

Long-Term Dynamics of Bird Dispersal Network Structures Associated with the Functions in Bird Migration and Fruit Abundance

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Abstract

In temperate zones, the complex network of seed dispersal by migrant birds is formed and the structure is dynamic on long time scale. Over 12 years, we examined interannual variability of structures of bird dispersal networks and factors affecting them by observing the characteristics of fruit abundance, bird migration and bird dispersal interactions in central Japan. The fruit abundance exhibited a remarkable fluctuation across years, with the number of fruiting trees and matured fruits fluctuating repeatedly every other year, leading to the periodic fluctuations. The abundance of migrants was also fluctuated.

According to the abundance of fruits and migrants, the 12 years as study period was classified into three types. The seed transporting frequency and the dispersal networks were investigated by collecting faeces of migrants. Of the 6652 samples collected from 15 bird species, 1671 (25.1%) included seeds from 60 plant species. Main dispersers were composed of *Turdus pallidus*, *T. obscurus* and *Zosterops japonicus*. The structures of bird dispersal networks were highly nested over 12 years, suggesting the networks are stable. Specifically, the nested structure developed in years when fruit abundance was low. GLM analyses showed the abundance of migrants, particularly *T. pallidus* and *T. obscurus*, had strong positive effects on construction of nested structure. The development of nested structure may be caused by the fact the two *Turdus* species were more frequently functioning as generalist dispersers when fruit abundance was lower. Our study revealed one of the mechanisms determining the structure of bird dispersal network on long time scale.

Introduction

Frugivore–plant interaction is one of the fundamental interactions of an ecological community. In these communities, the complex networks of interactions that connect species are formed. Intrinsically, the structure of such networks is dynamic and determines community structure. These dynamic network structures emerge directly from temporal changes in some population characteristics in the network, e.g., species composition, relative species abundance, resource availability, and other factors (Burkle and Alarcón 2011; Olesen et al. 2010; Trøjelsgaard and Olesen 2016). Dispersal of seeds by birds (endozoochory) is a mutualistic interaction between frugivorous birds and fleshy-fruited plants (Ridley 1930; Snow and Snow 1988; Corlett 1998; Herrera 2002). In the middle-latitude regions of temperate zones, migrant frugivorous birds play an important role in seed dispersal. In the autumn season, frugivorous birds migrate from high- to low-latitude regions where ample plants are in their fruit-bearing stages. The birds consume a large number of mature fruits and consequentially contribute to seed dispersal. The fruit diversity is maximised during this season due to the visits of several frugivorous bird assemblages visit (Thompson and Willson 1979; Herrera 1984; Skeate 1987; Levey 1988; Noma and Yumoto 1997; Burns 2002; Masaki et al. 2012). Plein et al. (2013) reported that bird–plant dispersal networks are constantly created at a local level despite spatial and temporal fluctuations in bird and fruit communities, indicating that these networks are frequently created on a short time scale.

Long-term dynamics observed in network structures are also widely recognised, regardless of the limited information available about them. Some studies have shown interannual variability in the structure of

bird dispersal networks (Herrera 1984; Carnicer et al. 2008; Costa et al. 2020). The bird migration patterns are likely to fluctuate every year, migrant bird abundance, species composition of assemblages, movement frequency, and timing of movement (Herrera 1998, Newton 2008). These patterns are further influenced by climatic and weather conditions, resource conditions, human activities, and any endogenous factors of the migrant birds, including age, hormones, and other physiological conditions (Berthold 1993; 1996; Gwinner 1996; Marra et al. 2005; La Sorte et al. 2015). Moreover, fruit abundance patterns in plant communities fluctuate over time. Although fruit abundance is high from autumn to early winter in temperate zones, variable fruit abundance is observed across years. This is attributed to the fact that the amount of fruit produced by a tree and its population varies across years (Herrera 1998; Shibata et al. 2002). In some species of shrubs and woody plants, simultaneous flowering and fruiting has been confirmed (Herrera et al. 1998), resulting in an overabundance of fruits in plant communities. Furthermore, bird migration and fruiting patterns are likely to fluctuate across years and are devoid of annual correlations. If fruits are abundantly produced despite the low abundance of birds, the efficiency of seed dispersal by birds could be of lower relevance. This suggests that the seed dispersal networks of migrant birds are not stable, and the network structures may vary over a long period.

Recently, network theory was applied for the analyses of bird dispersal systems on scales ranging from local to global in temperate and tropical regions (Carnicer et al. 2009; Héleno et al. 2013; Vidal et al. 2014; García-Quintas et al. 2014; Saavedra et al. 2014; Sebastián-González et al. 2015; Ramos-Robles et al. 2018). This revealed the environmental and biological factors affecting the network structures and explained the formation of complex network structures based on various factors. In general, a network structure is described using two fundamental characteristics: nestedness, i.e., specialist species interacting with a subset of generalist species, and modularity, i.e., presence of semi-independent groups of highly interactive specialist species. These two characteristics are strongly and mutually correlated, depending on the connectance among the mutualists in the network (Fortuna et al. 2010). Most bird dispersal networks exhibit high nestedness and low modularity patterns. This is because one bird species typically has various plant partners (Wheelwright 1985). In some cases, a few species that function as generalist dispersers are the main contributors to the formation of nested network structures (Vidal et al. 2014; Ramos-Robles et al. 2018). Ramos-Robles et al. (2016) confirmed that nested structures in seasonal tropical forests were more developed when fruit abundance was higher. However, a reduction in nested network structures was observed due to changes in bird species composition. Therefore, it can be inferred that the development of nested structure in the bird dispersal network depends on the presence of generalist dispersers and high abundance of fruits.

In the seed dispersal network of migrant birds in temperate zones, it is predicted that nested structures are more prevalent in years which fruit abundance is high as generalist species of migrant birds can interact with many plant species. For verification of this prediction, the structures of bird dispersal networks should be monitored to determine the influence of fluctuations on bird migration and fruiting (Herrera 1998). Many frugivorous birds migrate to north and west Japan in autumn and winter. These birds contribute to seed dispersal of many freshly-fruited plants (Higuchi 2014). Migration patterns of frugivorous birds fluctuate with area and time (Yamashina Institute for Ornithology 2002). For some

frugivorous species, the timing of arrival and length of stay at the wintering sites differ across years. Similarly, the fruit abundance of some bird-dispersed plants also fluctuates across years (Osada 2005; Naoe et al. 2018). Since 2005, we have examined the seed dispersal network of migrant birds and fluctuations in bird migration and fruit abundance patterns at the Otayama Bird Banding Station in Fukui Prefecture of central Japan. This was undertaken to observe and monitor long-term seed dispersal networks. In this study, we quantified variation in the structures of bird dispersal networks across years using a network approach. The following factors were analysed from the long-term data: (1) fluctuation in fruit abundance in the fleshy-fruited plant community, (2) fluctuations in abundance and species composition of migrant frugivorous birds, (3) classification of time periods based on bird migration and fruit abundance patterns, and (4) relationships between structures of bird dispersal networks (nestedness and modularity) and patterns of bird migration and fruit abundance. Finally, we considered the factors affecting structures of bird dispersal networks. In particular, we evaluated the influence of generalist dispersers and high fruit abundance on the development of nested network structures.

