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Impact of the spatial uncertainty of seed dispersal on tree colonization dynamics in a temperate forest

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An aggregated distribution of dispersed seeds may influence the colonization process in tree communities via inflated spatial uncertainty. To evaluate this possibility, we studied 10 tree species in a temperate forest: one primarily barochorous, six anemochorous and two endozoochorous species. A statistical model was developed by combining an empirical seed dispersal kernel with a gamma distribution of seedfall density, with parameters that vary with distance. In the probability density, the fitted models showed that seeds of Fagaceae (primarily barochorous) and Betulaceae (anemochorous) were disseminated locally (i.e. within 60 m of a mother tree), whereas seeds of *Acer* (anemochorous) and endozoochorous species were transported farther. Greater fecundity compensated for the lower probability of seed dispersal over long distances for some species. Spatial uncertainty in seedfall density was much greater within 60 m of a mother tree than farther away, irrespective of dispersal mode, suggesting that seed dispersal is particularly aggregated in the vicinity of mother trees. Simulation results suggested that such seed dispersal patterns could lead to sites in the vicinity of a tree being occupied by other species that disperse seeds from far away. We speculate that this process could promote coexistence by making the colonization rates of the species more similar on average and equalizing species fitness in this temperate forest community.

Keywords: aggregated dispersal, anemochory, barochory, endozoochory, Ogawa Forest Reserve, seed dispersal kernel, stochastic process

Introduction

The process that determines which species will colonizes a vacant space in communities of sessile organisms is often stochastic and can influences the species assembly (Hubbell 2001, Kitagawa et al. 2017). In a tropical forest with low seasonality and largely asynchronous seed production among species, a newly created vacant site will likely be colonized by a species that happens to produce and disperse seeds at that time, and this stochastic process may have important effects on the colonization rates of

various species (Usinowicz et al. 2017). In temperate forests, by contrast, seed production tends to synchronize among tree species within a year, and even among years (Shibata et al. 2002, Usinowicz et al. 2017), suggesting that temporal stochasticity of seed production has a smaller impact than in tropical forests. Instead, the spatial stochasticity of seed dispersal may have more important effects on specific colonization rates in temperate forests. For example, in an undulating temperate forest, Masaki et al. (2015) showed that habitat preferences were nearly identical among most species at the colonizing stage (i.e. environmental homogeneity in terms of seedling recruitment). Therefore, future studies should address the spatial uncertainty associated with seed dispersal, including whether simultaneously dispersed seeds from multiple species in a temperate forest display aggregated patterns, and which species reach a vacant site in the absence of environmental heterogeneity.

In this study, we examined seed dispersal patterns in a temperate forest focusing on spatial uncertainty. If the seed density near the mother tree shows strong spatial variation, sites without its offspring arise, which can be colonized by chance by seeds from other species. To evaluate the likelihood of such stochastic colonization dynamics, it is necessary to determine whether spatial uncertainty occurs in the seed dispersal process, which would potentially provide opportunities for all species to recruit in the vicinity of heterospecific reproductive trees.

Spatial uncertainty in seed dispersal can be considered from three main viewpoints. The first is based on interspecific differences in seed dispersal patterns. In general, seed dispersal patterns differ among the species in a community (Clark et al. 1999, Muller-Landau et al. 2008). To quantify these interspecific differences, a systematic approach using functions that describe dispersal kernels for comparisons of seed dispersal patterns is helpful (Clark et al. 1999, Muller-Landau et al. 2008, Bullock et al. 2017, García et al. 2017). Seeds are transported through several modes. Common seed transport modes for trees include falling naturally (primarily barochory; depending on the species, this is often followed by synzoochory), being carried by wind (anemochory), and travelling within the gut of a moving vertebrate (endozoochory). Although these modes have different mechanisms, the resulting seedfall patterns can be described using a probability density function of the distance from a seed source (i.e. a mother tree), referred to as a dispersal kernel. By fitting a versatile function to observed seedfall distributions, we can quantitatively compare seed dispersal patterns among species (Muller-Landau et al. 2008, Bullock et al. 2017) without fitting specific mechanistic models to particular dispersal modes (e.g. Trakhtenbrot et al. 2014 for anemochory).

The second viewpoint is based on the implications of the absolute number of seeds dispersed. The outcome of competition among species depends strongly on the number of individuals of each species in a location. Even when the probability density of seedfall for a species is lower than that for a second species at the same location, the first species may

have a numerical advantage if its fecundity is greater than that of second species (Tanaka et al. 1997). If interspecies differences in the probability density functions of seed dispersal are offset by variation in fecundity among species, different species might have similar absolute densities of seed dispersal.

The third viewpoint involves aggregated seed dispersal (Schupp et al. 2002, Wright et al. 2016), and is most relevant to this study. Most previous research estimated the parameters of dispersal kernels assuming a Poisson distribution of seeds at a given distance (Martínez and González-Taboada 2009) wherein two parameters, the mean and the variance, are of equal value. However, if aggregated seed dispersal is pervasive, these two parameters should have different values (i.e. overdispersion). In such cases, we must assume other probability distributions, such as a negative binomial distribution (Muller-Landau et al. 2008, Martínez and González-Taboada 2009).

To our knowledge, no studies have accounted for all of these viewpoints. Furthermore, some studies using probability distributions with high spatial variation, such as the negative binomial distribution, have assumed that parameters related to aggregation are constant (Muller-Landau et al. 2008, Jansen et al. 2014), but these factors may vary with the distance from the mother tree. For instance, birds that travel long distances after collecting fruit might cause different seedfall patterns than birds that move within a small area. Thus, we must expand seed dispersal models to relax such assumptions and better evaluate the spatial uncertainty in seed dispersal patterns.

This study examined how spatial uncertainty in the seed dispersal leads to variation in colonization rates among species. We analyzed the seedfall data for 10 tree species in an old-growth temperate deciduous forest, including two primarily barochorous species, six anemochorous species and two endozoochorous species. We fit dispersal kernels to these data to estimate the probability distributions of seed dispersal distance as well as the total number of seeds dispersed for each mother tree (i.e. fecundity). In this fitting, we mixed a gamma distribution with spatially variable parameters and a Poisson distribution to evaluate the degree of aggregation in seed dispersal. Based on these estimates, dispersal patterns were compared quantitatively among the 10 species, and local competition among species was evaluated in terms of the number of seeds arriving at a location.

