

Effects of temporal variation in community-level fruit abundance on seed dispersal by birds across woody species

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PREMISE OF THE STUDY: In animal-dispersed plants, seed dispersal patterns of the same species in the same habitat can greatly differ among individuals and temporally. Many studies have revealed the pervasive effects of spatial variation in fruit abundance on seed dispersal of individual plants. By contrast, very few studies have investigated the temporal variation in seed dispersal.

METHODS: We investigated the effects of conspecific and community-level fruit abundance on fruit removal rate and seed dispersal distance of six bird-dispersed woody species in a Japanese temperate forest for 3 yr. The six species share similar fruit characteristics but have different fruiting seasons. In addition, we also considered the effects of bird seasonality in diet and species composition on seed dispersal.

KEY RESULTS: Inter-annual and inter-seasonal variation in community-level fruit abundance determined both fruit removal and the seed dispersal distance across species, but the effect differed with seasonal changes in bird behavior. Abundant fruit satiated fruit removal by birds only during fruit-feeding periods, not during insect-feeding periods. A scarcity of fruit increased the dispersal distance, but only during the migratory period. This difference was probably due to the different foraging behaviors of passing migrants and territorial birds.

CONCLUSIONS: Our results illustrated that temporal variation in community-level fruit abundance could be a determining factor for seed dispersal in temperate forests. The effects of temporal variations in fruit abundance on seed dispersal patterns should be investigated in other ecosystems in order to understand their importance and associations with frugivore phenology.

KEY WORDS endozoochory; fleshy-fruited plant species; fruit abundance; fruit removal; Ogawa Forest Reserve; plant–animal interactions; seasonality; seed dispersal distance; temperate forest.

Seed dispersal is one of the few means of movement for plants. Among the various modes of seed dispersal, seed dispersal by fruit-eating animals (i.e., frugivores) is the commonest (e.g., Herrera, 2002). Because numerous factors can affect animal movement and consequently seed dispersal, the shadows of dispersed seeds in the same habitat can change depending on these factors.

Many field and theoretical studies have been focused on the factors that explain variation in seed dispersal between individuals within the same habitat, particularly the effect of spatial variation in fruit abundance (e.g., Manasse, 1983; Herrera, 1984; Sargent, 1990; Carlo, 2005). Fruit abundance affects seed dispersal by regulating frugivore abundance and their foraging behavior. High

fruit abundance in a habitat attracts frugivores from other habitats (Kinnaird et al., 1996; Hampe, 2008; Naoe et al., 2011), and the fruit removal rate will increase if frugivore satiation does not occur. High neighboring conspecific fruit abundance may increase the fruit removal rate by attracting more frugivores in a habitat (Sargent, 1990; Carlo, 2005) or decrease the fruit removal rate by satiating the frugivores (Manasse, 1983; Smith and McWilliams, 2014). Morales et al. (2012) reported that high neighboring conspecific fruit abundance also decreased seed dispersal distance, because frugivores did not travel long distances searching for fruit in such situations. Herrera et al. (2011) reported similar effects of fruit abundance of all fleshy-fruited woody species sharing frugivores (hereafter

“community-level fruit abundance”), although whether conspecific or community-level fruit abundance is more influential in seed dispersal remains unknown.

By contrast, few studies have investigated temporal variation in seed dispersal within a year or across years (Yamazaki et al., 2016). Fruit abundance, an important factor causing spatial variation in seed dispersal, may also be influential in temporal variation in seed dispersal. Fruit abundance in a habitat is known to exhibit seasonal and annual variation in many ecosystems. In temperate forests, fruit production is concentrated during autumn and winter (Thompson and Willson, 1979; Herrera, 1995; Noma and Yumoto, 1997); in seasonal tropical forests, fruit production is concentrated during the rainy season (Lieberman, 1982). Annual variation in fruit abundance arises because synchronous fruiting within and between species occurs intermittently (i.e., masting; Wheelwright, 1986b; Herrera, 1998; Sakai et al., 1999; Shibata et al., 2002). However, seasonal and/or annual variation in frugivore abundance in a forest may be much lower than seasonal and/or annual variation in fruit abundance, because frugivore abundance is limited by the ability to move between habitats and by breeding. Although frugivore abundance may fluctuate to some extent, several studies have reported a mismatch between temporal variation in fruit and frugivore abundance in a forest (Herrera, 1998; Hanya, 2005; but see Noma and Yumoto, 1997; Blendinger et al., 2012). In such cases, dispersal patterns may change between abundant and poor fruiting seasons and/or years. In fact, annual variations in fruit removal rate (Martínez et al., 2014) and seed dispersal distance (Martínez and González-Taboada, 2009; Yamazaki et al., 2016) were reported in temperate forests, and annual and/or seasonal variation in fruit abundance was suggested as possible factors. However, their discussions were based on simple comparison of seed dispersal results and fruit abundance among years and among seasons, and thus how and to what extent temporal variation in fruit abundance affects seed dispersal were not explicitly shown.