Methods

Study site

From 2005 to 2016, field research was conducted at the Otayama Bird Banding Station and the forested area on Mt. Ota in Fukui Prefecture, central Japan (35.9777°N , 136.0191°E , 500 m.a.s.l.). The elevation was approximately 500 m above sea level. The vegetation at the site was divided into two types: cedar forest and secondary broad-leaved forest. The areas along the ridge and forestry roads were covered with broad-leaved trees, while the large area of the mountain slope was covered with cedars. The broad-leaved forest was composed mainly of *Quercus crispula*, *Acer palmatum* var. *matsumurae*, and *Clethra barbinervis*. The station was used as a laboratory and mist nets were built on site.

Monitoring of fruit abundance at the study site

To evaluate fruit abundance and species composition of fleshy-fruited plant communities, we carried out a field census of fruiting plants and matured fruits. At the study site, the census route was set up in the capturing area (0.6 ha) and the area around the mountain path ($10\text{ m} \times 10\text{ km}$: 10 ha). Within the area, we searched for fruiting trees with binoculars by walking at 1 km/h. When fruiting trees were found, we identified the species and counted the number of matured fruits in each tree. In addition to woody species, herbaceous and liana species with fruits were also examined. In cases where the number of fruits was very large, we estimated the total fruit number by calculating the average number of fruits on an infructescence, infructescence on a branch, and branches on a tree. The census was carried out using the same route during 3 days on late October every year. Species name of plants was identified and referred based on the YList (Yonekura and Kajita 2003).

Capturing of migrant frugivorous birds and monitoring of migration patterns

Bird banding research at the station was managed by the Yamashina Institute for Ornithology. The capture of migrants was carried out for approximately two weeks from mid-October to early November every year. A total of 49 mist nets (height: 2.6 m, length: 12 m, and 36 mm mesh) were set up covering approximately 0.5 ha of the capturing area on the mountain ridge near the station. During fine-weather days, all nets were kept open from 6:00 to 18:00. Nets were checked every hour, and all captured birds were kept in cloth bags (size: 30 cm L × 40 cm W). After recording the bird species, sex, and age, and marking them with number rings, they were released unharmed.

The number and species composition of frugivorous bird species were confirmed from the banding data collected at the Otayama Bird Banding station from 2005 to 2016 (Yamashina Institute for Ornithology 2005 – 2016). Species name was identified and referred by check list of Japanese birds (The Ornithological Society of Japan 2012). Data concerning frugivorous families were used in the analyses, including Turdidae, Muscicapidae, Pycnonotidae, Cettiidae, Phasianidae and Picidae. Data for the families Columbidae, Emberizidae and Fringillidae were excluded from the analyses, because they are seed crushing species, and their functions as seed dispersers is regarded to be very low. Species of the family Bombycillidae were not captured. The capturing number per day was used in the analyses.

Collection of fecal samples from frugivorous birds

During banding, the frequency of seed transport and patterns of frugivorous species were investigated by collecting of faeces containing seeds and fruits. All captured birds were kept in cloth bags for 10-20 min, to allow them to drop their faeces and vomits. Then, the faeces and vomits left in the bags were collected in small paper bags (size: 10 cm L × 15 cm W). All faecal samples were brought back to the laboratory, and dried for over 48 h. Under a binocular microscope, each sample was dissected with forceps, and the contents were observed and collected. The contents were classified as seeds, fruit pericarps, crushed seeds, and insect or arthropod parts. In all seed samples, the number per faeces was counted, and the species were identified using a seed identification manual and reference samples that had been previously collected at the study site. Using this method, the transport frequency of bird-dispersed plants by each species was estimated.

Data analyses

To examine the fluctuation pattern of fruit abundance in the freshy-fruited plant community across years, the number of fruiting plants and abundance of matured fruit was compared among years using the G-test. The plant community in each year was classified using principle component analysis (PCA) based on the number and species composition of fruiting trees and fruits. For the analyses, the tree and fruit numbers were log-transformed. To confirm the fluctuation in fruit abundance for each plant across years, the coefficient of variation (CV) for the fruit number was used as the index because it has been previously applied to evaluate the spatial heterogeneity of some plant characteristics (Wilson 2000; Terradas et al. 2009). Furthermore, the synchronisation of fruiting among plant species was tested using Spearman's rank correlation. Next, to examine and compare the patterns of bird migration across years, the frequency and species composition of frugivorous birds were compared among years using the G-test. The

frugivorous bird community in each year was classified using PCA based on the number and species composition of captured birds. The relationships between the classification and abundance of migrants were analysed using linear regression.

For the bird dispersal networks, we explored two patterns: nestedness (Bascompte et al. 2003) and modularity (Olesen et al. 2007; Donatti et al. 2011; Mello et al. 2011). For nestedness, the qualitative degree was calculated for each matrix using the NODF (nestedness overlap and decreasing fills, Almeida-Neto et al., 2008), while quantitative nestedness was calculated using the WNODF (the weighted NODF, Almeida-Neto and Ulrich 2011). As the variation in the number of interactions across species could influence the degree of nestedness, we compared the observed NODF and WNODF values for each matrix with the NODF and WNODF values of 100 matrices constructed following a null model. In the null model for WNODF, the species-specific probabilities were proportional to the relative number of species interactions (Vázquez et al. 2007). In addition, the nestedcontribution as the degree to which the interactions of each bird species increase or decrease the community nestedness, was estimated for the three major disperser species to clarify their contribution to the nested structure (Bascompte et al. 2003; Saavedra et al. 2011). We calculated values and conducted null model analyses using the Bipartite package in R (Dormann et al. 2009).

To evaluate whether the modules were formed of cohesive subgroups of closely connected species, the modularity of the network was explored. The degree of modularity for each qualitative binary dataset was estimated as the metric M using MODULAR software (Newman and Girvan 2004; Olesen et al. 2007; Marquitti et al. 2014). The quantitative modularity metric Q was also calculated by the developed QuanBiMo algorithm using the Bipartite package in R (Barber 2007; Dormann and Strauss 2014). Both M and Q vary from 0 to 1, with large values characteristic of networks with a large number of modules and/or very isolated modules (Olesen et al. 2007; Sebastián-González et al. 2015). To test the significance of the modularity, we generated 100 random networks, fixing the probability that two species interact based on observations of the real networks. Then, we calculated the modularity of the networks and evaluated whether the observed modularity fell within the 95% confidence interval calculated from the randomised matrices. Additionally, to characterise the variation in network parameter values, the following parameters were calculated: interaction strength (IS), web asymmetry (WA), connectance (C) and network-level specialisation (H_2) (Ramos-Robles et al. 2016).