Specifically, the following questions related to the three viewpoints were assessed. 1) Is dispersal distance greatest for endozoochorous species, moderate for anemochorous species, and smallest for primarily barochorous species? 2) Is the numerical superiority of any species in terms of the seedfall probability density at a given distance regularly undermined by fecundity differences among species? 3) Does seedfall of endozoochorous species show greater spatial variation (i.e. aggregation) at a given distance from a conspecific mother tree than that of other species, reflecting the complex movement of frugivorous vertebrates? After answering these questions and conducting simple simulations, the impacts of

uncertainty in seed dispersal on colonization dynamics were evaluated for a temperate forest with a greater degree of synchrony in seed production than exhibited in tropical forests among years and among species.

Methods

Study sites

The study was conducted in a 6 ha plot (300 × 200 m²) in Ogawa Forest Reserve, Japan, which was established in a hilly forest area in 1987 (36°56′N, 140°35′E, 610 m a.s.l.). The study site is an old-growth temperate deciduous forest where anthropogenic disturbances have been rare for at least 100 years. The site is characterized by microtopography (Supplementary material Appendix 1 Fig. A1), but soil is not eroding and the stand has continuously been covered with a developed canopy (Tanaka and Nakashizuka 1997). The dominant species in terms of basal area in the 6 ha plot are *Quercus serrata*, *Fagus japonica* and *Fagus crenata* (Masaki et al. 1992). Within the plot, approximately 60 woody species are present with stem diameters at breast height >5 cm (Masaki et al. 1992). Nakashizuka et al. (1992) and Masaki et al. (2015) provided general information about species composition and tree population structure and dynamics. For endozoochorous species, the main seed-dispersing vertebrates are avian species such as the Japanese white-eye *Zosterops japonicas* and brown-eared bulbul *Hypsipetes amaurotis* (Naoe et al. 2011). Large mammals that climb trees and disperse seeds, such as the macaque *Macaca fuscata* and black bear *Ursus thibetanus*, are presently very rare or absent in this forest (Masaki et al. 2012).

Field methods

We selected 10 species of Betulaceae (four species), Fagaceae (two species), Rosaceae (one species), Sapindaceae (two species) and Cornaceae (one species) for which we were able to sample sufficient number of seeds (Table 1). These species disperse seeds in late summer to autumn, except for *Cerasus*, which disperses seeds in early to mid-summer. We used seed traps to measure seedfall of these species. A funnel-shaped trap made of 2 mm mesh polyethylene cloth (circular receiving face of 0.5 m² and 70 cm in depth) was held in place by three pipes, with its receiving face about 1 m above the ground (Supplementary material Appendix 1 Fig. A2).

The year and amount of effort expended for data acquisition differed among seed dispersal modes. Barochorous (Fagaceae) and anemochorous (Betulaceae and Sapindaceae) species were studied in 1988 in a 1 ha plot (100 × 100 m²) within the 6 ha plot. In total, 221 seed traps were set up within the 1 ha plot in a grid with an inter-trap distance of 7.1 m (Supplementary material Appendix 1 Fig. A1). Endozoochorous (Rosaceae and Cornaceae) species were studied within the entire 6 ha plot (Supplementary material Appendix 1 Fig. A1) because one of the primary endozoochorous species, *Cerasus leveilleana*, was found mostly outside the 1 ha plot, and its dispersal distances were likely too great to investigate in a 1 ha plot (Yamazaki et al. 2016). In 2007, 326 seed traps were deployed within the 6 ha plot in a grid with an inter-trap distance of 14.1 m (Supplementary material Appendix 1 Fig. A1, A2).

During the fruiting seasons of 1988 (1 ha plot only) and 2007 (entire 6 ha plot), litter, fruits and seeds were retrieved from the seed traps every two weeks, and apparently sound (i.e. mature with no signs of insect damage) seeds (anatomically, the diaspores of some species are fruits, but for convenience we refer to them as 'seeds') were extracted, counted and summed over the fruiting season for each trap. Immature seeds and those with signs of predation were excluded from the sample. For *Cerasus leveilleana* and *Cornus controversa*, only seeds without fleshy parts (anatomically, the exocarp and mesocarp) were analyzed; we assumed that these were disseminated by frugivores. Seeds of these species with an intact exocarp and mesocarp were found within 10 m of conspecific (presumably mother) trees, where seed and seedling mortality were much greater than elsewhere (Masaki et al. 1998,

Table 1. Information on the species investigated in this study related to dispersal mode and sampling methods. The number of mother trees includes those living in the outer margin (20 m width) of the study areas for some species (see Supplementary material Appendix 1 Fig. A1 for details). The nomenclature follows the BG plants Japanese–Scientific name index (YList; <http://ylist.info>) of Yonekura and Kajita (2003). The range of distance is the maximum distance between the traps and mother trees for each species. The total number of seeds retrieved is the number of seeds collected for each species over the entire dispersal season for the study year.

Species	Abbreviation	Primary dispesal mode	Seedfall season	Data year	Area (ha)	No. of trap	No. of mother trees	Range of distance (m)	Total no. of seeds retrieved
Betula grossa	*B.g.*	anemochory	Sep–Nov	1988	1.0	221	8	187.9	10 838
Carpinus cordata	*Ca.c.*	anemochory	Sep–Nov	1988	1.0	221	17	184.7	5054
Carpinus japonica	*Ca.j.*	anemochory	Oct–Nov	1988	1.0	221	5	139.3	3653
Carpinus laxiflora	*Ca.l.*	anemochory	Oct–Nov	1988	1.0	221	18	139.7	9279
Fagus japonica	*F.j.*	barochory	Oct–Nov	1988	1.0	221	14	111.0	42 936
Quercus serrata	*Q.s.*	barochory	Sep–Oct	1988	1.0	221	14	130.1	1248
Cerasus leveilleana	*Ce.l.*	endozoochory	Jun–Jul	2007	6.0	326	22	351.7	219
Acer amoenum	*A.a.*	anemochory	Sep–Nov	1988	1.0	221	5	127.8	2426
Acer pictum	*A.p.*	anemochory	Oct–Nov	1988	1.0	221	6	137.9	14 549
Cornus controversa	*Co.c.*	endozoochory	Aug–Oct	2007	6.0	326	39	349.9	1975

Masaki and Nakashizuka 2002), and we excluded these non-dispersed seeds from further analysis. We sampled more than 1000 seeds of each species, except for *Cerasus leveilleana* in 2007 (approximately 200 seeds). In both 1988 and 2007, these species produced more fruits than in an average year (Shibata et al. 2002, S. Naoe unpubl.), suggesting that seeds from these years were likely to contribute to substantial recruitment of each species into the community.