In addition to fruit abundance, frugivore species composition and diet also change seasonally, particularly in temperate regions (species composition: Thompson and Willson, 1979; Noma and Yumoto, 1997; Naoe et al., 2011; diet: Wheelwright, 1986b; Yui, 1988; Carnicer et al., 2009). Fruit requirements of frugivores and their foraging ranges often differ, exhibiting different fruit removal rates and seed dispersal distances (Dennis and Westcott, 2007; Jordano et al., 2007; McConkey and Brockelman, 2011). Even the same frugivore species may seasonally change their dependency on fruit in their diets (Wheelwright, 1986b; Yui, 1988). Therefore, the function of frugivores as seed dispersers should also change seasonally (Naoe et al., 2016). To understand temporal changes of seed dispersal patterns, the seasonal changes of frugivore species composition and diet should be considered, in addition to changes in fruit abundance.

In the present study, we investigated the factors that caused temporal change in seed dispersal of six bird-dispersed woody species with different fruiting seasons during 3 yr. Specifically, we asked the following three questions: (1) Does seed dispersal change within a year and/or across years depending on fruit abundance? (2) If so, is conspecific or community-level fruit abundance more important? (3) Do seasonal changes in bird species composition and diet affect seed dispersal? As indices of seed dispersal, we measured the fruit removal rate and seed dispersal distance. The fruit removal rate is a better index than the number of fruit removed for determining whether the fruit satiated the frugivores and indicates whether there is competition for seed dispersal within plant populations and

communities (Hampe, 2008). The seed dispersal distance is determined by frugivore foraging distances, which are likely to change with differences in fruit abundance. We hypothesized that the fruit removal rate and seed dispersal distance would be determined by temporal variation in fruit abundance.

MATERIALS AND METHODS

Study sites and species

The study was conducted in the Ogawa Forest Reserve (OFR, ~98 ha in area) in the southern Abukuma Mountains, Honshu, central Japan (36°56'N, 140°35'E; 610–660 m above sea level). The annual precipitation in the OFR is ~1910 mm, and the mean annual temperature is 10.7°C, with average monthly temperatures ranging from –0.9°C in January to 22.6°C in August, according to the data from a meteorological station in Ogawa (Moriguchi et al., 2002). The maximum snow depth in winter is ~50 cm.

The OFR has been preserved as an old-growth, cool-temperate, broad-leaved forest (Miyamoto and Sano, 2008) and contains 56 tree species, has a total basal area of 32.5 m²/ha, and contains trees ≥5 cm in diameter at breast height (DBH), with a density of 897 trees/ha (Masaki, 2002; Abe et al., 2008). The dominant woody species in the canopy layer are *Quercus serrata* Thunb., *Fagus japonica* Maxim, and *F. crenata* Blume (26.3%, 20.4%, and 8.5% of the community-level basal area, respectively). Fleshy-fruited woody species, which are dispersed by frugivores, are abundant in the OFR, occupying 12% of the community-level basal area and accounting for 43% of the total number of woody species. Disturbance associated with human activity, grazing, and fire plagued the forest until the 1930s (Suzuki, 2002). In the central part of the OFR, a 6 ha (200 × 300 m) permanent plot was established in 1987. All the stems in the plot with DBH ≥5 cm have been measured, tagged, and identified to species level (Masaki, 2002).

We selected the six most abundant fleshy-fruited woody species (*Swida controversa* (Hemsl.) Soják *Prunus verecunda* (Koidz.) Koehne, *Ilex macropoda* Miq., *Acanthopanax sciadophylloides* Franch. & Sav., *P. grayana* Maxim., and *Rhus ambigua* Lavallée ex Dippel in descending order of basal area) that fruited in 2006, 2007, and 2008. *Swida controversa* is the most dominant species and accounts for 32.0% of the total fleshy-fruited woody species in terms of basal area (Masaki et al., 1994). Ecological traits of the species are shown in Appendix S1 (see Supplemental Data with this article, Masaki et al., 2012; Mori et al., 2016). They have relatively similar fruit dimensions but different fruiting seasons (Fig. 1). At the study site, they share dispersers and are mainly dispersed by a common guild of frugivorous birds composed of permanent residents and migrants. Representative permanent residents are the brown-eared bulbul (*Hypsipetes amaurotis*) and the Japanese white-eye (*Zosterops japonicus*). Representative migrants are the narcissus flycatcher (*Ficedula narcissina*) and Naumann's thrush (*Turdus naumanni*). Seed dispersal of the target species by frugivorous mammals may be very limited at the site, because mammalian feces containing seeds are rarely found (Naoe et al., 2011).

Monitoring fruit abundance

To monitor fruit abundance and seed dispersal, seed traps were regularly set over the plot using the preexisting grid (20 m spacing;

