Structure and characteristics of plant-frugivore network in Guilin Botanical Garden

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Abstract

The interaction between plants and frugivores plays a critical role in sustaining ecosystem function and community diversity, but little is known about the structure of interaction networks between fruit plants and frugivore birds in urban green spaces. We observed the interactions between plants and birds throughout the year in the Guilin Botanical Garden and assessed the characteristics of the total plant-frugivore and seasonal networks. We also analyzed the relationship between the network roles of species and ecological traits to explore the structure and characteristics of the plant-frugivore network. The interactions between a total of 14 frugivore birds and 13 fruit plant species were analyzed in the study area, the autumn and winter interaction connections contributed 38.79% and 33.15% to the total network, respectively. The specialization (H2´), and interaction evenness (E2) of the network were higher in spring and summer than that in autumn and winter. However, connectance (C), nestedness, and interaction diversity (H2) were contrary to the specialization and interaction evenness of the network. Compared to the networks (N=1000) generated by the null model, the observed network exhibited lower connectance (C), interaction diversity(H2), interaction evenness (E2), and higher nestedness and specialization (H2´). A correlation analysis combining ecological traits and network roles showed that plants with black fruit had higher species strength, whereas the other traits of plants and birds were not significantly correlated with their network parameters.

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Abstract

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KEYWORDS

Guilin Botanical Garden; urban green spaces; plant-frugivore network; bird

1. Introduction

The interaction between frugivorous and fleshy-fruited plants is an important ecological process that links successive generations of plants and influences vegetation dynamics (García et al., 2018; Rumeu et al., 2020). Many fleshy-fruited plants rely on birds for seed dispersal because of their high diversity, mobility, diversified habitat selection (Carlo & Morales, 2016; Camargo et al., 2020), and differences in body characteristics that can concurrently remove a variety of fruit species (Wang et al., 2019). The relationship between fleshy-fruited plants and frugivorous birds can form a complex interaction network. Therefore, unraveling the structure and dynamics of the interaction network can provide novel insights into co-evolution theory (Schleuning et al., 2015), and can be used to describe the diversity of interactions, reveal ecological patterns, and plan conservation efforts (Ramos-Robles et al., 2016; Beal-Neves et al., 2020).

Rapid urbanization has had significant effects on ecosystem structure, leading to habitat loss, degradation, and homogenization (Kiers et al., 2010). Changes in landscape configuration and composition affect the movement and community diversity of bird (Pena et al., 2017), and ultimately reduce the stability of the interaction network structure and ecosystem service function, leading to serious consequences in ecological and evolutionary processes (Harrison & Winfree, 2015; Guenat et al., 2019). For instance, urbanization can negatively affect plant-bird interactions by decreasing bird richness and increasing interaction evenness (Schneiberg et al., 2020). Urban green spaces are a multitude of different open spaces in cities, such as patched native vegetation and artificially managed parks, which play a crucial role in maintaining species diversity and act as ecological corridors by connecting natural vegetation remnants (Daniels et al., 2020; Zhang et al., 2022). Urban green spaces comprise a range of garden plants, which not only provide sufficient food resources and suitable alternative habitats for birds but also influence the dispersal behavior of birds that can connect different patches (Silva et al., 2016; He et al., 2022). For instance, 19 bird species foraged on 21 fleshy-fruited plants in the Nanjing Botanical Garden Mem. Sun Yat-Sen during autumn and winter and then dispersed these seeds to different types of habitats (Li et al., 2001).

With the decline in urban bird diversity and the continuous enrichment of urban green space vegetation types, the characteristics of plant-frugivore networks in urban green spaces have aroused great interest. Previous studies have further shown that the richness and diversity of bird-plant interaction networks are affected by different factors, as suggested by changes across phenology, fruit size, color, and crop of plants that directly affect the foraging choice of frugivore birds (Plein et al., 2013; Zhang et al., 2022), while the body size, mouth-beak length, and tail length of frugivore birds are associated with feeding amount, mode, and flight

ability, and this variability in functional characteristics might increase the functional complementarity within networks (Dehling et al., 2016; Sebastián-Gonzalez, 2017).