During the seed-trap sampling periods, mature trees of the target species were visually assessed for fruiting within the focal plot (1 ha or 6 ha) and a surrounding margin of 20 m width if necessary (Supplementary material Appendix 1 Fig. A1), and fruiting trees were considered candidate seed sources. The locations of these candidate trees were mapped, and the distance was calculated between each trap and a centroid of the projected crown of each candidate tree. For the barochorous and anemochorous species studied in the 1 ha plot, these distances were no more than ca 190 m, and for the endozoochorous species studied in the 6 ha plot, they were no more than ca 350 m (Table 1).

Hierarchical model and parameter estimation

We used the 2Dt function introduced by Clark et al. (1999), which includes species-specific parameters (a shape parameter, p, and a scale parameter, u) and is formulated as:

$$f(r) = \frac{p}{\pi u \left[1 + \frac{r^2}{u}\right]^{p+1}} \tag{1}$$

where r and $f(r)$ represent the distance from a mother tree and probability density of seedfall (i.e. relative seedfall density) at that distance, respectively. The expected mean number of seeds retrieved from the i-th trap (μ_i) is calculated using the following equation:

$$\mu_i = A_i \sum_{j=1}^{n} F_j f(r_{ij}) \tag{2}$$

where A_i, F_j and r_{ij} represent the area of the i-th seed trap (0.5 m² for any trap), the number of seeds produced by the j-th mother tree, and the distance between the i-th trap and j-th mother tree, respectively.

The parameters p, u and F_j can be estimated using the statistical model:

$$N_i \sim \text{Poisson}(\mu_i) \tag{3}$$

where N_i represents the observed number of seeds in the i-th trap. We refer to Eq. 3 as the Poisson model. In this model (as well as those described below), fecundities (F_j) were estimated as an unknown parameter for each tree, not as a function of diameter at breast height (DBH). This procedure was used because the DBH of some trees located outside of the 6 ha plot was not measured and because some trees had smaller crowns (and consequently lower seed production)

than predicted from their DBH due to breaking of large branches.

To evaluate overdispersion, we expanded this model hierarchically by adding a gamma distribution with mean value of μ_i and a fixed shape parameter k. The expected number of seeds in the i-th trap (ν_i) was assumed to be a random draw from this gamma distribution, while N_i was assumed to be a random draw from a Poisson distribution with ν_i as the event rate parameter:

$$\nu_i \sim \Gamma(k, k/\mu_i) \tag{4}$$

$$N_i \sim \text{Poisson}(\nu_i) \tag{5}$$

The parameters p, u, k, F_j and ν_i were estimated. We refer to this model as the Poisson and parameter-fixed gamma mixture model.

In preliminary analyses, we found a linear relationship on a log–log scale between the mean seedfall density and its variance in terms of the distance from a focal trap to the nearest seed source tree for all tree species tested (Supplementary material Appendix 1 Fig. A3), suggesting that the parameters of the gamma distribution were variable. Based on this empirical finding, we assumed that variance in the number of seeds at the i-th trap (σ_i^2) was represented by a power function:

$$\sigma_i^2 = a\mu_i^b \tag{6}$$

In this equation, the parameters a and b are species-specific unknown parameters. Using μ_i and σ_i^2, the shape parameter α_i and the rate parameter β_i of a gamma distribution at the i-th trap was calculated with the following equations:

$$\alpha_i = \mu_i^2 / \sigma_i^2 \tag{7}$$

$$\beta_i = \mu_i / \sigma_i^2 \tag{8}$$

Then the expected number of seeds in the i-th trap (λ_i) was assumed to be a random draw from the gamma distribution including the above parameters, while N_i was assumed to be a random draw from a Poisson distribution with λ_i as the event rate parameter:

$$\lambda_i \sim \Gamma(\alpha_i, \beta_i) \tag{9}$$

$$N_i \sim \text{Poisson}(\lambda_i) \tag{10}$$

The unknown parameters of this Poisson and parameter-variable gamma mixture model were p, u, a, b, F_j and λ_i.

The parameters of these three models were estimated using the Bayesian framework. We employed STAN (R ver. 3.3.2 with 'rstan' package ver. 2.14.1) (<www.r-project.org>, Stan

Development Team 2017) to run a Markov chain Monte Carlo (MCMC) procedure to sample values from the posterior distributions of the parameters. This sampling procedure was implemented independently for each species. Uninformative prior distributions were provided for each parameter based on a flat Cauchy distribution ($x_0 = 0$, $\gamma = 5$). One chain was generated through 10 000 steps, of which the first 5000 were discarded as a burn-in period; the remaining chain of 5000 steps was sampled every five steps, resulting in 1000 values per chain sampled from the posterior distribution. We ran four chains, obtaining a total of 4000 samples for each parameter for every species. All of the generated MCMC chains appeared to converge well, with Gelman and Rubin's convergence diagnostic ($\hat{R}$) (Gelman and Rubin 1992) never exceeding 1.04. To compare the predictability of the three models, we calculated a Watanabe–Akaike information criterion (WAIC) values, which is an information criterion for structured (e.g. hierarchical) models (Gelman et al. 2013), for each species and each model.

In addition to the 2Dt function, we tested the log-sech, exponential power and lognormal functions, which are all probability density functions that have been used to describe seed dispersal kernels (Bullock et al. 2017). The 2Dt model provided a better fit to the data for more species in terms of WAIC (Supplementary material Appendix 1 Table A1–A4). Other studies (Muller-Landau et al. 2008) have also shown a good fit of the 2Dt model to tree dispersal data. Therefore, we used the 2Dt function for our comparison of seed dispersal patterns among species.