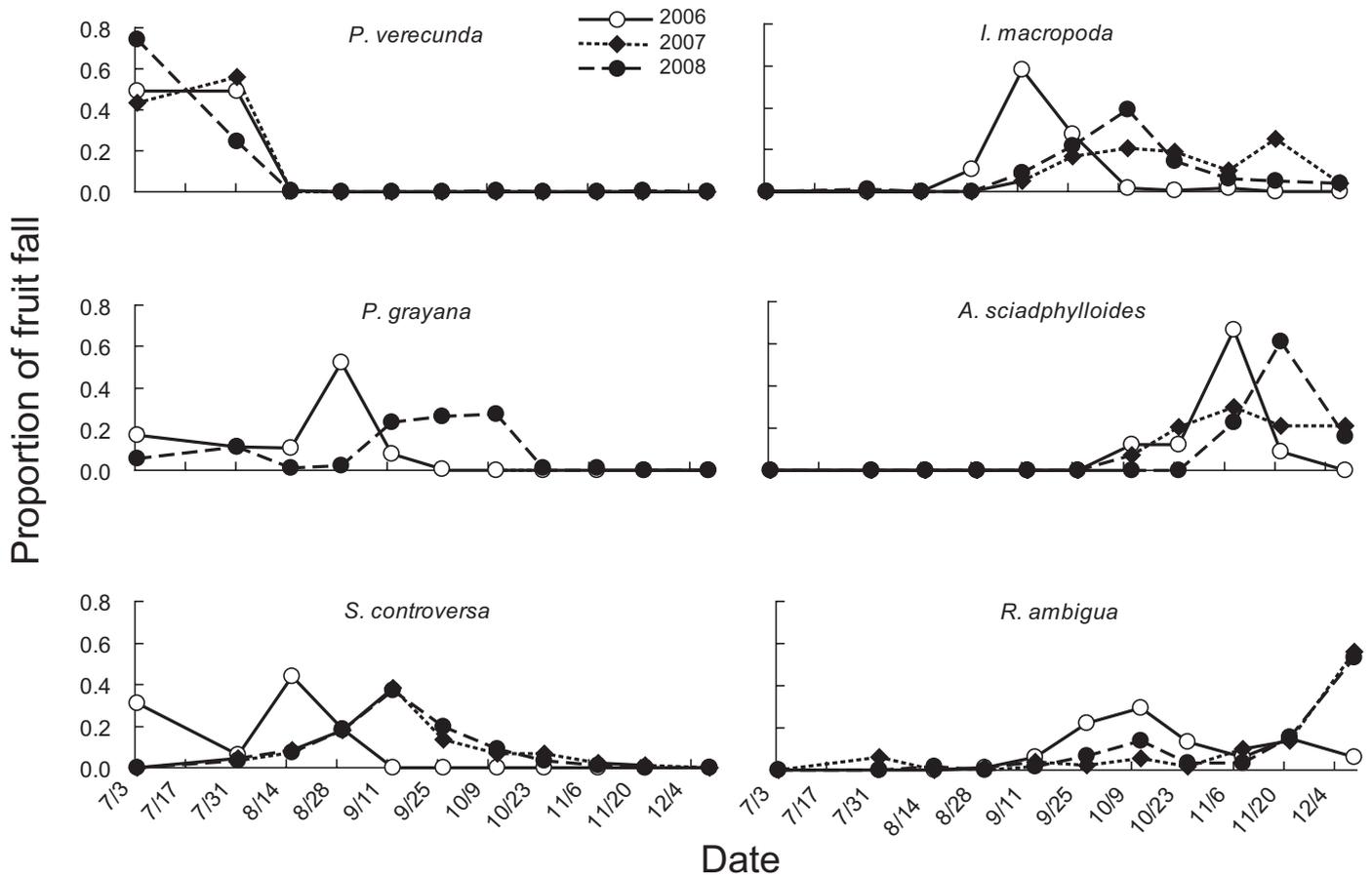


FIGURE 1. Seasonality in the fruit fall of each species, obtained by regular seed trap collections. The proportions of each season's fruit fall in 2006, 2007, and 2008 are shown. Please note that the actual census dates were not necessarily the same among the 3 yr: they may have differed by a few days (this is the same for Fig. 2 and Appendix S2).

see Masaki et al., 1992). Seed traps were placed at the grid intersections and in the center of each 20×20 m square (326 traps in total). The nearest inter-trap distance was ~ 14 m. Each trap had a surface area of 0.5 m^2 and was made of nylon cloth (1 mm mesh size). The traps were set 1 m above the ground to avoid seed predation by large Japanese field mice (*Apodemus speciosus*). Seeds from all fleshy-fruited woody species that fell into the traps were usually collected twice a month from June to December in 2006, 2007, and 2008. This period covers the entire fruiting season for all fleshy-fruited woody species, except mistletoe (*Viscum album* L.), which bears fruit during mid-winter. All the collected seeds were identified to species level. We excluded aborted and predated seeds from the analyses because of the difficulty in quantifying them. We estimate that predated seeds accounted for $\leq 5\%$ of total seeds produced (S. Naoe, personal observation). Pulpless seeds were considered to have been dispersed by birds, either by regurgitation or by defecation (Masaki et al., 1994; Hanya, 2005; Hampe, 2008). For community-level and conspecific fruit abundance, we used the number of fruit that had been removed or had naturally fallen during the fruiting season of focal species in the focal year. The fruiting season was defined as the period during which 90% of fruit of the focal species had fallen in each year, excluding periods when the first and the last 5% of fruit had fallen. This was because most of the early-fallen fruit were immature, and fruit remaining till the end of the season had dried up

and had not been removed by frugivorous birds, and thus including these fruit could have underestimated the effect of fruit abundance. The fruit production of each species was estimated by dividing the seed production (the sum of the naturally fallen and bird-dispersed seeds) by the number of seeds per fruit. In addition, conspecific and community-level fruit abundance in the forest was estimated on the basis of the number of calories the fruit contained, because this is considered a better indicator of food abundance for frugivores than the number of fruit counted (Peters et al., 2010). For each species, we multiplied the calorie content of the fruit pulp obtained from the literature (Masaki et al., 2012; T. Masaki, Forestry and Forest Products Research Institute, Japan, unpublished data) with the number of fruit caught in the seed traps. We could not estimate the calorie content of 0.1% of the obtained fruit because of a lack of calorific data for several species.