Lastly, we tested whether the network metrics (NODF, WNODF, M and Q) over 12 years were related to the patterns of bird migration and fruit abundance by model selection using generalised linear model (GLM) analysis and logistic regression analysis. For these analyses, the network metrics standardized as Z-scores: Z-NODF, Z-WNODF, ZM and ZQ (Sebastián-González et al. 2015). As predictor variables, the following values for the patterns of bird migration and fruit abundance were used: the captured number of migrant birds (bird abundance), number of mature fruits (abundance of fruits), the first and second principal components of bird and plant communities in PCA, and the interactions between bird and fruit abundance. The number of migrant birds and mature fruits were log-transformed. The interactions among predictor variables were also considered. We began with a full model, then constructed various

models with different combinations of explanatory variables, with the final model selected according to the lowest AICc (Akaike's information criterion) value. For the models, a Gaussian-type error distribution was used. The analyses were carried out using the lme4 and MuMIn packages in R 3.6.2. (R Core Team 2019, <http://www.r-project.org>). Moreover, the relationships between the network metrics and any factors were analysed using logistic regression.

Results

Fluctuations in fruit abundance and synchronization of fruiting

A total of 8067 trees (0.076 tree/m²) from 97 species (41 families, 29 orders), comprising 64 woody, 15 liana and 18 herbaceous species, were observed in the route census of fruiting plants from 2005 to 2016. The number of fruiting trees was significantly different among years (annual average: $672.3 \pm SD 419.1$, range: 168–1367, $\chi^2 = 2873.7$, $P < 0.0001$, G-test). In *Daphniphyllum macropodum*, *Sorbus gracilis*, *Viburnum wrightii*, *Vaccinium oldhamii*, and *Callicarpa japonica*, more than 400 trees were confirmed over the 12 years. The total number of matured fruits was 10507534 (99.1 fruit/m², annual average: 875627.8 ± 795960.7 , range: 64023–2781101), and the fruit number was significantly different among years ($\chi^2 = 7958961.0$, $P < 0.0001$). In *Zanthoxylum ailanthoides* and *Mallotus japonicus*, more than twenty thousand of fruits were produced per tree. Additionally, these species occupied 22.9% – 88.7% of all fruits each year.

The fruit abundance of the freshy-fruited plant communities exhibited a remarkable fluctuation across years, with the number of fruiting trees and matured fruits fluctuating repeatedly every other year from 2005 to 2016 (Fig. 1A). The fruit number fluctuation corresponded to that of tree number. The plant communities could be classified into years when the fruit abundance was high and low (Supplementary Fig. 1). The CV values for the fruit numbers of 97 species were shown in Fig. 1B. They were less than 1.0 in only seven species *Aralia elata*, *Eurya japonica*, *Clerodendrum trichotomum*, *Ampelopsis glandulosa* var. *heterophylla*, *Tripterospermum japonicum*, *C. japonica*, and *Z. ailanthoides*. To confirm whether the fruiting patterns synchronise among species, the relationships between the fruit numbers were analysed in 31 dominant species, of which the number of fruiting trees was more than 20 over the 12 years. There were significant positive correlations in 133 (28.6%) of the 465 relationships among the 31 species (Spearman's rank correlation, Supplementary Table 1). The fruit numbers of 14 species were positively correlated with those of the other 12–20 species. Specifically, a high correlation was confirmed in even three species with a CV was less than 1.0, *C. trichotomum*, *T. japonicum* and *C. japonica*. This means that most freshy-fruited plant species produced fruits repeatedly every other year, synchronising mutually, only four species (*A. elata*, *E. japonica*, *Z. ailanthoides*, and *A. glandulosa* var. *heterophylla*) constantly producing fruits every year. The synchronisation of fruit production among species leads to the periodic fluctuations in fruit abundance within plant communities.

Migration pattern of frugivorous birds and classification of the 12-year study period

From 2005 to 2016, a total 16722 individuals of 20 frugivorous species were captured and released. The number of birds captured per day was 35.9–122.2, which were significantly different among years ($\chi^2 = 114.0$, $P < 0.0001$, G-test, Supplementary Fig. 2). Concerning all captured birds, 76.2%–90.2% were composed of the Japanese white-eye *Zosterops japonicus*, pale thrush *T. pallidus*, and eyebrowed thrush *T. obscurus*. There were no significant relationships between the number of birds captured per day and the number of fruiting trees and matured fruits (tree number: $P = 0.12$; fruit number: $P = 0.87$). However, the fruit abundance was associated with the species compositions of migrant birds. The communities of migrants were classified into three groups by PCA (Fig. 2). The first and second principle components explained 27.7% and 16.8% of the total variation, respectively. The classification was associated with fruit abundance. First, in 2007, 2009, 2011, and 2013, when the fruit abundance was relatively high, the communities were characterised by *Z. japonicus*, *Luscinia calliope*, *Horornis diphone*, *Phylloscopus xanthodryas* and *T. cardis* (Fig. 2B). Second, in 2006, 2010, 2012 and 2014 when the fruit abundance was relatively low, the communities of frugivores were characterized by *T. pallidus*, *T. obscurus*, *T. chrysolaus*, *T. eunomus*, *Ficedula mugimaki*, and *Tarsiger cyanurus*. Third, in 2005, 2008, 2015 and 2016, the frugivore communities were characterized by *Hypsipetes amaurotis*, *F. narcissina*, and *Syrmaticus soemmerringii*.

In addition, the classification was also strongly associated with the abundance of migrant birds. The first principal component was significantly correlated with the number of birds captured in one day ($R^2 = 0.78$, $P < 0.001$, Fig. 3). In particular, the bird abundance in 2005, 2008, 2011, 2015 and 2016 was lower (average number: 35.9–122.2). In conclusion, the 12-year study period could be classified according to fruit and bird abundance and species composition of migratory birds as shown in Fig. 3: years when the abundances of both frugivores and fruits were high (2007, 2009 and 2013; FA group), years when the fruit abundance was low but frugivores were abundant (2006, 2010, 2012, and 2014; FP group), and years when the abundance of frugivores was low (2005, 2008, 2011, 2015, and 2016; BP group).

Seed-dispersal Networks Of Migrant Frugivorous Birds

The faeces and vomit were collected from total 6652 individuals of 15 bird species. Of the collected samples, 1671 (25.1%) included seeds from 60 plant species (Table 1). The species composition of seed dispersers and transported seeds differed among years (birds: $\chi^2 = 356.7$, $P < 0.0001$; seeds: $\chi^2 = 447.4$, $P < 0.0001$, G-test, Supplementary Fig. 3). Of the bird species, 68.4% – 97.6% were composed of *T. pallidus*, *T. obscurus*, and *Z. japonicas* and 48.8% – 90.1% of the seeds were composed of *A. elata*, *Z. ailanthoides*, *E. japonica*, *C. japonica* and *Cornus macrophylla*. In all 12 years, the average number of interactions was larger in bird species than plant species. Each bird species interacted with 2.7–9.2 plant species, whereas each plant species interacted with 1.7–3.2 bird species (Table 1). The numbers of bird and plant species, interaction numbers and interaction strengths in the networks were larger in the FP group, despite of low fruit abundance. The frequency of seed transport was also higher in the FP group, though the difference

was not significant (FA: 0.19–0.34, FP group: 0.25–0.39, and BP group: 0.15–0.27, $P = 0.09$, ANOVA for GLM, Table 1).