The Guilin Botanical Garden, located in the Guilin city, Guangxi Zhuang Autonomous Region, Southwest China, serves as a typical ex-situ plant protection base in an urban green space (Tang et al., 2009). It has more than 300 endangered plants, and these plants produce large amounts of fruit every year, providing an adequate source of food for birds. However, very little information is available regarding the interaction network structure and characteristics between birds and fruit plants. In this study, we report the structure of the plant-frugivore network and the trophic relationships between the network roles and functional traits of two trophic species in the Guilin Botanical Garden. We aimed to answer the following questions: (1) whether seasonal variation affects interactions between frugivorous birds and plant species and (2) whether species traits influence the functional roles of plants and animals in interaction networks. We predicted that (*i*) the network is more complex in autumn and winter because of sufficient fruit resources and (*ii*) the role of species in interaction networks is affected by their traits.

2.MATERIALS AND METHODS

2.1 Study site

Field experiments were performed in the Guilin botanical garden (107deg17'E,25deg01'N) in Guangxi Zhuang Autonomous Region, Southwest China (Fig.1). The altitudes range from 180~300 m above sea level. The climate in this region is dominated by the mid-subtropical zonal monsoon and the average annual air temperature is approximately 19.2 degC, ranging from -4.2 degC in January to 36 degC in July. The annual average precipitation is 1800 mm and the mean annual relative humidity is more than 78% (Tang et al., 2009). The Guilin botanical garden is a comprehensive research base integrating ex-situ protection of endangered plants, domestication and planting of garden ornamental plants. The local vegetation is a middle subtropical evergreen and deciduous broad-leaved mixed forest, and the fruits of plant species, such as *Cinnamomum camphora* , *Machilus thunbergii* , and *Ficus concinna* can provide sufficient food resources for birds.

2.2 Experimental design

2.2.1 Plant–frugivore bird network

Based on the distribution characteristics of fruit plants, we set up four transects (2-3km for each transect) in the survey area to observe the feeding behavior of birds from September 2020 to August 2021. Once birds were found to forage for plant fruits, we recorded which bird species fed on which plant, the number of fruits that were removed by each bird species either by swallowing or carrying away from the parent tree, the number of birds per visit, and the total foraging time (from arrival to departure). Observations were recorded during two foraging periods of 7:00-10:00 a.m. and 14:00-17:00 p.m. with Safari l0x26 zoom binoculars until no more fruits remained on the mother trees. The observation frequency at least eight per month. If frugivorous birds visited trees in conspecific flocks, foraging behavior was recorded for a single, randomly chosen individual and was assumed to be representative of the entire feeding flock (Breitbach et al., 2010). During the field observations, we found that some birds were foraging the fruits by pecking, and made it difficult to record realistic feeding quantity. Thus, to avoid the influence of bird feeding patterns on the network structure (Jordano et al., 2016; Zhang et al., 2022), we took the frequency of bird visits to plant species to build the interaction networks between birds and fruits plants.

2.2.2 Fruit and frugivoretraits

We measured the traits of all plant and bird species relevant to their roles in interaction networks. Plant traits included fruit diameter (d, mm), length (l, mm), mass (m, g), volume (v, mm^3), and color (co). Fruit length, fruit diameter, and fruit mass were measured from 20 fruits obtained from one to three trees per species for each fruiting plant species using Vernier calipers and an electronic balance. The fruit volume was calculated using ellipsoid volume calculation: v=4/3 ($\pi \times$l/2$\times$d/2$\times$d/2) (Zhang et al., 2022). Bird traits included bill width (bw, mm), body length (bl, mm), body mass (bm, g), wing length (wl, mm), and wing loading (wlo) as a proxy of bird movement capacity: Wlo=bm/2$\times$wl. With increasing wing loading value,

the movement capacity of a bird species decreases (Camargo et al., 2020). These bird traits were obtained from a field guide to the birds of China (Mackinnon and Phillipps, 2000) and A Handbook of the Birds of China (Zhao, 2001).