Monitoring frugivorous birds

To assess the abundance of frugivorous birds, six bird census sites (40×100 m) were set in the permanent plot in the OFR (for details, see Naoe et al., 2011). We sat at the center of each site and counted birds within the site, from July to December in 2006 and from June to December in 2007 and 2008. For each census, all the birds found at the census site (by sight or call) within 15 min were identified to

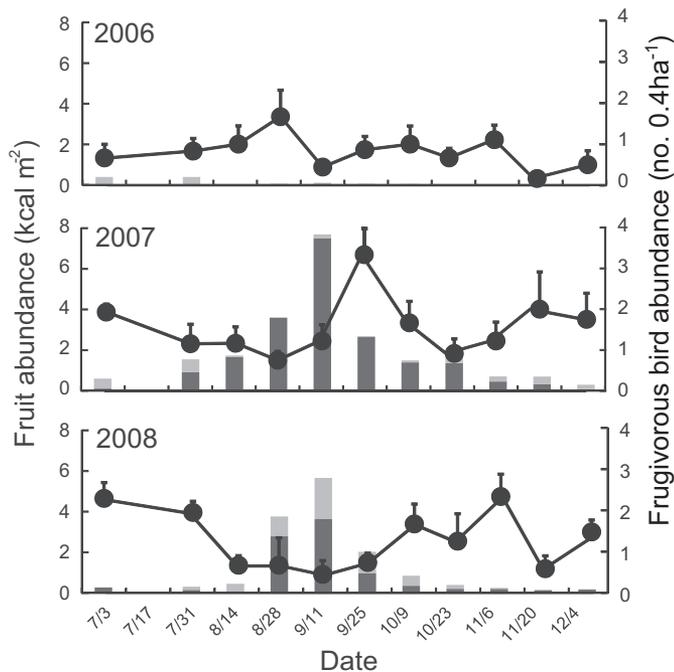


FIGURE 2. Seasonal changes in community-level fruit abundance and frugivorous bird abundance in 2006, 2007, and 2008. Bars indicate community-level fruit abundance (dark gray: *S. controversa*; light gray: the other fleshy-fruited woody species). Solid circles and bars indicate average \pm SE frugivorous bird abundance.

species level and recorded. Basically, three censuses were conducted (i.e., three census sites were visited) in a day during a period of 3.5 h after sunrise. A series of censuses was conducted 2–10 days/month (when permanent plots were visited to collect seeds) and was intensified during the bird migratory period, because temporal variations in bird abundance and species composition were assumed to be greater during the migratory period. We did not conduct surveys when rain, fog, or strong wind could interfere with detection. In total, 366 censuses were conducted. Bird species were considered to be seed dispersers if they frequently fed on fleshy fruit and did not damage the seeds (Kiyosu, 1966; Higuchi et al., 1996, 1997; Weir and Corlett, 2007).

Seasonality of frugivorous birds

To evaluate the effects of seasonal changes in frugivore species composition, we categorized migratory and nonmigratory periods depending on the presence or absence of passing migrants. Passing migrants were species that temporarily used the study site as a stopover during autumn and/or winter, from a few days to a few months. We identified passing migrants by referring to the literature (Takagawa et al., 2011) and by field observations. The abundance of passing migrants was apparently underestimated, because some individuals of bird species that were identified as non-passing migrants behaved as passing migrants (Higuchi et al., 1997), but these were not distinguishable from the other individuals. Passing migrants move longer distances for food than other species, because they are nonterritorial (Fukui, 1995; Taylor et al., 2011). Because passing migrants begin to arrive in the OFR in October (Appendix S2), we considered the period from October as the migratory period.

According to this classification, *P. verecunda* fruited in all years; *P. grayana*, *S. controversa*, and *I. macropoda* in 2006 fruited during the nonmigratory period; and *P. grayana* in 2008, *S. controversa* and *I. macropoda* in 2007 and 2008, and *R. ambigua* and *A. sciadophylloides* in all years fruited during the migratory period.

To evaluate the effects of seasonal changes on frugivore diet, we identified two components of frugivore diet seasonality. In temperate forests, particularly in deciduous forests, the main diet of frugivorous birds in spring is insects, because herbivorous insects are abundant in spring, when plant leafing and flowering occur (Wheelwright, 1986b; Yui, 1988; Carnicer et al., 2009). We defined the period May–July (when plant leafing and flowering are greatest at the study site; Kawarasaki and Hori, 2001; Shibata et al., 2002) as the insect-feeding period, and the period August–December as the fruit-feeding period. According to this classification, *P. verecunda* fruiting was determined to occur during the insect-feeding period and that of the other species during the fruit-feeding period.

Seed dispersal

To evaluate the fruit removal rate at the population level of each plant species in each year, we calculated the proportion of its bird-dispersed seeds to all seeds collected in the seed traps. We used species that produced >0.1 seeds m^{-2} in the focal year for the analysis; *P. grayana* in 2007 did not meet this criterion.