Table 1

Frequency of seed removal and the characteristics of dispersal network from 2005 to 2016. The 12 years were classified with three groups by the abundance of migratory birds and fruits; FA group: years when the abundance of both frugivores and fruits were high, FP group: years when the fruit abundance was low, though frugivores were abundant, and BP: years when the abundance of frugivores was low.

Characteristics of interaction networks									
Interaction number									
Year	Group	N	Species number	Seed removal frequency	Species number		Average ± SD		
					Birds	Plants	Total	Birds	Plants
2005	BP	477	16	0.15	12	19	48	4.0 ± 2.1	2.5 ± 1.9
2006	FP	1166	15	0.31	10	30	92	9.2 ± 8.0	3.1 ± 2.3
2007	FA	831	14	0.19	9	23	52	5.8 ± 6.1	2.3 ± 1.3
2008	BP	377	14	0.26	11	18	51	4.6 ± 3.6	2.8 ± 2.4
2009	FA	257	10	0.33	8	17	35	4.4 ± 5.4	2.1 ± 1.2
2010	FP	554	13	0.34	9	20	52	5.8 ± 4.7	2.6 ± 1.8
2011	FA	164	13	0.26	4	13	22	5.5 ± 3.9	1.7 ± 0.5
2012	FP	253	13	0.39	10	11	27	2.7 ± 2.3	2.5 ± 1.9
2013	FA	295	12	0.24	7	17	38	5.4 ± 4.2	2.2 ± 1.5
2014	FP	790	14	0.24	10	21	55	5.5 ± 5.3	2.6 ± 2.1
2015	BP	729	15	0.26	13	24	76	5.8 ± 5.4	3.2 ± 2.5
2016	BP	478	19	0.2	6	21	45	7.5 ± 4.8	2.1 ± 1.4

Figure 4 shows the networks of the three groups in which the interaction data were pooled. In all groups, *Z. japonicus*, *T. pallidus*, and *T. obscurus* mainly interacted with four plant species, including *A. elata* (ID No 3), *Z. ailanthoides* (ID No 47), *E. japonica* (ID No 22), and *C. japonica* (ID No 27). In all groups, *Z. japonicus* frequently transported seeds of two species *A. elata* and *Z. ailanthoides* that constantly produced fruits. Through 12 years, more than 40% of *A. elata* and *Z. ailanthoides* seeds were transported by *Z. japonicus* (average *A. elata*: 50.1%, *Z. ailanthoides*: 68.8%). The two *Turdus* species tended to have more interactions than *Z. japonicus*. In particular, in the FP group, *T. pallidus* and *T. obscurus* interacted with 29 and 33 species, respectively, whereas *Z. japonicus* interacted with 17 species. In the FP group, these species frequently transported not only seeds of woody species but also those of herbaceous and liana plant species; 14 of 29 (48.3%) and 14 of 33 (42.4%) were herbaceous and liana species (Fig. 4, Supplementary Table 2).

In 11 of the 12 years, the networks were significantly and highly nested, excluding 2011 (BP group) (Table 2). The NODF and WNODF values were significantly higher in the FP group than in the other two groups (NODF: $F_{2,5,8} = 2.9$, $P = 0.05$, WNODF: $F_{2,7,6} = 2.9$, $P = 0.02$, ANOVA for GLM). In the networks of the pooled data, the values were higher in the FP group than in the other two groups (Supplementary Table 3). Additionally, nestedcontribution values for *T. pallidus*, *T. obscurus*, and *Z. japonicus* in the FP group were 5.15, 6.0, and 3.31, respectively. This suggests that the nestedness structures were developed according to the functions of the two *Turdus* species as generalist dispersers. All networks through 12 years were also significantly modular (Table 2). Although the values of M and Q values were not different among years (M: $P = 0.99$, Q = 0.98, ANOVA for GLM), they tended to be higher in the FA group. However, when the interaction data of each group was pooled and the networks were created using the QuanBiMo algorithm, the modular structures of the groups differed. Specifically, the composition of modules in the FA group remarkably differed from that in the FP group (Supplementary Fig. 4). The number of interactions among the modules was relatively small in the FA group (average: 5.8 ± 3.9), and the modules tended to be mutually independent. In these networks, *Z. japonicus*, *T. pallidus*, and *T. obscurus* belonged to different modules respectively. In the FP group, 8 and 9 species of herbaceous and liana plants were included in the modules of *T. pallidus* and *T. obscurus* (Supplementary Fig. 4). In the module of *Z. japonicus*, *A. elata* and *Z. ailanthoides* were included in the two networks. As shown in the nested structures, there were specific interactions among these species.

Table 2

Descriptors of interaction networks between migratory birds and plants in each year. N: number of individuals transporting seeds; IN: interaction number; IS: interaction strength, WA: web asymmetry; C: connectance. Significance of nestedness and modularity was tested by comparing the values observed in real network and expected from the null model.

Descriptors of interaction networks												
Year	Group	N	IN	IS	WA	C	Nestedness		Modularity			M/Q
							NODF	WNODF	M	Q		
2005	BP	73	48	82	0.23	0.21	44.5**	19.6**	0.41*	0.34*	1.2	
2006	FP	368	92	525	0.5	0.31	70.9**	48.7**	0.27*	0.19*	1.44	
2007	FA	158	52	202	0.44	0.25	54.7**	38.7**	0.32*	0.26*	1.23	
2008	BP	100	51	138	0.24	0.26	54.2**	35.5**	0.34*	0.27*	1.27	
2009	FA	87	35	127	0.36	0.26	62.4**	39.4**	0.32*	0.25*	1.29	
2010	FP	190	52	251	0.38	0.29	58.6**	36.0**	0.31*	0.24*	1.3	
2011	BP	42	22	52	0.53	0.42	32.8	20.7	0.34*	0.24*	1.41	
2012	FP	98	27	131	0.05	0.25	51.7**	36.3**	0.40*	0.18*	2.21	
2013	FA	71	38	92	0.42	0.32	60.0**	36.0**	0.30*	0.27*	1.11	
2014	FP	197	55	255	0.35	0.26	65.2**	45.4**	0.3*	0.26*	1.13	
2015	BP	192	76	261	0.30	0.24	61.3**	40.0**	0.29*	0.23*	1.26	
2016	BP	97	45	132	0.56	0.36	57.9**	38.1**	0.31*	0.24*	1.27	