2.3 Data Analysis

2.3.1 Network structure

We used foraging frequency to construct the interaction network, and divided the whole year into four seasons, spring (March, April, and May), summer (June, July, and August), autumn (September, October, and November), and winter (December, January, and February), to analyze the differences in plant-frugivore network characteristics between different seasons. We characterized the structure of weighted interaction network using the following nine statistics through the function "network-level" in the "bipartite" package (R Core Team, 2022): (1) number of bird species (b); (2) number of plant species (p); (3) network size (b×p); (4) number of links (n); (5) connectance (C), the proportion of links that are realized among the pool of all possible links (n/b×p) (Cruz et al., 2013); (6) nestedness (nestedness), which quantifies the degree to which species with few interactions are connected to highly connected species and has been proposed to be associated with network stability (Ramos-Robles et al., 2016); (7) specialization (H_2'), which quantifies the overall specialization within a network, that is, whether species in a network tend to separate or share their interaction partners (Blüthgen et al., 2006); (8) interaction diversity (H_2), a Shannon index based measure of diversity estimated from interaction frequencies, which reflect whether the links are strong (high interaction frequencies) or weak (low interaction frequencies) (Zhang et al., 2022); (9) interaction evenness (E_2), which depicts heterogeneity in the distribution of interactions across species in the network, with high values indicating more even distribution (Sakai et al., 2016).

We used the function "null model" to randomize plant-frugivore interactions, and compared the differences of structure between the observed network and null model (1000 iterations). Randomizations can determine which nodes (species) interact with one another and how strong the interactions are under a simple null hypothesis and determine whether interaction frequencies between consumers and resources are a consequence of the relative abundances of the potential resources (Vaughan et al., 2018). The null model can reshuffle interactions while maintaining the observed matrix dimensions and connectance to reduce the influence of sampling effects on the network interpretation (Pigot et al., 2016).

2.3.2 Network roles of fruit plants and frugivore birds

We characterized the network roles of plants and birds based on five parameters: (1) degree (D), which describes the proportion of available partners a species interacts with and is related to the importance of the species for network cohesion and stability of the total number of connected species (Costa et al., 2020); (2) species strength (Ss), which represents the sum of the dependencies of each species' relevance across all partners (reflecting quantitative importance of a species for the other) (Bascompte & Jordano, 2007); and (3) partner diversity (Pd), which represents the diversity of interaction partners for each species. It is a quantitative analog to the qualitative species degree, the richness of interaction partners (Kaiser-Bunbury & Blüthgen, 2015); and (4) effective partners (Ep), which interpret the variety of partners a species interacts with in a given network (Quitián et al., 2017); and (5) specialization (d'), which measures how strongly a species deviates from a random sample of interaction partners, assuming that all species interact according to their total frequencies (Rumeu et al., 2020). All analyses were performed using the function "species-level" in the "bipartite" package version 4.20 (Vollstädt et al., 2018).

We conducted a correlation analysis between species traits and network parameters to test whether the role of plants and birds in the network were driven by species traits. Plant traits included fruit mass, fruit length, fruit diameter, fruit volume, and fruit color, whereas bird traits included body mass, body length, bill length, wing length, and wing-loading. Their network parameters included degree, species strength, partner diversity, effective partners, and specialization. The analysis between them was performed in the "cor" package version 4.2.0 (R Core Team, 2022), the function "pairs" were used to realize graphic visualization, and the statistically significant difference was set as $P < 0.05$.