To evaluate seed dispersal distance at the population level, we estimated the seed dispersal kernel, which describes the change of bird-dispersed seed density with distance from a source tree, for each species in each year, and then the mean dispersal distance. The seed dispersal kernel and seed production comprise the seed shadow of a single source tree (i.e., the distribution of dispersed seeds from a source tree). Overlaps of seed shadows from each source tree form seed rain (i.e., the sum of the dispersed-seed distributions of each source tree), which is available from seed traps mentioned above. Therefore, we estimated seed shadows and consequently seed dispersal kernel on the basis of the locations and number of bird-dispersed seeds in the seed traps and the location of fruiting trees within the study plot, by employing a hierarchical Bayesian approach. We observed all the trees with DBH ≥ 5 cm in the 6 ha plot and with DBH ≥ 10 cm in the surrounding area (2.3 ha) to check whether they produced fruit or not in their beginning of fruit maturation over a period of 3 yr (see, e.g., Appendix S3). With regard to the vine species *R. ambigua*, the locations of the fruiting trees were unknown; therefore, the locations of the seed traps that collected naturally fallen fruit multiple times during the season were considered the locations of fruiting trees for this species. A hierarchical Bayesian approach considers the probability of seed arrival as a function of the distance from a fruiting tree and considers fecundity as a function of the sum of the bird-dispersed seeds within the traps near the fruiting tree (i.e., in a 20 m radius) and then calculates the expected seed rain into each trap. We regarded the seed rain into each trap as the sum of the contributions from every conspecific fruiting tree on the plot (as determined by their distance from the trap and their fecundity). We then identified the functions that produced the best fit to the observed seed rain. The seed dispersal kernel predicted that the seed density would decline monotonically with the distance from the fruiting tree. We considered all fruiting trees within a species to have the same dispersal kernel. The dispersal kernel we used was a bivariate Student's *t* (2Dt), which Clark et al. (1999) derived as a continuous mixture of Gaussian

densities, with the dispersal parameter distributed as an inverse χ^2 . This fits the dispersal data better than traditional exponential or Gaussian kernels and widely used for animal-dispersed woody species (e.g., Muller-Landau et al., 2008; Caughlin et al., 2015; but see Hardesty et al., 2006). We used the Markov chain Monte Carlo method (MCMC) to characterize the posterior distributions of the seed shadow parameter. To run the MCMC algorithm for model fitting, we used Stan (the Program R version 3.3.2 and the package “rstan” version 2.14.1; R Development Core Team, 2016; Stan Development Core Team, 2016). The sampling was implemented for every species. The uninformative prior was given automatically by Stan for each parameter (fully wide uniform distribution). We ran the MCMC algorithm for four independent chains of 10,000 iterations. In each chain, the first 5000 iterations were abandoned as a burn-in and the remaining chain of 5000 iterations was thinned every five steps, resulting in 1000 values per a chain sampled from the posterior. Finally, 4000 samples were obtained from four chains and were used to yield the posterior distributions and to summarize the parameters for every species. The model convergence was assessed using \hat{R} values (the Gelman–Rubin statistic); the \hat{R} values of all parameters were <1.002 , indicating that our model convergence was good (Gelman and Hill, 2007). Mean dispersal distance was estimated using the dispersal kernel. Mean seed dispersal distance can be affected by the tail end of dispersal kernel, so we estimated the mean seed dispersal distance using the dispersal kernel from 0 to 500 m in distance from seed sources, considering that small birds (i.e., <100 g in body weight), which all of the abundant frugivorous species in our study site are (Naoe et al., 2011), rarely disperse seeds over 500 m (Jordano et al., 2007; Yamazaki et al., 2016). We targeted the same species that were used for fruit removal rate.

Generalized linear mixed model analysis

To examine what factors influenced temporal variations in fruit removal across species, we conducted a generalized linear mixed model (GLMM) analysis with a log link and a negative binomial error. The number of fruit removed from each species in each year was the response variable of the model, and the number of fruit produced by the species was the offset variable. We used conspecific and community-level fruit abundance in the year, frugivore species composition seasonality (i.e., migratory vs. nonmigratory periods), and diet seasonality (i.e., insect-feeding vs. fruit-feeding periods) as the explanatory variables. Plant species identity was treated as a random effect. To examine the factors that influenced the seed dispersal distance across species, we used a GLMM with a log link and Gamma error. The mean seed dispersal distance of each species was the response variable of the model. Explanatory variables (conspecific and community-level fruit abundance in the year, frugivore species composition seasonality, diet seasonality), a random effect (plant species identity), and the model evaluation process (below) were the same as when we examined the factors influencing temporal variations in fruit removal.

We checked for multicollinearity among the four variables using a variance inflation factor (VIF), where $VIF >10$ is generally considered to indicate multicollinearity (Quinn and Keough, 2002). All the selected variables had $VIF <2.5$, which suggests that multicollinearity was not a serious concern. The fitted models were compared and hierarchically ordered using Akaike’s information criterion (AIC), a statistical method that rewards parsimony by penalizing the maximum likelihood for the number of model parameters

(Akaike, 1973). If the difference in the AIC between two models (ΔAIC) was <2 , they were considered equivalent (McCullagh and Nelder, 1989). Thus, if the AIC difference from best-fitting models was <2 , the support for the model was considered substantial and the model was accepted. The statistical analyses were performed using R 2.14 (R Development Core Team, 2011).

