# 亚洲热带雨林两种鸟类媒介互利系统的比较[*]

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**摘　要**　了解植物形态学性状如何影响鸟类传粉者和种子散布者的拜访, 有助于阐明植物-鸟类相互关系的进化. 本研究选取云南省西双版纳 4 类不同人类干扰程度的热带森林, 比较植物-鸟类在种子散布和传粉基础上所构建的网络系统. 结果表明: 植物-食果鸟网络系统高度不对称, 而植物-鸟类传粉者网络系统未出现类似的不对称现象. 两类网络系统的差异主要表现在鸟类丰富度、鸟类活动能力以及适合鸟类拜访的一系列植物性状上. 对这两个互利共生系统差异的了解有助于深入理解植物-鸟类互利关系的进化.

**关键词**　人为干扰　食果鸟　果实性状　花朵颜色　互利共生系统　食蜜鸟

**Comparison of two plant-bird mutualistic systems in Asian tropical rainforests.** Sawat SANIT-JAN[1,2], CHEN Jin[1], WANG Bo[1,2] ( [1]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China*; [2]*Graduate University of Chinese Academy of Sciences, Beijing 100039, China*). -*Chin. J. Appl. Ecol.*, 2011, **22**(6): 1579−1584.

**Abstract**: To deeply understand how the morphological features of plants affect the visiting of pol-len- and seed dispersal birds is beneficial to elucidate the ecological and evolutionary consequences of plant-bird interactions. In this paper, a comparative study was conducted on the avian pollen- and seed dispersal networks across four tropical rainforest habitats having experienced different lev-els of anthropological disturbance in Southwest China. It was observed that the inter-active network of plant-frugivorous bird was highly asymmetrical, while that of plant-seed dispersal bird was not asymmetrical. The differences between the two networks mainly manifested in the bird abundance, bird movable capability, and plant features attracting bird visiting. The understanding of these differences allowed us to reveal the mutualistic relationship between plant and bird.

**Key words**: human disturbance; frugivorous bird; fruit feature; flower color; mutualistic system; nectarivorous bird.

Interactions between plants and their animal polli-nators as well as seed dispersers have promoted the biodiversity enrichment[1]. Flower pollination and seed dispersal are both critical processes in plant reproduc-tion[2]. More than 90% reproduction of tropical plant species related to animals, especially to frugivorous birds[1], which dominate in the seed dispersal in the Old World tropics[3]. The abundance of frugivory has been reported for birds in tropical region of Asia, at least 13 orders (of 17), 41 families (of 82, but 23 of families without frugivores are largely aquatic), 260 genera (of 560) and an estimated 900−1200 species (of 2471) of birds[4]. In pollination systems of angio-sperms, plants often promote successful reproduction through phenological and morphological adaptations, which are necessary for pollinator attraction[5]. Satisfy-ing their high requirements in energy, birds visit nu-merous flowers regularly, which increase the gene ex-changing among plants[6]. Nectarivorous birds often provide higher quality pollination than insects, particu-larly for self-incompatible flowers with patchy distribu-tions[6]. Birds pollinate about 500 genera of plants from 13500 genera[7].

Many studies have shown that plant-animal mutu-

alisms, *e. g.*, plant-frugivore and plant-pollinator network, are characterized by weak or asymmetric mutual dependences between interacting species, a feature that could increase community stability[8-10]. Bascompte *et al.*[11] analyzed quantitative plant-animal mutualistic networks and concluded that most of the bulk of pairwise dependences was weak and only a few were strong. Despite a strong current interest in ecological networks, the most of studies were devoted to the static descriptions of network structure, and very few analyzed their spatial and temporal dynamics[10].

Habitat fragmentation is well-known as one of the great threats to biodiversity worldwide[12]. Habitat quality and disturbance regime have considerable impact on both disperser and pollinator assemblages, as well as plant-animal interaction networks[13]. Habitat degradation and fragmentation can decrease the abundance and change composition of the frugivorous bird community[14] that lead to the rate decreasing of fleshy fruits consumption[15]. Habitat fragmentation reduces pollination success, due to reduced diversity and abundance of pollinators[16], and leads to reduced seed set or increased inbreeding for plants[16]. Habitat disturbance may also affect network structure, and as a consequence, on the dynamics and evolutionary processes of plant-disperser interactions[17], and plant-pollination interactions[17-18]. However, only a few studies devoted to the impact of the habitat modification on the seed dispersal and pollination networks[18].