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RESULTS

Year and seasonal plant-frugivore network

During the observations throughout the year, we recorded 2235 interactions events between 14 bird species (2 Order 7 families) and 13 plant species (9 Order 10 families) connected by 110 links (Fig.2). Each plant species interacted on an average with 7.08±1.01 (Mean±SD) birds, and each bird species interacted on an average with 6.13±1.15 plant species (Fig.2). We registered 9,106 fruit-eating individual birds, and 92.89% of them foraged fruits of more than five individual plants (Fig.2). Passerine frugivores were relatively important in our study system, involving 13 species that consumed fruits, representing 98.26% of the total interaction number (Fig.2). The plant species most commonly consumed by birds was *Cayratia japonica* with 724 interactions (32.39%), while the bird species most frequently recorded was *Pycnonotus xanthorrhous* with 644 interactions (28.81%) (Fig.2).

Compared with the predicted networks generated by the null model (N=1000), the observed plant-frugivore network exhibited relatively a lower connectance ($C = 0.604$), lower interaction diversity(H_2 =3.91), lower interaction evenness (E_2 =0.751), higher nestedness (nestedness=0.715), and higher specialization ($H´$ =0.091) (Fig.3). These results indicated that the observed network had fewer realized connections and a more stable subset of interactions than that of the predicted network, species exhibiting higher feeding dependence, and lower interaction frequencies.

The contributions of the interaction connections, to the total connections of the network, in different seasons were different (Fig.4). Interaction connections contributed 13.38% and 14.68% to the annual network in spring and summer, and 38.79% and 33.15% to the annual network in autumn and winter, respectively. The specialization ($H_2´$), and interaction evenness (E_2) of the network were higher in spring and summer than that in autumn and winter. However, connectance (C), nestedness, and interaction diversity (H_2) were contrary to the specialization and interaction evenness (Table1). The number of frugivore bird and fruit plant species was positively correlated with the contributions of the interaction connections between birds and fruit plants in different seasons (R_b^2=0.954, P=0.023; R_p^2=0.297, P=0.455).

Fig.4 The connections of different seasons contribution to the total plant-frugivore network, the color bars with the gradient of pink to yellow below the main figure indicate the proportion of interaction connections to the total network in different seasons.

Table 1 Main quantitative description of seasonal variation of interaction network

The relationship between species' traits and their functional roles

None of the bird traits that we investigated were significantly related to the functional roles of species in the network structure (Fig.5). The relationships between the network parameters and fruit traits showed that only fruit color had significant effects on species strength (Pearson correlation coefficient: r=0.666, *P* =0.013) (Fig.6), and the species strength of plants with black fruits (2.69±1.25) was significantly greater than that of plants with red fruits (0.358±0.057). Thus, only fruit color could explain species strength; that is, plants with black fruits had greater species strength.

Fig.5 Correlation matrix between network parameters and bird traits

Fig.6 Correlation matrix between network parameters and plant traits

DISCUSSION

We recorded 2235 interactions events between 14 bird species and 13 plant species in our study area (Fig.2), suggesting that even in urban green spaces with relatively small biodiversity, interaction networks can be highly complex and dynamic. Passerine birds occupied a dominant position in the whole interaction network (Fig.2), which may be related to their wide feeding niche, foraging on a variety of fruits, and high adaptability to disturbed urban habitats. Thus, the existence of passerine birds with different body traits in cities can increase the cumulative connection of the plant-frugivore bird networks in urban ecosystems.

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However, compared with the random network generated by the null model, the observed network had a lower connectance (C), lower interaction diversity (H_2), lower interaction evenness (E_2), higher nestedness, and higher specialization (H') (Fig.3). The results indicated that the structure of the observed network was simpler than that expected by the null model, and these shifts in the network structure can be explained by the intrinsic mathematical behavior of the null model tends to generate more connected matrices than that observed (Dormann et al., 2009; Costa et al., 2016). The higher degree of specialized interaction in the null model, which is consistent with other studies (Blüthgen et al., 2008), but these highly specialization interactions are more easily lost from the networks because extinction of one of the species may have fatal consequences for its specialist interacting partners (Sebastián-González et al., 2015). Hence, disturbed urban habitats may show more nestedness and less modular structures because the most specialization interactions have been lost due to human activities.