RESULTS

Annual and seasonal fluctuations in fruit abundance

Community-level fruit abundance exhibited very large annual and seasonal variation (Fig. 2). The coefficient of variation (CV) of community-level fruit abundance between years was 0.86, and CV between seasons was 1.49, 1.05, and 1.44 in 2006, 2007, 2008, respectively. The annual community-level fruit abundance was lowest in 2006 (1.13 kcal m⁻²), highest in 2007 (22.06), and intermediate in 2008 (13.77). The most important determinant of the annual variation was fruit abundance of *S. controversa*, which accounted for 1.5%, 87.2%, and 39.0% of the fruit abundance in 2006, 2007, and 2008, respectively (see also Appendix S1). The seasonal community-level fruit abundance was the highest in mid-September (Fig. 2), when most *S. controversa* fruit fall (Fig. 1).

Annual and seasonal fluctuations in frugivore abundance

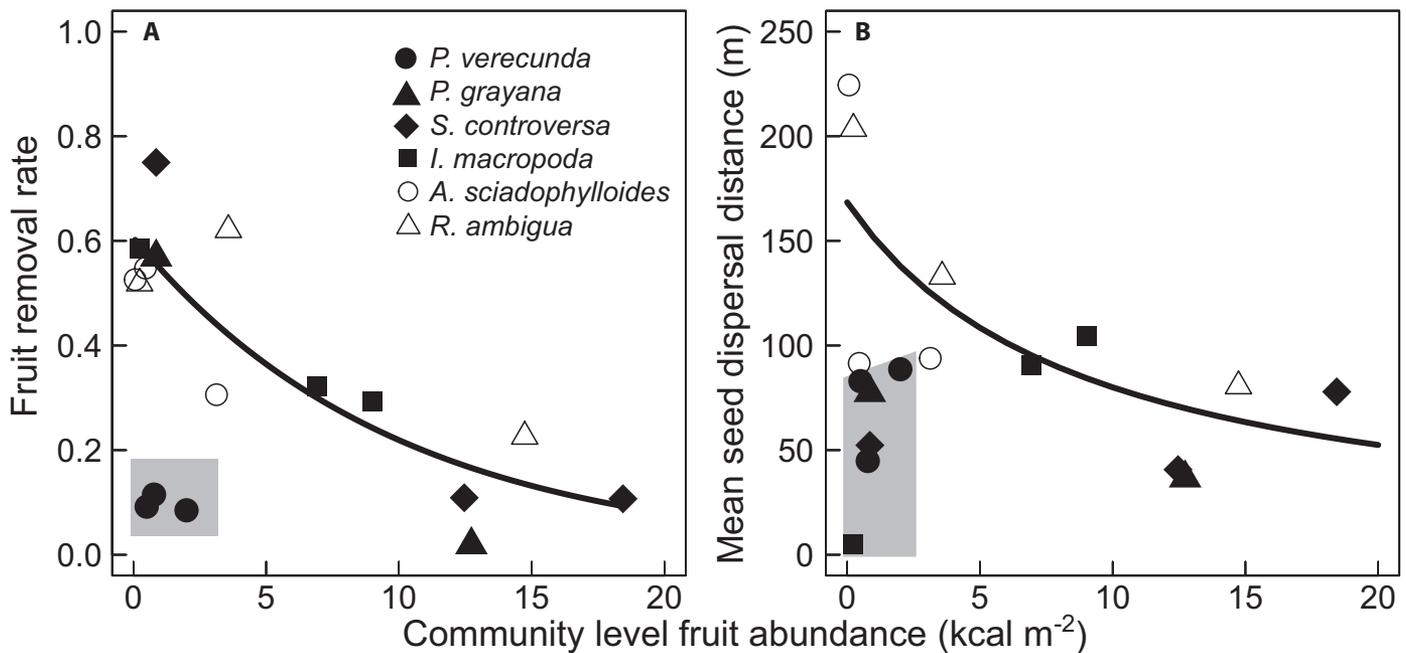
Annual frugivorous bird abundance positively corresponded with community-level fruit abundance to a certain degree—it was lowest in 2006 (mean = 0.81 individuals 0.4 ha⁻¹), highest in 2007 (1.56), and intermediate in 2008 (1.28) (Fig. 2). However, the annual variation in frugivorous bird abundance was much smaller than the variation in community-level fruit abundance, and the CV of frugivorous bird abundance between years was 0.31. There was a 20-fold difference in community-level fruit abundance between 2006 and 2007, whereas there was only a 2-fold difference in frugivorous bird abundance. There were no clear relationships between community-level fruit and frugivorous bird abundance in all years (Spearman correlation, 2006: $\rho = 0.089$, $S = 200.49$, $P = 0.7954$; 2007: $\rho = -0.4315$, $S = 314.93$, $P = 0.1851$; 2008: $\rho = -0.4335$, $S = 315.37$, $P = 0.1829$; Fig. 2). Seasonal variation in frugivorous bird abundance was much smaller than community-level fruit abundance, and CV between seasons was 0.49, 0.46, 0.55 in 2006, 2007, 2008, respectively. There was a 56-fold seasonal difference in community-level fruit abundance (mid-September vs. late November in 2008), whereas there was only a 5-fold difference in frugivorous bird abundance (mid-September vs. early November in 2008). The most abundant frugivorous bird was *H. amaurotis* (this species accounted for 37.5% of the frugivorous bird abundance), followed by *Z. japonicus* (27.8%), *T. naumanni* (7.3%), *F. narcissina* (6.0%), and *T. cardis* (4.8%); *H. amaurotis* and *Z. japonicas* are basically permanent residents; *F. narcissina* and *T. cardis* are summer birds; *T. naumanni* is a passing migrant.

