bulbul		F	0.1	0.0	0.0	0.0	0.0
Pycnonotus aurigaster	Sooty-headed bulbul §	B 3	F	12.6	5.7	1.1	0.0	8.3
Pycnonotus flavescens	Flavescent bulbul §	B 24	F	0.0	0.0	0.0	2.8	0.4
Pycnonotus jocosus	Red-whiskered bulbul §	B 1	F	53.3	38.8	59.0	14.2	46.1
Pycnonotus melanicterus	Black-crested bulbul §	B 5	F	2.7	4.7	11.6	11.7	5.2
Pycnonotus sinensis	Chinese bulbul §	B 23	F	0.0	0.0	0.0	7.3	0.9
Pycnonotus xanthorrhous	Brown-breasted bulbul §	B 26	F	0.3	0.0	0.0	0.0	0.2
Sturnidae								
Sturnus malabaricus	Chestnut-tailed starling §	B 14	O	0.4	3.8	0.0	0.0	1.0
Sturnus sinensis	White-shouldered starling §	B 28	O	1.8	1.9	0.00	0.00	1.4
Sylviidae								
Phylloscopus coronatus	Eastern crowned warbler §	B 25	I	0.2	1.9	1.40	1.58	0.9
Timaliidae								
Garrulax chinensis	Black-throated laughingthrush		O	0.0	0.6	1.40	2.21	0.6
Zosteropidae								
Zosterops japonicus	Japanese white-eye §	B 6	O	19.6	5.1	2.81	3.47	12.7
Zosterops palpebrosus	Oriental white-eye §	B 21	O	3.5	3.8	1.40	1.58	3.1