From the values of μ and σ^2 estimated for the Poisson and parameter-variable gamma mixture model, we calculated σ^2/μ for every species as an index of overdispersion at various distances; when this value was greater than 1, the seedfall distribution was more spatially variable than was assumed by the Poisson distribution, and when it was less than 1, the seedfall was distributed more uniformly. For the Poisson and parameter-fixed gamma mixture model, this index was given by $1/k$ and for the Poisson model, this index was 1.

Simulation study

To evaluate how spatial aggregation influences colonization by multiple species in terms of local seedfall density, the models described above were used to calculate seedfall densities in a virtual community composed of 11 trees: one focal tree of a particular species was placed near the center and 10 trees (one conspecific and nine heterospecific) were placed farther away. A distance of 10 m from the center was chosen for the focal tree; distances closer to the mother tree caused much greater distance-dependent mortality of seeds and seedlings in some species (Masaki and Nakashizuka 2002). We chose 50 m as the distance of the distant tree, which is the distance within which most seeds of the species investigated in this study were dispersed, as well as 100 m, which is simply double that distance. The density of specific seedfall at the center was predicted using stochastic simulations based on models with the estimated parameters and mean fecundity for each

species: seeds from the focal tree close to the center and seeds from the 10 trees located farther away from the center. This simulation was conducted separately for each species as the focal tree.

We assumed that successful colonization by a species was determined by numerical advantage based on seed arrival, such that when the seedfall density of a tree, whether near or far, exceeded those of other trees, the location was assumed to be occupied by the offspring of that tree. We repeated the simulation 100 000 times for each of the 10 species in the role of the focal tree and calculated the probability that the center would be occupied by offspring of other trees farther away, rather than by those nearby. When the winner was a distant tree of a different species, the probability indicated the degree of ecological drift, and when they were conspecific, it indicated the degree of gene flow. By comparing the results of these simulations, we determined how spatially aggregated seed dispersal might affect colonization dynamics in the studied forest community.

Data deposition

Results

Table 2 and Supplementary material Appendix 1 Table A1 summarize the estimates of species-specific parameters of the three models. In terms of WAIC, inclusion of the parameter-variable gamma distribution improved the predictive power of the models. The WAIC values for the Poisson–parameter variable gamma mixture models were lower than the Poisson–parameter fixed gamma mixture models for seven species with absolute differences of the values ranging ca 12–27 for six species and ca 2 for one species, and vice versa for three species with smaller absolute differences of the values ranging ca 1–5 (Table 2). WAIC values for the Poisson model were much greater than those of the other two models (Supplementary material Appendix 1 Table A1). Based on this, we subsequently use the results of the Poisson–parameter variable gamma mixture model unless otherwise noted. The estimates of b in this model were greater than 1, showing that the variance of seedfall density became disproportionately greater when the mean seedfall density was greater (i.e. nearer to a mother tree).

Estimated dispersal kernels are shown in Fig. 1. In terms of relative seedfall density (i.e. the probability that a seed will fall within a 1-m^2 area at each distance), the two *Acer* species, *Cerasus* and *Cornus*, showed values greater than 10^{-6} at all distances within 100 m of a mother tree. Two *Carpinus* species (*C. japonica* and *C. laxiflora*) and *Fagus* had seedfall densities >10^{-6} only within 80 m. *Betula* and *Carpinus cordata* showed more concentrated distributions around mother trees (>10^{-6} within approximately 60 m), and the

Table 2. Estimates of parameters for the two dispersal models. For the Poisson–parameter variable gamma mixture model, we estimated the parameters of the dispersal kernel function (p and u of the 2Dt function) and the power function (a and b) representing the relationship between variance and mean seedfall density. For the Poisson–parameter fixed gamma mixture model, we estimated the parameters of the dispersal kernel function (p and u) and the shape parameter of the gamma distribution (k). By fitting these models, the fecundity of each candidate seed source tree (F) was estimated, and the mean value for each species is presented in this table (estimates for each tree are presented in Supplementary material Appendix 1 Fig. A5). These estimates are presented with the mean and 95% confidence intervals of the posterior distributions in parentheses. WAIC values were calculated for each species and each model. For each species, the minimum WAIC value is indicated in underlined bold text. See Supplementary material Appendix 1 Table A1 for estimates for the Poisson model where we estimated only the parameters of the dispersal kernel function (p and u).