Fruit removal rate

The effects of community-level fruit abundance and frugivore diet seasonality on the fruit removal rate were selected and significant in all best and competitive GLMMs as judged by AIC value (Table 1). Community-level fruit abundance was negatively associated with the fruit removal rate (Table 1 and Fig. 3A). The fruit removal rate of

TABLE 1. Results of best and competitive GLMMs to predict the fruit removal rate, including coefficients, standard errors (SE), and *P* values for each explanatory variable (*P* < 0.05 in bold).

	Explanatory variables				AIC	ΔAIC
	Community-level fruit abundance	Conspecific fruit abundance	Frugivore diet seasonality (insect-feeding vs. fruit-feeding periods)	Frugivore composition seasonality (migratory vs. nonmigratory periods)		
Best model					188.6	0.0
Coefficient	-0.1017		-1.7222			
SE	0.0308		0.4805			
Z	-3.3060		-3.5840			
<i>P</i>	0.0009		0.0003			
Competitive model 1					188.5	1.9
Coefficient	-0.0967		-1.8268	0.1661		
SE	0.0346		0.5915	0.5342		
Z	-2.7920		-3.0880	0.3110		
<i>P</i>	0.0052		0.0020	0.7559		
Competitive model 2					188.6	2.0
Coefficient	-0.1040	0.0046	-1.7290			
SE	0.0401	0.0512	0.4868			
Z	-2.5970	0.0890	-3.5520			
<i>P</i>	0.0094	0.9291	0.0004			
Null model					220.0	33.4

**FIGURE 3.** Relationship between seed dispersal and community-level fruit abundance. (A) Fruit removal rate. Symbols in gray area indicate species that fruit during the avian insect-feeding period. Solid line was estimated by GLMM for species that fruit during the avian fruit-feeding period. (B) Mean seed dispersal distance. Symbols in gray area indicate species that fruit during the avian nonmigratory period. Solid line was estimated by GLMM for plants that fruit during the avian migratory period.

P. verecunda, which produces fruit during the avian insect-feeding period, was lower than that of plants that produce fruit during the fruit-feeding seasonality (Fig. 3A).

Seed dispersal distance

The effects of community-level fruit abundance and frugivore species composition seasonality on mean seed dispersal distance

were selected and significant in all best and competitive GLMMs as judged by AIC value (Table 2). Community-level fruit abundance was negatively associated with mean seed dispersal distance (Table 2 and Fig. 3B). Mean seed dispersal distance of plants that produced fruit during the avian migratory period was longer than that of plants that produced fruit in the nonmigratory period (migratory period: 107.1 m; nonmigratory period: 58.5 m). Mean seed dispersal distance of *I. macropoda*, whose fruiting season

TABLE 2. Results of best and competitive GLMMs predicting mean seed dispersal distance, including coefficients, standard errors (SE), and *P* values for each explanatory variable (*P* < 0.05 in bold).

	Explanatory variables				AIC	ΔAIC
	Community-level fruit abundance	Conspecific fruit abundance	Frugivore diet seasonality (insect-feeding vs. fruit-feeding periods)	Frugivore composition seasonality (migratory vs. nonmigratory periods)		
Best model					185.2	0.0
Coefficient ^a	0.0007			0.0106		
SE	0.0003			0.0040		
Z	2.2300			2.6410		
<i>P</i>	0.0258			0.0083		
Competitive model 1					185.9	0.7
Coefficient ^a	0.0007		−0.0087	0.0159		
SE	0.0003		0.0077	0.0067		
Z	2.3250		−1.1230	2.3640		
<i>P</i>	0.0200		0.2613	0.0181		
Competitive model 2					186.9	1.7
Coefficient ^a	0.0008	−0.0003		0.0108		
SE	0.0004	0.0006		0.0040		
Z	2.0750	−0.6140		2.7200		
<i>P</i>	0.0380	0.5393		0.0065		
Null model					188.7	3.5

^aThe interpretation of a positive or a negative coefficient value is inverse in gamma distribution.

was extended to October when passing migrants arrived in the intermediate and abundant fruiting years, tended to increase as community-level fruit abundance increased (Fig. 3B). Mean seed dispersal distance of *A. sciadophylloides* and *R. ambigua*, whose fruiting seasons occurred when the passing migrants were present regardless of whether their fruiting seasons were extended or not, tended to decrease as community-level fruit abundance increased. Finally, *P. verecunda*, *P. grayana*, and *S. controversa* did not exhibit any clear pattern.