We found that the characteristics of the interaction network varied with season, and most interactions were detected in autumn and winter (Fig.4), which is consistent with our prediction (i). This difference could be explained by the decrease in other food sources such as insects and the arrival of wintering populations, which intensifies competition for food resources (Cruz et al., 2013; Yang et al., 2013). The number of ripe fruit species and participating frugivore birds were positively correlated with the interaction connections in different seasons, and other studies have also shown that an increase in fruit abundance significantly improves bird richness and network complexity (Ramos-Robles et al., 2016; Schneiberg et al., 2020). The connectance (C), nestedness, and interaction diversity (H_2) for the autumn and winter networks were higher (Table1), indicating more efficient use of resources (i.e. higher number of realized links among all possible links). Interaction evenness (E_2) was higher in spring and summer, which means that there was a more homogeneous distribution of the frequency of links in these networks; whereas, in autumn and winter a few highly frequent interactions dominated the network, particularly *Cayratia japonica* and *C. camphora*. Higher specialization in spring and summer may arise as a response of the higher trophic level to low plant diversity (He et al., 2022), which also means a high degree of niche differentiation (Blüthgen, 2010; Sebastián-González et al., 2015) and decreasing competition between different birds to facilitate species coexistence (Silva et al., 2016).

There was no significant correlation between species traits and their network roles, except for the effect of fruit color on species strength (Fig.5; Fig.6). This is contrary to the results of previous studies (Saavedra et al., 2014; Pigot et al., 2016) and is inconsistent with our prediction (ii). These differences can be explained by the following two factors: First, individual species play important roles, and their contribution to the network is much higher than the average value of species with the same traits; therefore, the differences cannot be shown in the analysis. Second, the small sample size for the weighted analyses may have caused this contrasting result (Costa et al., 2016). Plants with black fruit have greater species strength, which means they can attract more frugivorous birds. This, could be explained by the black aril of mature fruits that can create a strong visual contrast with the green background of the surrounding plants attracting birds to feed on their fruit (Duan et al., 2014; Zhang et al., 2022), and there is a significant positive correlation between the lipid nutrients and color; thus, color may be a signal of seed maturity and nutritional rewards (Schaefer et al., 2014). Finally, the evergreen fruit plants, such as *C. camphora* and *B. javanica* can provide temporary shelter when birds forage in highly disturbed urban habitats and the long-term interaction adaptation between these plants and frugivore birds has resulted in bird foraging preferences for these species.

Our results suggested that there are significant seasonal differences in the structure and characteristics of the interaction network between plants and frugivore birds in urban green space, and none of plant and bird traits were significantly related to the functional roles of species in the network structure, except for the effect of fruit color on species strength. This result may be caused by the sample size and the area limitation. Therefore, it is necessary to expand research area in the next research to further understand the impact of urbanization on the characteristics of the interaction network between plants and frugivore birds.

Ethical standard

This article does not contain any studies with human participants or animals performed by any of the authors.

Statement of conflict of interest

The authors declared that there is no conflict of interests regarding the publication of this article.