| | Poisson–parameter variable gamma mixture model | | | | | | Poisson–parameter fixed gamma mixture model | | | | |
	p	u	a	b	Mean fecundity (10³)	WAIC	p	u	k	Mean fecundity (10³)	WAIC
Betula grossa	1.34 (0.96–1.79)	69.96 (21.04–156.27)	2.06 (1.27–3.07)	2.06 (1.93–2.21)	977 (487–1895)	817.7	1.35 (0.98–1.80)	71.35 (22.27–150.58)	0.43 (0.34–0.54)	963 (485–1852)	**814.7**
Carpinus cordata	1.36 (0.89–1.99)	81.66 (38.66–154.14)	1.49 (0.70–2.77)	1.63 (1.39–1.87)	34 (30–40)	**1078.1**	1.53 (1.07–2.18)	91.52 (43.96–168.55)	2.07 (1.55–2.72)	39 (32–47)	1094.2
Carpinus japonica	0.32 (0.21–0.46)	5.26 (0.54–14.79)	0.45 (0.21–0.77)	1.98 (1.77–2.21)	155 (111–245)	**945.8**	0.32 (0.21–0.46)	5.06 (0.51–14.79)	2.65 (1.89–3.67)	158 (112–248)	947.8
Carpinus laxiflora	1.02 (0.78–1.33)	229.22 (123.26–381.92)	0.21 (0.08–0.47)	2.06 (1.80–2.32)	338 (249–484)	1389.0	1.03 (0.78–1.32)	232.72 (128.01–379.05)	4.41 (3.45–5.55)	336 (247–484)	**1388.2**
Fagus japonica	0.71 (0.42–1.07)	33.10 (15.38–61.32)	77.99 (27.60–195.47)	1.18 (0.97–1.37)	365 (318–426)	**1395.5**	1.56 (0.85–2.53)	94.52 (24.89–232.41)	0.44 (0.36–0.52)	529 (355–815)	1407.5
Quercus serrata	2.28 (1.13–4.73)	68.58 (22.80–183.62)	4.31 (2.68–7.02)	1.33 (1.10–1.57)	10 (8–12)	**485.2**	8.47 (2.70–25.21)	358.78 (74.40–1206.05)	0.65 (0.45–0.92)	12 (8–17)	512.5
Cerasus leveilleana	0.12 (0.05–0.25)	90.93 (9.21–380.29)	2.62 (1.67–3.94)	1.77 (1.38–2.28)	11 (7–17)	**511.7**	0.12 (0.05–0.26)	98.24 (8.39–361.73)	0.42 (0.26–0.63)	11 (7–18)	524.7
Acer amoenum	0.26 (0.12–0.47)	26.02 (9.41–63.23)	1.41 (0.80–2.29)	1.68 (1.46–1.92)	82 (63–113)	**969.6**	0.32 (0.13–0.59)	37.24 (8.73–96.39)	1.46 (1.10–1.89)	77 (59–106)	984.7
Acer pictum	0.24 (0.12–0.39)	36.15 (19.85–60.77)	4.17 (2.16–7.39)	1.42 (1.26–1.59)	390 (308–544)	**1487.7**	0.12 (0.05–0.22)	21.17 (5.69–45.05)	1.88 (1.53–2.29)	601 (395–977)	1514.9
Cornus controversa	0.09 (0.05–0.15)	19.90 (3.60–43.95)	0.47 (0.22–0.88)	2.21 (1.88–2.53)	56 (39–79)	1386.0	0.09 (0.05–0.15)	21.87 (5.79–45.86)	1.57 (1.23–1.97)	55 (38–78)	**1380.8**

shortest dispersal distances were found for *Quercus* ($>10^{-6}$ only within 35 m). Generally, the expected values of the seed-fall density (μ) were well-correlated with the observations (Supplementary material Appendix 1 Fig. A4). The exceptions were the endozoochorous species *Cerasus* and *Cornus*, for which the observed seedfall often greatly exceeded the expected values for relatively large values of μ (i.e. close to the mother tree), suggesting greater kurtosis of seed distribution patterns around zero distance than is assumed in the dispersal kernel function. A similar trend was observed, albeit to a lesser degree, for *Acer amoenum*.

Based on estimates of the shape and scale parameters of the 2Dt function, p and u, the cumulative proportions of seeds dispersed over a given distance were calculated (Fig. 3 and values shown in Fig. 1). For Betulaceae and Fagaceae, most seeds were deposited within 50 m of the mother tree. *Acer* species showed further dispersal, and endozoochorous species showed much further dispersal of seeds. Bird-dispersed species showed the greatest 50th percentile (i.e. median) distance of about 200 m, followed by *Acer* species (about 20 m). Fagaceae and Betulaceae species showed the shortest median distances (mostly <10 m). The 95th percentile distances showed similar tendencies; those of Fagaceae and Betulaceae were less than 50 m, except for *Carpinus japonica* (extrapolated value >200 m). The 95th percentile distances of *Acer* species and endozoochorous species were estimated to be much greater, at 1700–3000 m and $>10^6$ m, respectively.

The mean estimated fecundity varied greatly among species (Table 2, Supplementary material Appendix 1 Fig. A5). The most fecund species was *Betula* ($>900 \times 10^3$ seeds) followed by some *Carpinus* species, *Fagus* and *Acer pictum* ($>100 \times 10^3$). The least fecund species were *Quercus* and *Cerasus* ($<11 \times 10^3$). The relative seedfall density was slightly positively correlated with fecundity at 10 m from mother trees ($r = 0.62$, $p < 0.1$), and as a result, absolute seedfall density (= fecundity × relative seedfall density) was strongly correlated with fecundity at that distance ($r = 0.97$, $p < 0.05$) (Supplementary material Appendix 1 Fig. A6). By contrast, at distances of 50 m and 100 m, the relative seedfall density tended to be correlated negatively, although not significantly, with fecundity ($r = -0.22$, $p > 0.1$ and $r = -0.32$, respectively) when *Quercus* was excluded from analyses as an outlier due to its much lower seedfall densities (10^{-9}–10^{-7} m^{-2} in relative density and 10^{-5}–10^{-3} m^{-2} in absolute density), while a positive relationship was found between absolute seedfall density and fecundity (with *Quercus* excluded) at 50 m ($r = 0.85$, $p < 0.05$) and at 100 m ($r = 0.59$, $p < 0.1$) (Supplementary material Appendix 1 Fig. A6). Among the species with lower relative seedfall densities at distances of 50 and 100 m, the absolute seedfall densities of *Betula* and *Fagus* were greater than (50 m) or similar to (100 m) others, reflecting their greater fecundities (Supplementary material Appendix 1 Fig. A6).

We calculated the index of overdispersion in seedfall σ^2/μ for every species over distances of 0–100 m. The results showed that seedfall density in the vicinity of a mother tree varied more than expected from a Poisson distribution in all species (Fig. 2). This value decreased with distance from the mother tree and was smaller than 1 at distances >60 m for all species except *Fagus japonica* and *Acer pictum*, suggesting rather uniform seedfall distributions beyond that distance.

The results of simulations using the Poisson–parameter variable gamma mixture model, as well as the Poisson model as a control, are shown in Fig. 4. The results of the former model showed that sites near species other than *Carpinus laxiflora* and *Acer pictum* were susceptible to colonization by different species located 50 m away. In particular, the probability of colonization by other species was greater for *Betula* (ca 0.15), *Quercus* (ca 0.6), *Cerasus* (ca 0.8) and *Cornus* (ca 0.4) than other trees. These tendencies persisted when considering colonization from trees 100 m away. *Acer pictum*, *Carpinus laxiflora* and *Fagus* showed strong colonization abilities from 50 m away. From 100 m away, *Acer*, the two *Carpinus* species and *Cornus* had greater colonization rates. By contrast, the simulation with the Poisson model suggested that locations in the vicinity of only *Quercus* and *Cerasus* were likely to be colonized by other species located far away (and for *Cornus*, colonized by other species 50 m away).