DISCUSSION

Our results indicate that temporal variation in community-level fruit abundance has an effect on the fruit removal rate and seed dispersal distance across species. The GLMM analyses indicated that the most important factors influencing the fruit removal rate of each species were community-level fruit abundance and frugivore diet seasonality. Removal rates decreased with increasing community-level fruit abundance; this was probably due to frugivore satiation, because frugivorous bird abundance changed in response to fruit abundance but with a much smaller amplitude (Fig. 2). An exception was the fruit removal rate of *P. verecunda*. Its removal rate was much lower than expected from community-level fruit abundance, although its fruit size and nutritional value are not remarkable compared to the other species, including the congeneric *P. grayana* (Masaki et al., 2012). Considering that *P. verecunda* produces fruit during the insect-feeding period when herbivorous insects are abundant, insects rather than fruit were likely to cause satiation of frugivorous birds and thus lower the removal rate of *P. verecunda*. Because of a negative association between community-level fruit abundance and the fruit removal rate, the timing of fruit fall in the intermediate (2008) and abundant fruiting years (2007) was later than that in the poor fruiting year (2006) in all focal species, except for *P. verecunda* (Fig. 1). Consequently, in the intermediate and abundant fruiting years, the fruit fall of *P. grayana*, *S.*

controversa, and *I. macropoda* continued until October, when the passing migrants arrived (Appendix S1).

The GLMM analysis showed that frugivore species composition seasonality and community-level fruit abundance are primary determinants of seed dispersal distance. Mean seed dispersal distance when passing migrants were present was much longer, compared to when passing migrants were absent. And when passing migrants were present, the mean seed dispersal distance decreased with community-level fruit abundance (Fig. 3B). This was likely due to differences in the foraging behavior between passing migrants and other birds (i.e., permanent residents and summer birds). When fruit abundance was low, passing migrants would travel long distances searching for fruit, whereas the foraging areas of permanent residents and summer birds would be limited irrespective of fruit abundance, because residents and summer birds tend to stay in their territories (Gill, 2006). The home range size of the most common resident frugivorous bird (*H. amaurotis*) is 1.00–2.61 ha (Fukui, 1995; Yamaguchi and Saito, 2009), and that of the second most common (*Z. japonica*) is 0.01–1.15 ha (Higuchi et al., 1997; Abe et al., 2011). These dimensions roughly correspond to our estimated seed dispersal distance in the nonmigratory period (mean = 58.5 m). Interestingly, in years of high fruit abundance, the extended fruiting period caused by frugivore satiation probably greatly increased the proportion of seeds dispersed by passing migrants in *I. macropoda*. Although we lack direct observation of birds feeding in the focal abundant fruiting years, direct observations of fruiting *I. macropoda* trees revealed that passing migrants accounted for ≥63.8% of removed fruit in another abundant fruiting year, 2011 (A. Nakajima, Tohoku University, Japan, unpublished data), whereas residents removed most fruit in the poor fruiting year, 2006 (S. Naoe, personal observation). Increased seed dispersal by passing migrants would result in longer dispersal distances in the years of high fruit abundance. To the best of our knowledge, this is the first study to report that frugivore satiation changes the species composition of seed dispersers, resulting in greater seed dispersal distances by extending the fruiting period.

Although the GLMM analysis detected an effect of community-level fruit abundance on fruit removal and seed dispersal distance, the effects of conspecific fruit abundance were much smaller. These results are surprising, because quite a few studies have shown an effect of conspecific fruit abundance on seed dispersal, whether focused spatially or temporally (spatial: Sargent, 1990; Blendinger et al., 2011; temporal: Prasad and Sukumar, 2010). We consider that this is due to the differences in the dominance of target species. While we targeted six species of different dominance, previous studies have targeted a single dominant or common plant species. If the target plant species is dominant, as was *S. controversa* in our study, the conspecific fruit abundance should be comparable or almost identical to the community-level fruit abundance; therefore, seed dispersal could have been explained by the target species. Because the conspecific fruit abundance of low-density species was very low compared to the community-level fruit abundance, it would not affect frugivore behavior and abundance, and thus the resulting seed dispersal. Therefore, for low-density species, it is probably essential to evaluate community-level fruit abundance in order to understand their seed dispersal patterns.

We found that temporal variation in community-level fruit abundance had a strong effect on the fruit removal rate and seed dispersal distance across species, and that the significance of the effect changed with the phenology of the frugivores (i.e., seasonal variation in frugivore diet and species composition). Is large temporal variation in fruit abundance, as we observed, common in other geographic regions? One may assume that, in general, fleshy-fruited plants exhibit less temporal variation in fruit production compared with other plants, because a large number of fruit may satiate seed dispersers and decrease the seed removal rate (Kelly and Sork, 2002). However, mass fruiting habits in fleshy-fruited plants, probably associated with fluctuations in abiotic and biotic environmental factors, have been frequently observed (e.g., Herrera, 1998; Shibata et al., 2002; Norden et al., 2007; Prasad and Sukumar, 2010). Seasonal and annual variations in fruit abundance have been reported in various regions of the world (Thompson and Willson, 1979; Wheelwright, 1986a; van Schaik et al., 1993; Herrera, 1998; Sakai et al., 1999; Shibata et al., 2002). However, differences in the importance of the phenology of frugivorous birds among regions may exist. Seasonal changes in the diets and species compositions of frugivorous birds may vary among regions and may be relatively small in tropical rainforests. The effects of temporal variation in community-level fruit abundance on seed dispersal patterns in other ecosystems should be investigated to understand their importance and their association with frugivore phenology.

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DATA ACCESSIBILITY

Please see data in Appendix S4 for seasonality in the fruit fall of each species, S5 for seasonal changes in community-level fruit abundance and frugivorous bird abundance, and S6 for analyzing the relationship between seed dispersal and conspecific and/or community-level fruit abundance.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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