Author Contributions

Guo-hai Wang, Yang Huang, Wei Yao, Qi-ming Tang conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. Qiu-chan Huang, Yong-Ping Huang, Li-Juan Wei analyzed the data, prepared figures and/or tables. Qi-hai Zhou conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

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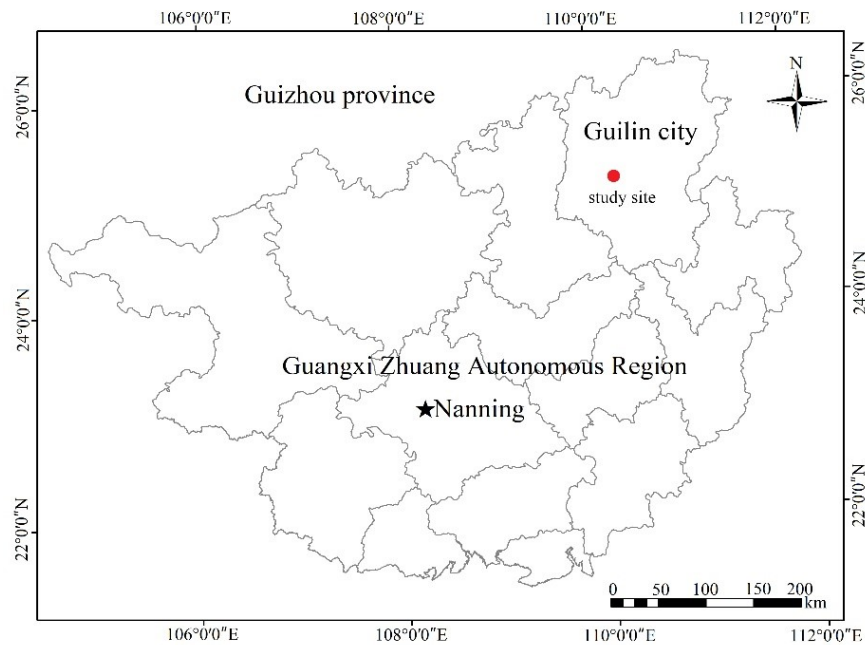
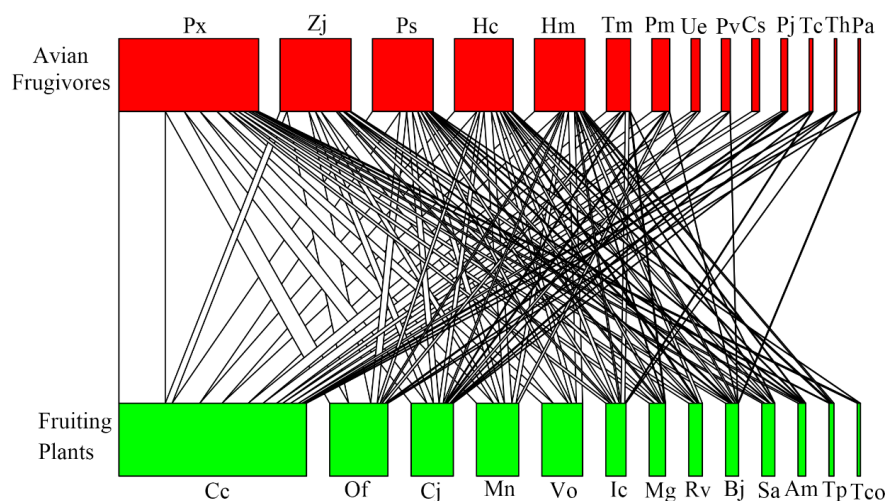Fig.1 Location map of Guilin Botanical Garden, China.jpg

Fig.2 Correspondence relationship between avian frugivores and fruiting plants based on feeding frequency. Widths of connecting lines denote the number of observed interactions (wider represents higher intensity of visiting). Avian frugivores: Px: *Pycnonotus xanthorrhous* ; Zj:*Zosterops japonicus* ; Ps: *Pycnonotus sinensis* ; Hc:*Hemixos castanonotus* ; Hm: *Hypsipetes mcclellandii* ; Tm:*Turdus merula* ; Pm: *Parus major* ; Ue: *Urocissa erythrorhyncha* ; Pv: *Parus venustulus* ; Cs: *Copsychus saularis* ; Pj: *Pycnonotus jocosus* ; Tc: *Turdus cardis* ; Th:*Turdus hortulorum* ; Pa: *Pycnonotus aurigaster* ; Plant species: Cc: *Cinnamomum camphora* ; Of: *Osmanthus fragrans* ; Cj: *Cayratia japonica* ; Mn: *Machilus nanmu* ; Vo:*Viburnum odoratissimum* ;