**: P < 0.01, *: P < 0.05

Table 3 shows the best-fit models from the GLM analysis concerning the effects on the nestedness and modular structures in the networks over 12 years. The abundance of migrant birds had a strong positive effect on the Z-NODF and Z-WNODF, though fruit abundance had also weak effects. Whereas, none of the factors had positive effects on ZM or ZQ, as the coefficients were low and seemed ineffective. The bird abundance was positively correlated with the Z-NODF and Z-WNODF (Z-NODF: $R^2 = 0.49$, $P = 0.004$; Z-WNODF: $R^2 = 0.69$, $P = 0.0002$, logistic regression). In particular, the abundances of *T. pallidus* and *T. obscurus* were significantly correlated with the Z-NODF (*T. pallidus*: $R^2 = 0.61$, $P = 0.0028$; *T. obscurus*: $R^2 = 0.34$, $P = 0.048$) and Z-WNODF (*T. pallidus*: $R^2 = 0.62$, $P = 0.002$; *T. obscurus*: $R^2 = 0.42$, $P = 0.02$), whereas *Z. japonicus* had weak correlation (Z-NODF: $P = 0.2$; Z-WNODF: $R^2 = 0.37$, $P = 0.03$). Consequently, the nestedness structure was developed from the high abundance of the two *Turdus* species functioning as generalist dispersers, particularly in years when fruit abundance was low. Furthermore, the development of nestedness structures appears to induce the low levels of modular structures.

Table 3

The best-fit models from the generalized liner model (GLM) analysis concerning the effects on the nestedness and modular structures in the networks over 12 years. As predictor variables, the following values for the patterns of bird migration and fruit abundance were used: the captured number of migrant birds (bird abundance), number of fruiting trees (abundance of fruiting trees), number of mature fruits (abundance of fruits), and the first and second principal components of bird and plant communities in PCA. The models with the fewest AIC value were selected as the best model. Asterisk means significant effect.

Response variables				
	Nestedness		Modularity	
Predictor variables	Z-NODF	Z-WNODF	ZM	ZQ
Bird abundance	9.8**	25.4**	27.2	0.4
PC1 of bird communities	-1.6*	-3.3	-1.1*	-0.2*
PC2 of bird communities	0.4	-	-	-
Fruit abundance	2.0	5.1*	8.9	0.2
PC1 of plant communities	-0.6	-1.6*	-0.4*	-0.1
PC2 of plant communities	-	1.1*	0.1	-0.05
Bird abundance × fruit abundance	-	-	-1.7	-
Intercept	-61.5*	-141.6*	-137.9	-7.5*
AIC	43.6	64.5	16.7	6.6

**: P < 0.005, *: P < 0.05

Discussion

There are few studies in which the fluctuations in bird migration, plant fruiting, and bird dispersal network structures have been monitored for more than 10 years. Herrera (1998) reported on the dynamics among frugivorous birds, freshy-fruited plants, and bird dispersal systems over 12 years in a Mediterranean montane forest of southeastern Spain. The long-term data presented in the aforementioned study showed that fruit abundance fluctuated among years, depending on the amount of rainfall in early spring, though this fluctuation had weak effects on bird abundance and the properties of bird dispersal. The data outlined in the present study also revealed fluctuations in fruit abundance across years. However, this fluctuation exhibited a high periodicity with the number of fruiting trees, and number of mature fruits repeatedly fluctuated every other year. In addition, synchronization of fruiting among dominant plant

species was confirmed. The variable and synchronous production of fruits by plant populations (masting) has been observed in diverse forests (Kelly 1994; Kelly and Sork 2002). In some freshy-fruited plant species, the synchronization of fruiting among conspecific individuals has been reported. Fruit production in the northern highbush blueberry, *Vaccinium corymbosum*, has been shown to exhibit a two-year periodicity (Vander Kloet and Cabilio 1984). In *Rhus trichocarpa*, masting and non-masting years was confirmed in a western Japanese forest (Osada 2005). However, the synchronization of fruiting among heterospecific individuals is very rare (Herrera 1998). It is likely that the case found in the present study can be explained using a resource accumulation hypothesis (Kelly 1994); plants must build up sufficient reserves before an abundant fruiting episode. Many freshy-fruited plants in the study site may need more than one year to store resources for fruiting, with the result that they can only produce fruits every other year. Although the proximate mechanism is unclear, resources, physiological aspects, and environmental factors appear to regulate the fruiting timing of synchrony (Pearse et al. 2016), leading to a high periodicity of fruiting among heterospecific individuals.

The properties of migrant bird communities also differed remarkably across years. In seven years (FA and FP group), the species composition of migrants was related to fruit abundance, whereas bird abundance was low in the other five years (BP group), regardless of fruit abundance. The bird abundance in the BP group may have been determined by factors other than fruit abundance. Bird migration patterns are influenced by various conditions (Herrera 1998; Newton 2008). As one hypothesis, weather conditions seem to regulate bird abundance. Analysis of the weather data collected in Fukui prefecture (Japan meteorological Agency 2020) showed the average daily daylight hours in September was significantly shorter in the BP group years than in the FA and FP group years ($U=-2.1$. $P = 0.03$, Mann-Whitney U-test, Supplementary Fig. 5). In central Japan, September represents an early stage of migration. Therefore, it is possible that the migration route and movement timing of migratory bird assemblages are altered in years with many rainy and cloudy days in September. Thus, fruit and bird abundances per year may be affected by physiological and environmental factors, respectively.

The fluctuation in fruit and bird abundances was linked to the structures of the bird dispersal network. Over the 12 years, these fluctuations were highly nested, although they were also modular. Many mutualistic networks exhibit nested structures, as these can emerge as a consequence of an optimization principle aimed at maximizing the species abundance in mutualistic communities (Bascompte et al. 2003; Almeida-Neto et al. 2008; Bastolla et al. 2009; Suweis et al. 2013; Fontain 2013). Namely, nested network structures possess community-level stability or persistence. Therefore, it can be suggested that the bird dispersal network among migrant birds and freshy-fruited plants in the study site has been stable for 12 years. The network structure is strongly dependent on the abundance of migrant birds, particularly *T. pallidus* and *T. obscurus*. The genus *Turdus* is one of the representative frugivorous bird groups in the temperate zone (Ridley 1930). In the networks, *T. pallidus* and *T. obscurus* frequently interacted with dominant plants, forming the core component of nested structures. The genus also interacts with many other plants, functioning as generalist dispersers. Specifically, they dispersed seeds of even herbaceous and liana plants under conditions in which fruit abundance in woody plant communities is poor. The functions of *Turdus* species as generalist contribute to the development of nested structures in bird

dispersal network in the study site. It appears that they play an important role in highly diverse plant-frugivore networks (Bascompte and Jordano 2007; Bastolla et al. 2009; Palacio et al. 2016).