Discussion

To answer the questions raised in the introduction, the probability distributions of seed dispersal distance for each species were largely determined by dispersal mode (farthest in endozoochory and shortest in barochory), the lower dispersal probability of a species at farther sites could be offset to a certain degree by greater fecundity, and the distribution patterns of seedfall were more aggregated than is assumed by a Poisson distribution in the vicinity of a mother tree, irrespective of species. These findings and the simulation results suggest that aggregated seed dispersal results in spatial uncertainty of seedfall and makes it possible for distant trees to colonize sites near mother trees instead of being filled with local offspring. In the following sections, the findings of this study are discussed in more detail.

Dispersal patterns of each species

First, we discuss the seed dispersal distances of the tree species in the study forest in descending order of dispersal distance. As might be expected (Bullock et al. 2017), endozoochorous species had the longest seed dispersal distances while barochorous species had the shortest distances; those of anemochorous species were intermediate. For endozoochorous species, more than half of the seeds were estimated to be dispersed over approximately 200 m from the mother tree. *Cerasus leveilleana* and *Cornus controversa* showed almost identical patterns of cumulative proportion with distance, despite the different fruiting phenologies of these species, which should be reflected in the different post-foraging behaviors of their frugivorous birds: *Cerasus* produces fruit
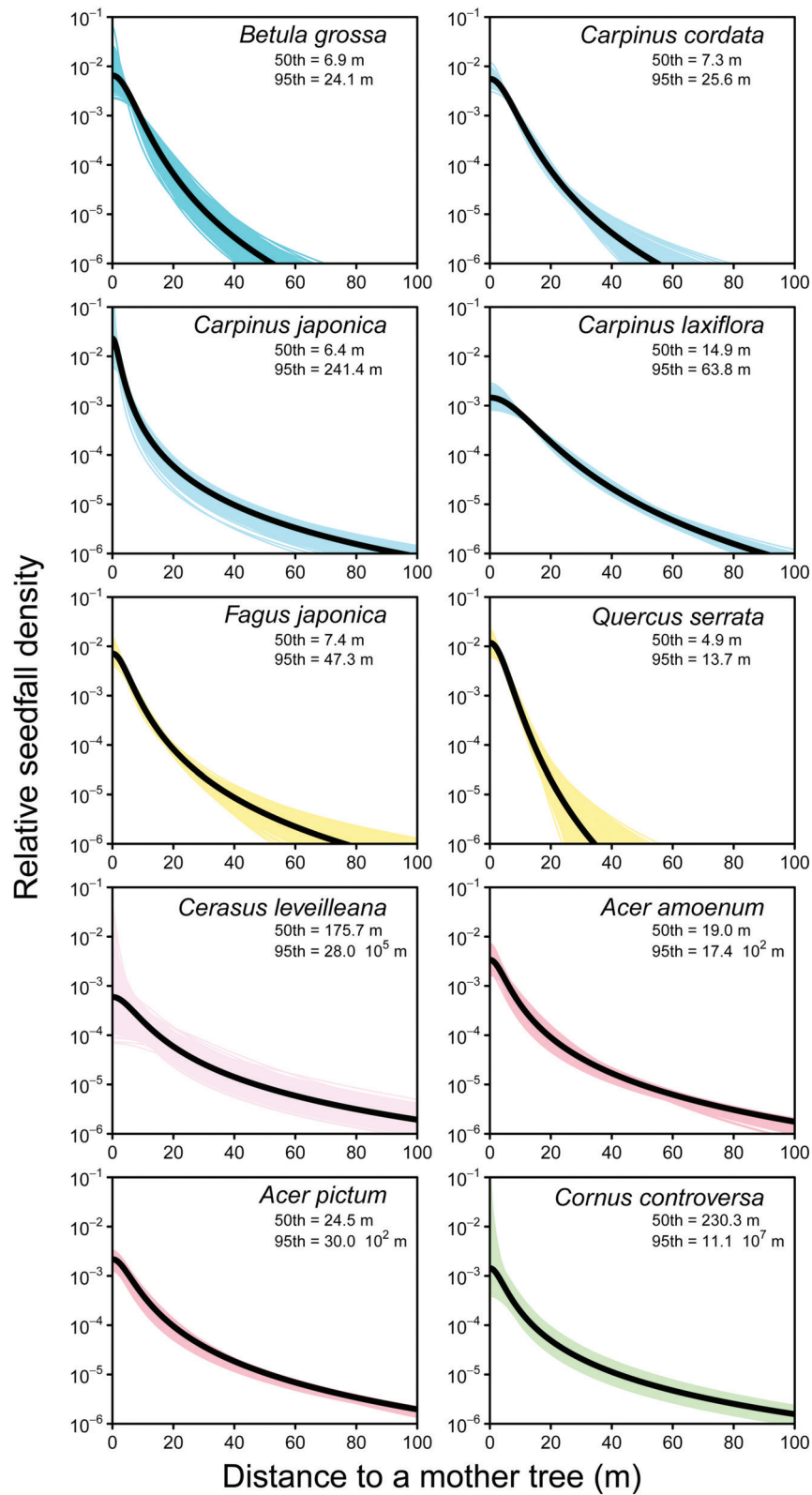
Figure 1. Fitted seed dispersal kernel functions (Clark's 2Dt model) from the Poisson–parameter variable gamma mixture model for 10 species without the variation given by the gamma distribution. The relative seedfall densities are shown as a function of the distance to a mother tree. Colored lines represent each of the 4000 Markov chain Monte Carlo (MCMC) samples, and the black line represents the posterior mean. The 50th and 95th percentile distances are shown in each panel.
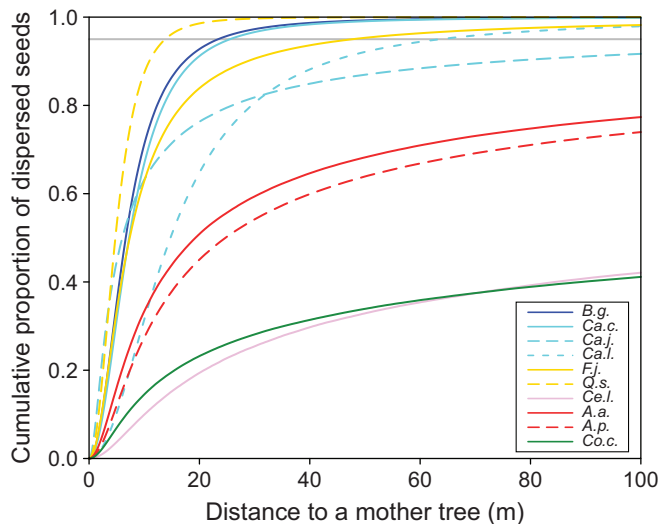
Figure 2. Cumulative proportion of dispersed seeds calculated using the estimated 2Dt functions against the distance from a mother tree for each species. The horizontal grey line indicates 0.95. See Table 1 for the species abbreviations.