Ic: *Ilex chinensis* ; Mg: *Magnolia grandiflora* ; Rv:*Rauvolfia verticillate* ; Bj: *Bischofia javanica* ; Sa:*Schefflera arboricola* ; Am: *Alocasia macrorrhiza* ; Tp:*Tetrastigma planicaule* ; Ico: *Ilex cornuta* .
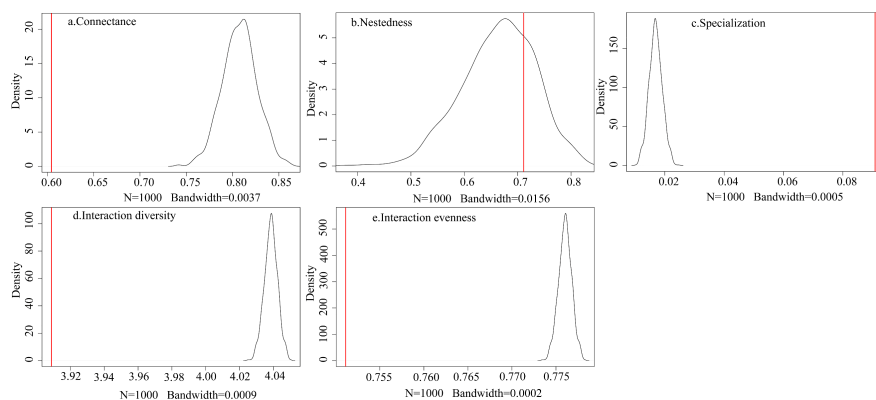

Fig.3 Comparision between observed network and networks generated by null mode
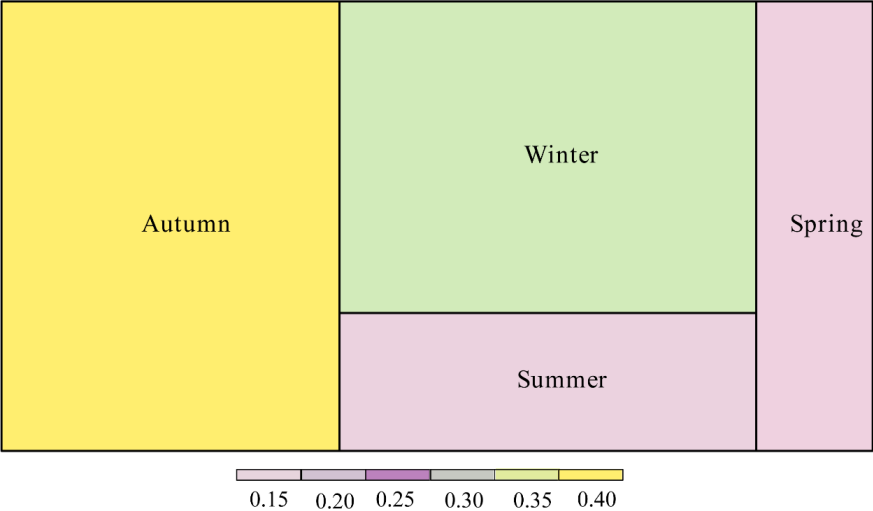
Fig.4 The connections of different seasons contribution to the total plant-frugivore network
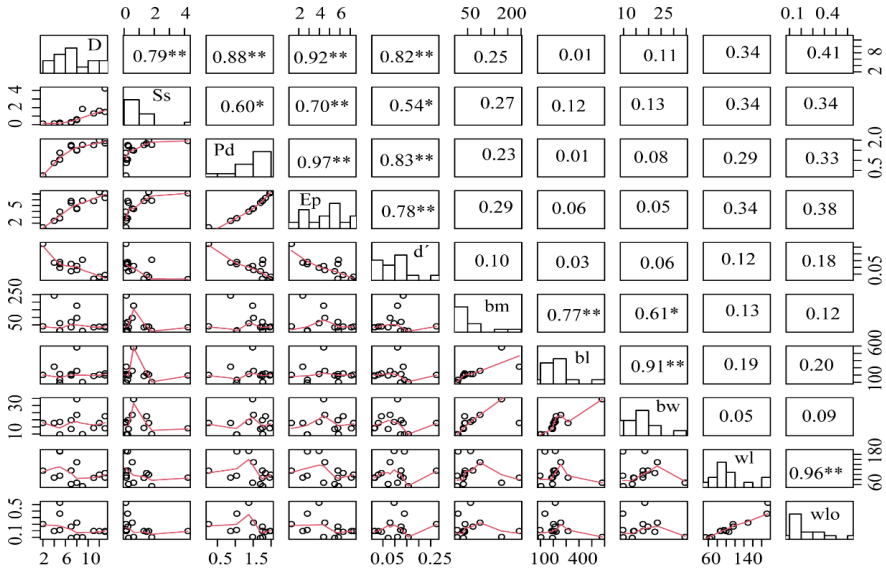