Located in southwestern China, the prefecture of Xishuangbanna is characterized by a climatic gradient transitioning from tropical to subtropical biomes that is rich in biodiversity[19-20]. The major tropical rainforest type distributed at <900 m above sea level, and the monsoon tropical rainforest has been fragmented and surrounded by large-scale rubber plantations[21]. In this study, we selected four sites within 2−9 km apart representing different microhabitats and different degrees of fragmentation and human disturbance (Fig. 1). The main purpose of our study were to investigate the differences between networks of plant-frugivorous birds and plant-flower visiting birds, and their development as a response to the changes of the habitat quality.

# 1 Study Site and Methods

## 1.1 Study Site

The study area (21° 55′ N, 101° 15′ E) is located in Mengla County, Xishuangbanna Prefecture of Yunnan Province, China. Elevation ranges from 550−600 m above sea level. The climate 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). The average air temperature is 21.8 ℃, average relative humidity 83%, and the annual rainfall is about 1400 mm. We selected four different sites representing different substrates and human disturbance level. The study sites are 2−9 km apart (Fig. 1). Ⅰ: The arboretum in Xishuangbanna Tropical Botanical Garden (XTBG arboretum): mostly open space with daily visits by tourists. Plants in this part of the garden are mainly introduced plants. Ⅱ: The forest in Xishuangbanna Tropical Botanical Garden (XTBG forest). This is a fragment of forest located at the east end of XTBG with an area of 100 hm². It was heavily logged in the 1970s and thereafter was strictly protected. Occasional visitors walk along trails inside the forest. Ⅲ: Limestone tropical rain forest (Limestone forest). This is an isolated piece of primary forest with an area of about 300 hm² belonging to the Menglun National Natural Reserve. Human activities are forbidden inside the forest.
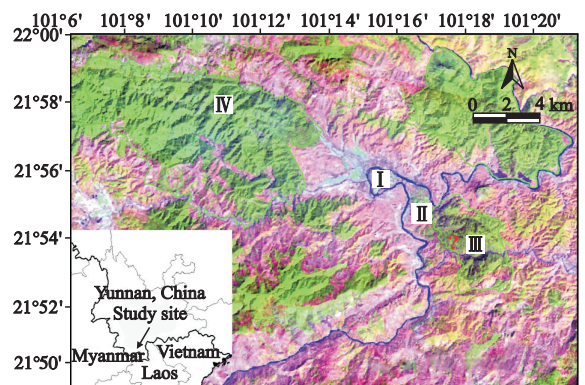


**Fig. 1** Location of the four study sites and the degree of fragmentation.

The pink areas represented rubber plantations and the green natural forest. Ⅰ: XTBG (Xishuangbanna Tropical Botanical Garden) arboretum; Ⅱ: XTBG forest; Ⅲ: Limestone forest; Ⅳ: ML (Menglun Natural Reserve) primary forest.

Ⅳ：Menglun National Natural Reserve primary forest (ML primary forest). This is a continuous primary forest with an area of about 3000 hm², and human activities are forbidden inside the forest.

## 1. 2 Survey for Bird Community, Frugivorous and Nectarivorous Birds

We conducted line transects and point counts between March 2004 and February 2005, documented the bird community and number of frugivorous and nectarivorous birds on fruit trees inside the four study sites. The survey was done during three seasons: dry and hot season (February−May), rainy season (June−October), and cool and dry season (November−January). A 1500 m-long transect line was set up in each of the four study site, and each transect line was divided into 30 sections of 50 m. Inside of each section, we spent ca. 6 minutes for observations within a radius of 25 m (measured by a ruler). The same transect lines were used for different seasons, and all birds were recorded. We did strong efforts for recognizing the individual bird features, in order to avoid recounting of the same individuals from adjacent plots. One observer walked along the transect with speed ca. 8. 3 m per min ( = 50 m/6 minutes). Censuses took place from 6:30 to 18:30. In order to not only decrease workload but also censor all the bird species active in different times, the censuses were divided into four periods: 6:30−9:30, 9:30−12:30, 12:30−15:30 and 15:30−18:30. Each study site was observed for 48 h per season, so a total of 576 h of observation were made over three seasons. Instead of continual observation for the 48 h per site, we often spend more than three days per site, depending on the weather and accessibility while we tried to minimize bias for different sites due to influence of weather during observation. Number of individuals and species of all birds within the radius along line transects were recorded. Numbers and species of frugivorous birds that visit and feed on fruits or seeds at the fruiting trees and shrubs within the 25 m radius along the transect were recorded per plant tree. Similarly, we recorded the number of individuals and species of nectarivorous birds feeding at flowering trees. Birds were observed with the aid of 8×50 binoculars and bird species were identified according to the bird field guide[22].