during the bird breeding season (early summer) (Naoe et al. 2011) and *Cornus* during the bird migration season (autumn) (Masaki et al. 1994, Yamazaki et al. 2016). However, the estimated 95th percentile distances (>100 km) of these endozoochorous species may be overestimates. The gut passage time of seeds in the brown-eared bulbul, a major frugivorous seed-dispersing bird in the study area (Naoe et al. 2011), is less than 30 min on average (Fukui 2003) and the average home range of this bird is approximately 300 m in diameter (Fukui 1995). Therefore, the tail of the dispersal curve for frugivorous birds will likely be truncated at long distances (Jordano
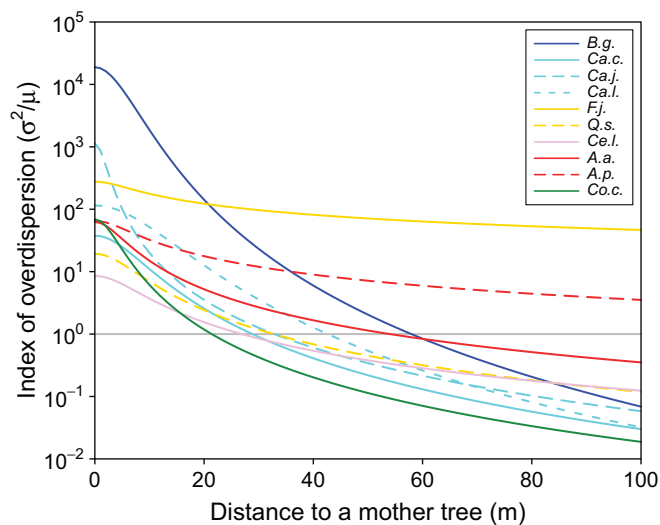

Figure 3. Change in the variance to mean ratio of seedfall density, as an index of overdispersion in seed dispersal, shown as a function of the distance from a mother tree for each species. The horizontal line shows where the mean equals the variance (i.e. an assumption of the Poisson distribution). See Table 1 for species' abbreviations.

2017, Pegman et al. 2017). In addition, the observed seedfall density near mother trees often exceeded the values predicted by the estimated kernel functions. The 2Dt model did not successfully recreate the high kurtosis in seedfall distribution around seed sources in this study. This deficiency might be due to dispersal by different bird species that have different post-foraging movement patterns; some might remain longer at seed sources, causing more concentrated seedfall around mother trees, while others might fly farther shortly after feeding on fruits. Mixtures of multiple kernel functions (Martínez and González-Taboada 2009) might be necessary, and the number of functions required would depend on the diversity of seed-dispersing frugivorous birds. However, such mixtures would introduce many more parameters and increase the risk of over-fitting (Bullock et al. 2017).

Within anemochorous taxa, there was substantial variation in dispersal distance, which was longest for *Acer*, intermediate for *Carpinus* and shortest for *Betula*, despite the fact that these species have similar seedfall velocities (Tanaka et al. 1997). Seed dispersal distance varied even within the genus *Carpinus*, being shorter for *Carpinus cordata* than for its congeners. This result might be explained by topographical differences in the habitats of related species (Trakhtenbrot et al. 2014). *C. cordata* is often found on the lower parts of slopes (Supplementary material Appendix 1 Fig. A1; also see Masaki et al. 1992), likely resulting in a shorter realized horizontal seed dispersal distance than that expected for trees on flat topography. By contrast, *C. laxiflora* and *C. japonica* are generally found on the upper parts of slopes (Supplementary material Appendix 1 Fig. A1; also see Masaki et al. 1992). The fundamental seed dispersal function (i.e. drawn on flat land) for *Carpinus* species is likely intermediate between that of *C. cordata* and those of its congeners. In comparison, *Betula* somewhat unexpectedly had the shortest dispersal distance. This species is found on relatively high parts of slopes (Supplementary material Appendix 1 Fig. A1; also see Masaki et al. 1992); its seed and dispersal appendage were the lightest measured (Tanaka et al. 1997), and mature trees of this species are the tallest among the 10 species investigated (Masaki et al. 2017). All of these traits may contribute to longer dispersal distances. One explanation for this discrepancy is that the seeds of this species might abscise without external forces such as strong wind, while seeds of other anemochorous species might tend to abscise more often under strong winds (Tanaka et al. 1997), which increase dispersal distances (Soons and Bullock 2008). Another explanation for this result is that fruits of *Betula* that contain seeds might fall near their mother tree before the seeds within them are dispersed. In this case, as well as for endozoochorous species, a mixture of two dispersal kernels for fruits and seeds might be necessary for a clearer understanding of the dispersal ecology of *Betula* seeds.