The generalist function of the two *Turdus* species may be due to the characteristics of foraging in *Turdus* species. In general, gape width directly constrains the range of fruit sizes that birds can forage (Wheelwright 1985; Jordano 2013). In the frugivores observed in the present study, the gape width of *Turdus* species was relatively larger than other species of the genus *Zosterops*, *Horornis*, *Tarsiger*, and *Ficedula*, making it possible for *Turdus* species to consume large-sized fruits that other species cannot forage. Many *Turdus* species also have various foraging modes, as they do not only forage on fruits on trees and shrubs but also forage on other organisms on the ground. Such a range of foraging behaviour allows *Turdus* species to behave as generalist dispersers. Contrary to the expectation, in years when fruit abundance was low (FP group), the nested structures of the networks were more developed, and the contribution of the two *Turdus* species to nestedness was also higher. Rather it was caused by the fact that the two *Turdus* species preferred fruits of a few plant species and modular structures in the networks were developed when fruit abundance was high (FA group). Moreover, they formed different modules in the networks, meaning that they prefer different fruit resources, even though they are closely-related and their morphological traits are similar. In some bird dispersal networks, frugivorous species exhibit functional specializations towards specific fruits, depending on the morphological traits of the fruits, changes in fruit abundance, and fruit availability (Carlo et al. 2003; Bender et al. 2018; Malanotte et al. 2019; Pires and Melo 2019). Probably, the higher fruit abundance and availability make it possible for the two *Turdus* species to utilize fruits more selectively. The various foraging behaviour strongly has affected the structures of bird dispersal networks in the study site.

Zosterops japonicus was also one of the main seed dispersers in the bird dispersal networks outlined in the present study, forming a core component of the nested structures within the networks. However, its interactions with plants were different from those of *Turdus* species. *Zosterops japonicus* frequently interacted with certain plant species regardless of fluctuations in fruit abundance across years. Specifically, modules including *Z. japonicus* and two plant species, *A. elata* and *Z. ailanthoides*, were constantly found in networks. In western Japanese sites, it has been reported that *Z. japonicas* is a major seed disperser of *A. elata* and *Z. ailanthoides* (Sato and Sakai 2004; 2006). As mentioned above, functional specializations of frugivorous birds towards specific fruits arise from many factors and determine the network structure. In the long-term observations of Herrea (1998), the structure of the bird dispersal network was determined by the strong preferences of two major dispersers, the Eurasian blackcap *Sylvia atricapilla* and the European robin *Erithacus rubecula* to certain fruit species, indicating the existence of modular structures within the network. In the present study, the function of *Z. japonicus* as a specialist disperser had less of an effect on the network structure than the functions of the two *Turdus* species did. However, its module was stably and independently constructed in the networks due to these specific interactions. The long-term bird dispersal networks in the studied site may be characterised by modular structures. It remains unclear why *Z. japonicus* prefers the fruits of *A. elata* and *Z. ailanthoides*. Possibly, the preference may be related to the foraging efficiency of *Z. japonicus* or to the nutritional composition of the fruits.

Conclusions

One of the most important components of community ecology is understanding which factors drive mutualistic interactions and the influences of these interactions on mutualistic networks. The present study showed that fluctuations in fruit and bird abundance across years determined the structures of bird dispersal networks among migrant birds and freshy-fruited plants. The abundance of birds fulfilling a 'generalist disperser' role had a strong effect on the construction of nested structures, though their functions were dependent on fluctuations in fruit abundance. Modular structures were also constructed as a result of species acting as specialist dispersers. Whether a species functions as a generalist or a specialist is determined by its specific foraging characteristics. The functions of other birds also should be considered. Particularly, the existence of specialists interacting with a subset of plants that also interact with generalist species is important in the formation of the nested structure. In the networks outlined in the present study, the Japanese Bush Warbler *Horornis diphone*, the Red-flanked bluetail *Tarsiger cyanurus*, and some *Turdus* species may play such roles. Furthermore, the structures and properties of networks are interconnected across years via interlayer links (Costa et al. 2020). The effects of bird and fruit abundance across years should be explored via a multilayer network approach.

Declarations

Conflict of interest statement

No potential conflicts of interest are disclosed.

Ethics approval

All applicable institutional and/or national guidelines for the capturing and use of animals were followed.

Availability of data and material

All data generated or analysed during this study are included in this published article and available from the corresponding author, K. Ohkawara, upon reasonable request.