## 1. 3 Statistical Analyses

To analyze the properties of frugivorous bird-plant network and nectarivorous bird-plant network, we followed Bascompte et al. [9] for 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 (AICS Research, Inc., University Park, NM, USA). The T value has been widely used in the measurement of nestedness, some arguments criticize its strong bias from the effect of sample size[23]. Thus, we also used a FORTRAN program (Nestedness, a FORTRAN program for calculating ecological matrix temperatures) to evaluate the properties of the interaction. The program gave the results for the matrix temperature, the observed matrix temperatures 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.

## 2 Results

### 2. 1 Frugivorous and Nectarivorous Bird Species at Four Study Sites

Totally, 52 bird species belonging to 16 families was recorded as frugivorous and nectarivorous birds at the four study sites, which represents 28. 7% of the total 181 recorded bird species (authors' observation) in the study sites (32. 7% of the 49 total families).

The large ML primary forest had the highest species number and Shannon diversity index (H) for frugivorous birds, followed by the XTBG forest, the XTBG arboretum, and the Limestone forest. The species number of nectarivorous birds did not differ significantly among different sites (Chi-square Test, P = 0. 994), and the Shannon diversity index (H) showed a similar pattern to species number for nectarivorous birds among different sites (Table 1).

### 2. 2 Network Properties of Bird-mediated Seed Dispersal and Pollination Systems

For frugivore-plant interaction, the nestedness structure occurred throughout the four sites (Table 2), while the degree of nestedness varied over sites. The

**Table 1  Species number ($Ns$) and species diversity ($H$) of frugivorous and nectarivorous birds in the four study sites**

| Site | Frugivorous birds | | Nectarivorous birds | |
|------|------|------|------|------|
| | $Ns$ | $H$ | $Ns$ | $H$ |
| XTBG arboretum | 15 | 0. 93 | 9 | 1. 61 |
| XTBG forest | 17 | 1. 61 | 10 | 2. 00 |
| Limestone forest | 9 | 1. 14 | 10 | 2. 23 |
| ML primary forest | 19 | 2. 29 | 10 | 2. 21 |

highest nestedness occurred at ML primary forest ($T_1 = 16. 4$), and the lowest occurred in the Limestone forest ($T_1 = 30. 1$). The $T$ value calculated by FORTRAN program of all sites was significantly lower than the randomly generated matrices of frugivorous bird-plant interaction.

For the plant pollinator interaction, XTBG arboretum showed the highest degree of nestedness, while XTBG forest showed the lowest. By using FORTRAN program, only XTBG arboretum showed a significantly low value of $T$ compared to the randomly generated matrices ($t$-test, $P < 0. 05$), while the other three sites did not differ significantly in $T$ value and the mean of 1000 randomly generated matrices (Table 2).