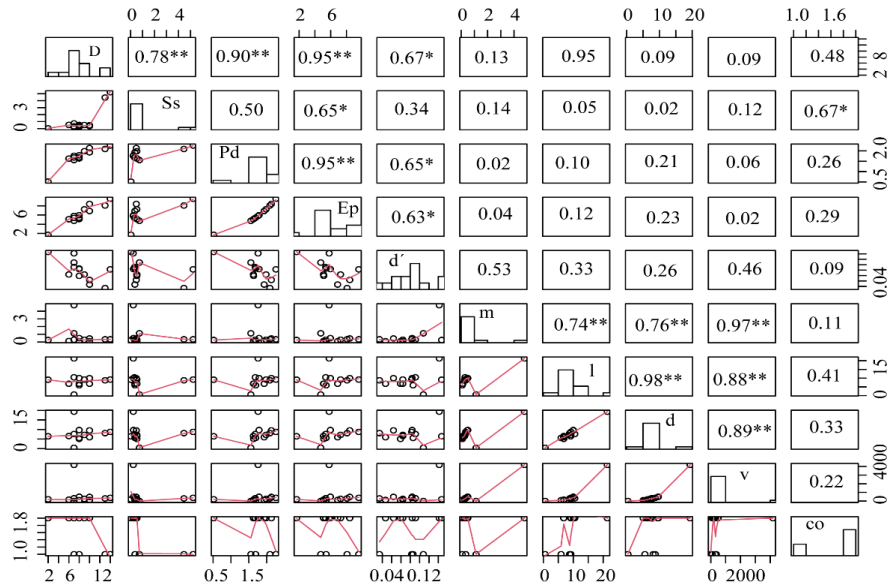Fig.5 Correlation matrix between network parameters and bird traits

Fig.6 Correlation matrix between network parameters and plant traits

Table 1 Main quantitative description of seasonal variation of interaction network

Parameter	Autumn	Winter	Spring	Summer
No. of bird species (b)	13	13	8	8
No. of plant species (p)	6	9	5	6
No. of links (n)	51	76	23	29
Network size (b × p)	78	117	40	48
Connectance (n/b × p)	0.65	0.65	0.58	0.60
Nestedness	0.65	0.78	0.56	0.35
Specialization ($H_2´$)	0.12	0.09	0.13	0.20
Interaction diversity (H_2)	3.18	3.60	2.42	2.92
Interaction evenness (E_2)	0.06	0.05	0.11	0.10

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