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Figures

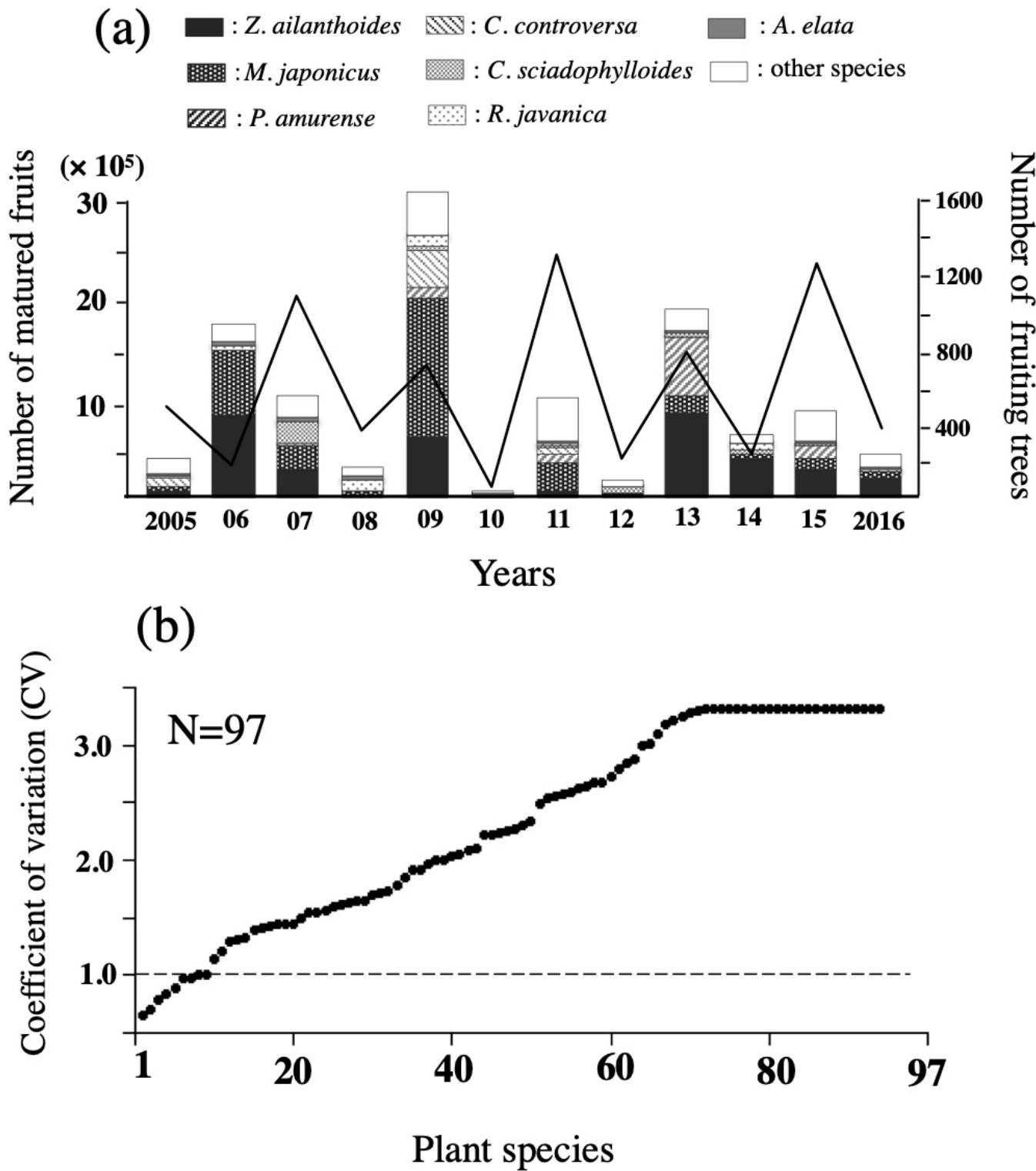


Figure 1

(A) Fluctuation of fruit abundance in freshly-fruited plant communities at the study site from 2005 to 2016. Bar graph shows the number and species composition of matured fruits. Line graph shows the number of fruiting trees. (B) Coefficients of variation (CV) of the fruit number in 97 plants observed in field census. X axis represents plant species arranged in an ascending order of the CV value.

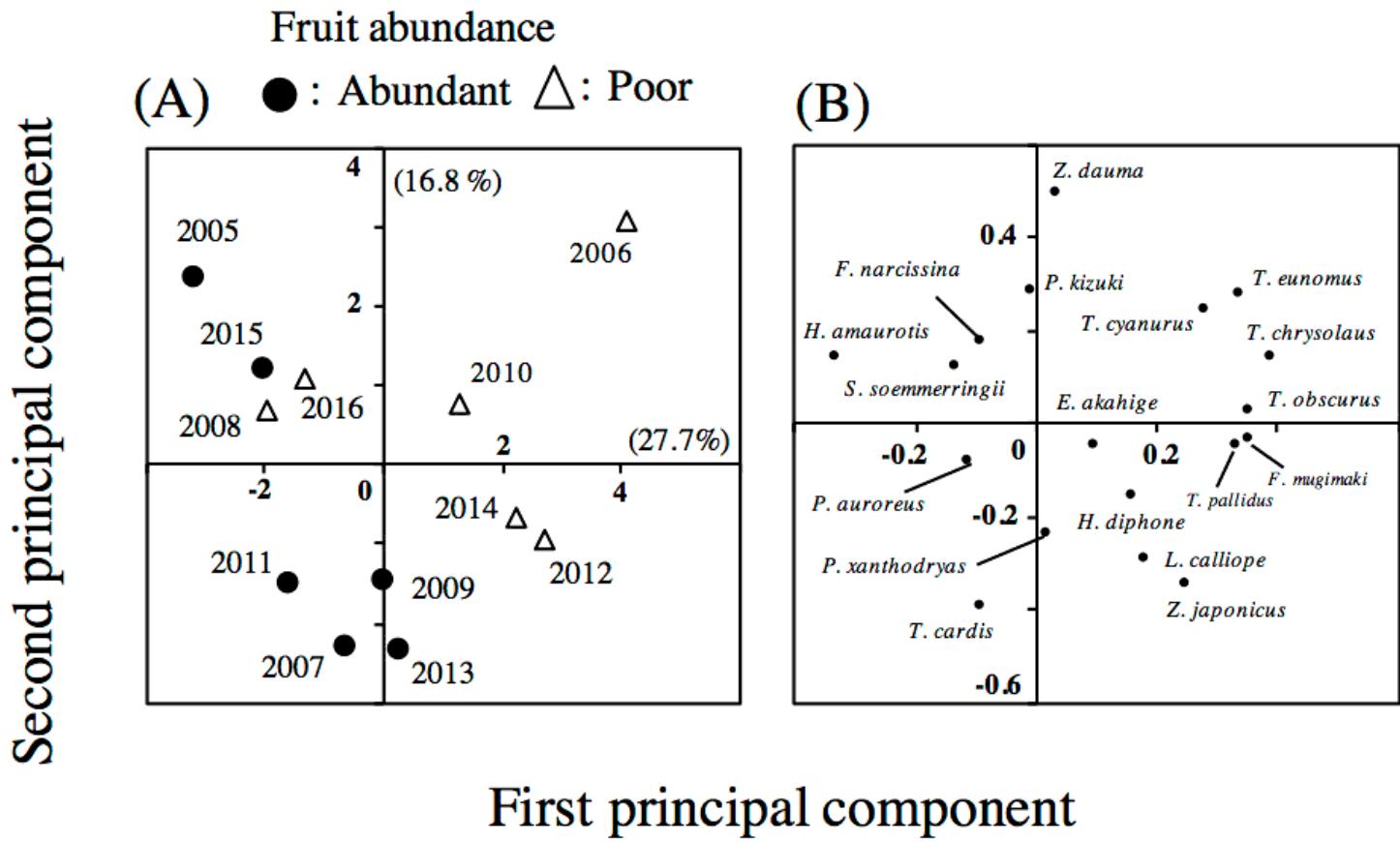
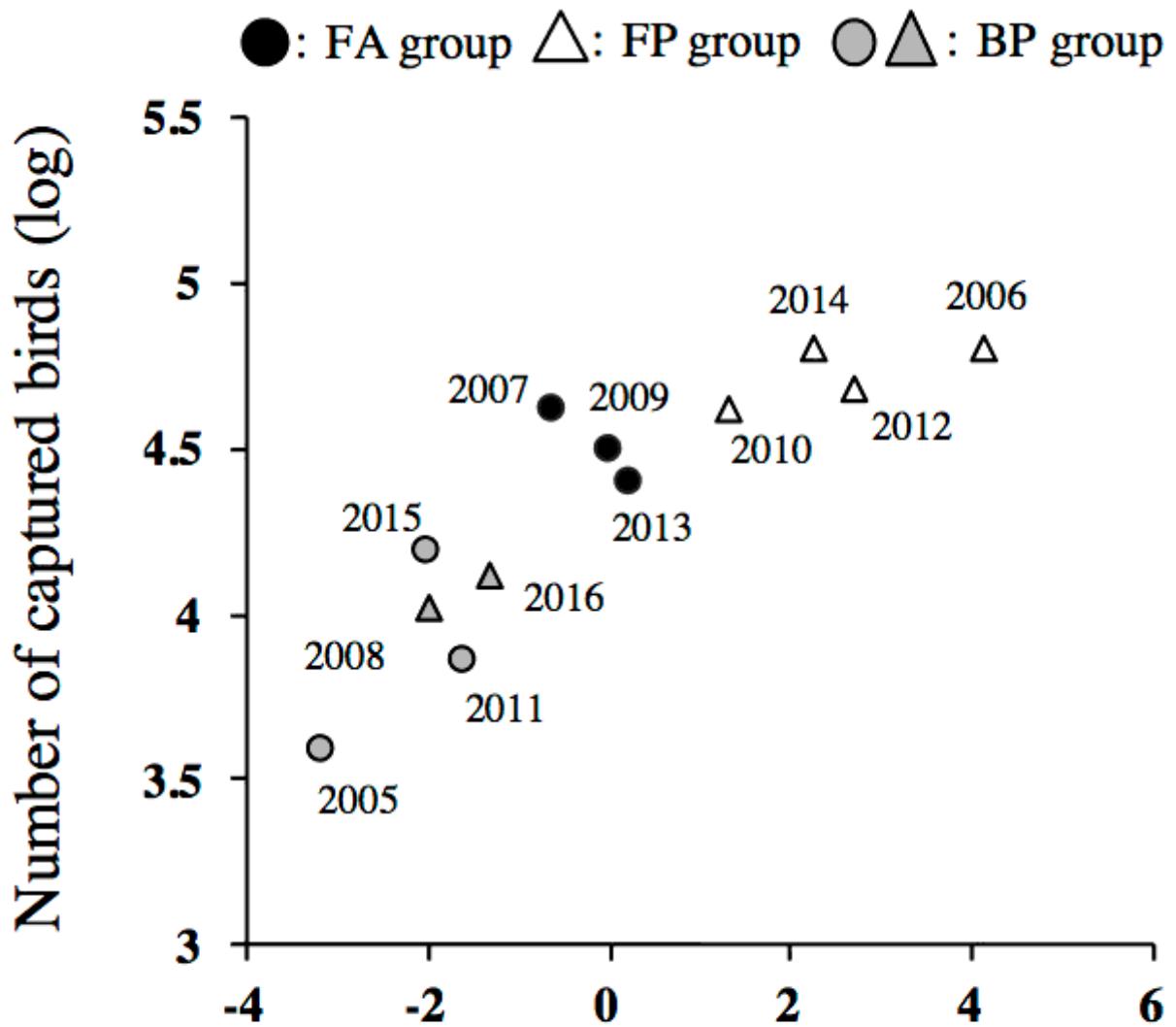