**Table 2  Summary of frugivorous bird-plant and nectarivorous bird-plant interactions at the four sites**

| Site | $n_1$ | $n_2$ | $I$ | $k_1 \pm SD$ | $k_2 \pm SD$ | $T_1$ (°) | $T_2$ (°) | | | |
|------|------|------|------|------|------|------|------|------|------|------|
| | | | | | | | Tem | SimT | StdDev | $P$ |
| Frugivorous bird-plant interactions | | | | | | | | | | |
| XTBG arboretum | 36 | 16 | 133 | 3. 69±2. 85 | 8. 31±9. 86 | 21. 9 | 2. 25 | 30. 40 | 3. 04 | <0. 001 |
| XTBG forest | 32 | 15 | 102 | 3. 19±2. 42 | 6. 80±7. 90 | 19. 5 | 3. 10 | 28. 19 | 3. 52 | <0. 001 |
| Limestone forest | 10 | 7 | 25 | 2. 50±1. 72 | 3. 57±2. 64 | 30. 1 | 9. 11 | 23. 66 | 5. 93 | <0. 05 |
| ML primary forest | 20 | 17 | 65 | 3. 25±3. 27 | 3. 82±4. 35 | 16. 4 | 3. 23 | 17. 46 | 3. 42 | <0. 001 |
| Nectarivorous bird-plant interactions | | | | | | | | | | |
| XTBG arboretum | 17 | 14 | 38 | 2. 20±1. 52 | 2. 70±2. 49 | 13. 8 | 8. 59 | 19. 23 | 3. 91 | <0. 05 |
| XTBG forest | 14 | 9 | 29 | 2. 10±1. 07 | 3. 20±2. 05 | 21. 3 | 19. 12 | 25. 18 | 5. 73 | >0. 05 |
| Limestone forest | 4 | 5 | 7 | 1. 75±1. 50 | 1. 40±0. 89 | 20. 0 | 7. 39 | 7. 92 | 4. 71 | >0. 05 |
| ML primary forest | 7 | 10 | 14 | 2. 00 ±1. 15 | 1. 40±0. 84 | 16. 6 | 9. 85 | 11. 75 | 6. 32 | >0. 05 |

$n_1$: Number of plant species involved, $n_2$: Number of bird species involved, $I$: Total no. links in network, $k_1$: Median number of interactions per plant species, $k_2$: Median number of interactions per bird species, $T_1$: A measure of matrix temperature calculated with Nestdness 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.

## 3  Discussion

In our study, by using two programs to measure the nestedness, we found that the $T$ value calculated by using FORTRAN program of all sites was lower than the randomly generated matrices of frugivorous bird-plant interaction (Table 2). However, the two results presented similar results that the network of fruit-eating birds and plants were much more nested than the network of nectar-feeding birds and plants. Similar pattern occurred also in other areas both in the Neotropics and the Paleotropics[24]. The reasons of this nestedness differences is a consequence of factors complex impact. The network size could be one of them. Plant and bird species involved in frugivorous bird-plant interaction was significantly higher than it was in nectarivorous bird system. Bascompte et al.[9] found that small networks generally did not show significant nestedness.

The relative species abundance has been recognized as important component to nestedness. For example, Krishna et al.[25] suggested that the relative species abundance explained 60%−70% of nested patterns in two real communities. The abundance of most frugivorous birds was much higher than that of the flower visiting birds.

One of the most puzzling questions to evolutionary ecologists is the appreciation of the degree involving of disperser or pollinator in the diffuse evolution process with their food plant[3,26]. Both dispersal and pollination mutualistic systems have been considered as nonspecific to plant morphology. Potential for tight co-evolution between plants and their pollinators has been thought to be greater than that between plants and seed dispersal agents[27]. However, a comparison between this review and an earlier one of seed dispersal in the same region[4] provides no evidence that this potential

is generally realized in practice[28]. Nested mutualistic networks have been theoretically recognized as facilitating the process of coevolution and generation of biodiversity[2]. By adapting real networks and simulations, Guimarães *et al*.[2] showed that network structure of different forms of mutualism affected evolutionary changes in distinct ways. However, how the interaction structure influence the evolutionary process is always the core part of the unsolved questions.

In our study area, the different habitats had more obvious influence on the assemblage of the frugivorous birds which visited different fruit trees than that on the nectarivous birds. Bird community structure has been recognized as a largely influenced by habitat fragmentation and landscape forest[14]. Durún & Kattan[29] demonstrated that capture rates of nectarivores correlated with resource abundance at sampling plot scale, but weak correlation was found for frugivores. They suggested understory frugivorous birds were apparently functioning at a larger spatial scale than the patchiness created by the two habitats. Nectarivorous birds are responding to small-scale patchiness in resource availability, but not to the different habitats. Our study also suggested the significant habitat effects on frugivores would be more across habitat moving than those small-body nectarivores; for the former, rather long distance seed dispersal was quite common in this area[30].

## 4　Conclusion

The interactions between plants and their mutualistic frugivorous and nectar feeding birds have been a long-time focus for ecological studies while studies comparing the network structures of these two systems are less frequent. In our paper, we presented a comparative study on the two mutualistic systems at the tropical rainforests in southwest China. The frugivorous bird and the food plant interaction were highly asymmetrically structured while the interaction between flower visiting birds and plants was mostly non-nested. Understanding the difference for the two important multicsitc systems would help us achieve a better comprehension on the evolutionary dynamics of the interaction.

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