Figure 2

Biplots of principal component analysis (PCA) for the data of number and species composition of migrant frugivorous birds. (A) First and second principal components of ordinations of the bird communities. Black and white circle mean years when fruit abundance was high and low respectively. (B) The ordinations of bird species for the principal components.



First principal component in the classification of bird communities

Figure 3

Relationships between abundance of migrant birds and first principal components in PCA of migrant bird communities. The 12-year study period could be classified with three groups. The symbols mean the fruit abundance in each year, circle: abundant, triangle: poor.

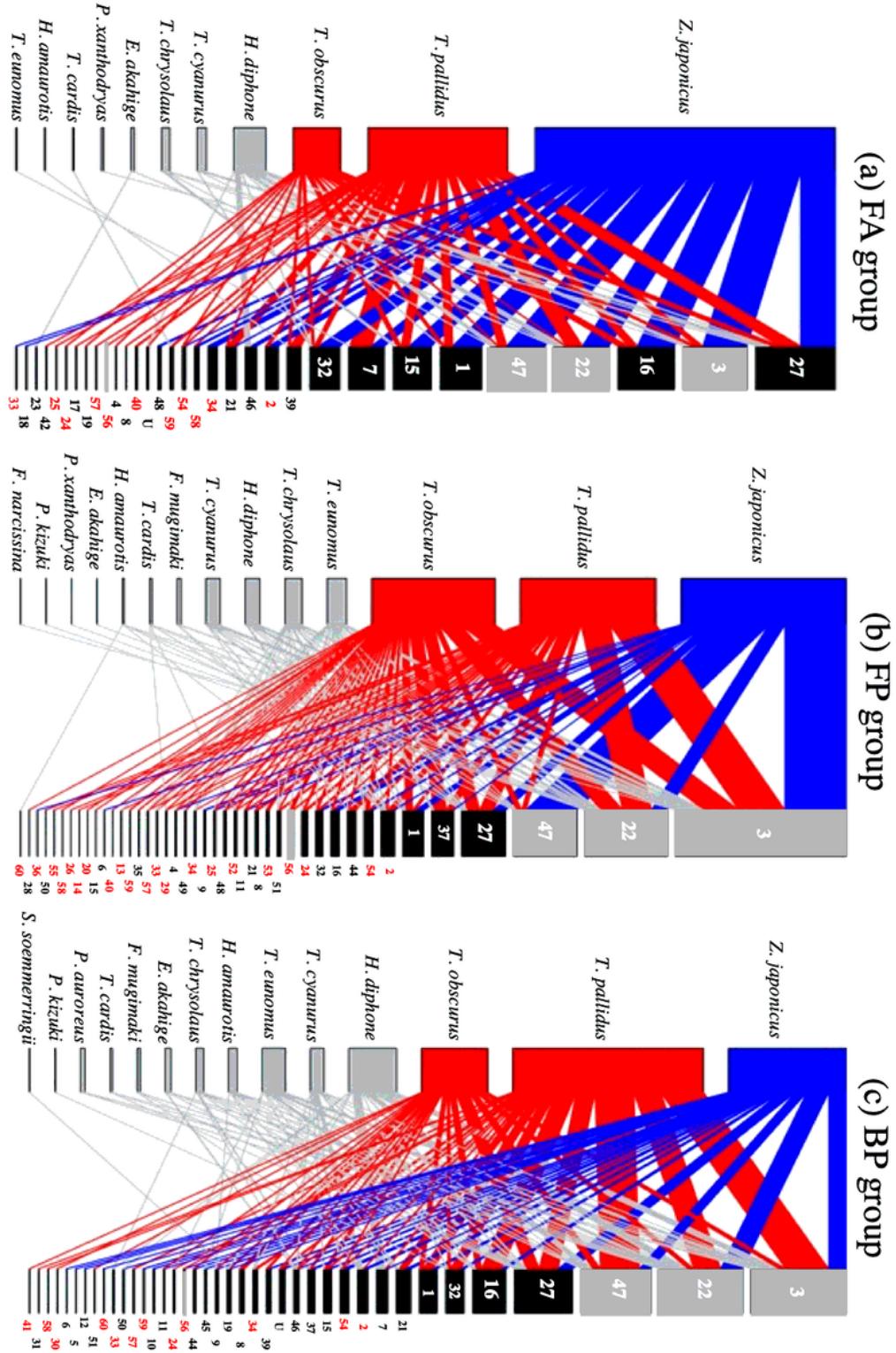


Figure 4

Seed dispersal networks among frugivores and plants in three groups, (A) FA, (B) FP and (C) BP group. The interaction data of each group was pooled. Numeral figures mean ID number of plants (Supplementary material Appendix 1 Table A2) and the red-colored number denotes herbaceous and liana species. Four plants colored background by light gray, *A. elata*, *E. japonica*, *A. glandulosa* and *Z. ailanthoides* (ID No 3, 22, 56 and 47) mean the species constantly produced fruits every year. The

interactions with three main dispersers, *T. pallidus*, *T. obscurus* and *Z. japonicus* are shown by the lines colored background by red and blue.

Supplementary Files

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