Unsurprisingly, *Quercus serrata* had the shortest dispersal distance. By contrast, the other barochorous species, *Fagus crenata*, had a greater 95th percentile distance, which was almost equivalent to those of *Carpinus* species. This finding might be explained partly by the architecture of *Fagus japonica*
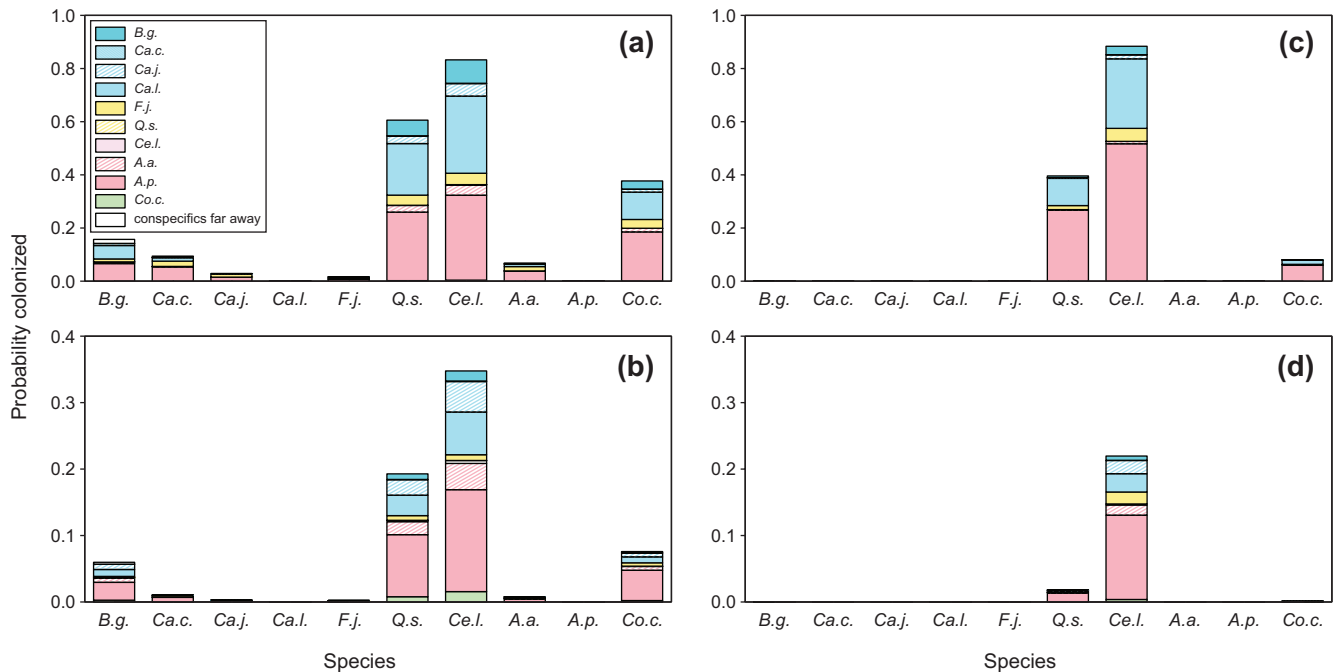
Figure 4. Simulation results for the probability of a site near a species being colonized by each of 10 tree species (one conspecific and nine heterospecific) located far away in a virtual community. The left panels (a–b) show results based on the Poisson–parameter variable gamma mixture model, and the right panels (c–d) show results based on the Poisson model. The upper panels (a–c) use 50 m as the distance of the far trees, and the lower panels (b–d) use 100 m for this distance. The probability of a site being colonized by a nearby mother tree (i.e. regeneration in situ) is not included in this figure.

trees. This species has multiple radial canopy-reaching stems (a genet; Ohkubo 1992), resulting in a larger individual canopy area than *Quercus* in this forest (approximately 230 m^2 and 120 m^2 for *Fagus* and *Quercus*, respectively; Masaki unpubl.). The median distance of seed dispersal has an established positive relationship with the radius of the canopy of the source (Shaw et al. 2006). Seed distributions within a three-dimensional crown might play an essential role in shaping the distribution of seed dispersal distances of *Fagus*, as well as other species.

Specific fecundity and its effects on absolute density of seedfall

There was considerable variation in fecundity among species, from ca 11×10^3 per tree for *Quercus* and *Cerasus* to ca 1000×10^3 per tree for *Betula*. This variation in fecundity influenced numerical aspects of seed dispersal differently depending on the distance from mother trees. At locations close to mother trees (i.e. 10 m away), mean relative and absolute seedfall density values of each species correlated strongly and positively with its fecundity. In particular, the relationship between absolute seedfall density and fecundity appeared almost deterministic. At 50 and 100 m away, the lower probability of dispersal was offset for some species (specifically *Betula* and *Fagus*) by their greater fecundity. Although the lower probabilities of *Carpinus cordata* and *Cerasus leveilleana* at greater distance was not fully offset by their fecundity, greater fecundity in general seemed to play a

substantial role in allowing nearly equivalent seedfall of different species at sites far away from the mother trees.

Spatial aggregation of seed dispersal in the context of colonization dynamics

All species tested in this study showed more overdispersion within ca 30 m of their mother trees than assumed by a Poisson distribution. This is unlikely to be a statistical artifact because the parameter μ, as the denominator of σ^2/μ, was greater at locations closer to mother trees. This trend was also reflected in estimates of the parameter b (>1) used in the Poisson–parameter variable gamma mixture model. This result suggests that these species showed aggregated seed dispersal patterns, particularly in the vicinity of mother trees, resulting in greater spatial variation within the local community. Furthermore, in contrast to a priori expectations, the values of σ^2/μ were greatest for non-endozoochorous species (*Betula*, *Carpinus*, *Fagus*) and smallest for endozoochorous *Cerasus*.

What caused this spatial uncertainty near mother trees? For anemochorous species, strong winds during the fruiting season (Abe et al. 2008) could be a causal factor; high wind speeds lead to aggregated seedfall distributions of anemochorous species (Wright et al. 2016). Among endozoochorous species, *Cornus* and *Cerasus* showed contrasting patterns of aggregated and relatively random distributions, respectively. We speculate that seasonal differences in bird activity might be reflected in seed distributions; some migratory birds

that feed on the fruits of *Cornus* in the study site are gregarious and forage as a flock (Naoe et al. 2011), possibly causing more non-random seedfall than seen during the breeding season. Breeding birds dispersing seeds of *Cerasus* might move randomly within their home ranges when searching for food. This speculation regarding seasonal variation in the activity of seed dispersing birds could be tested in the future by studying the movement of birds of various species. However, this reason does not fully explain why the values of σ^2/μ decreased. It is possible that pervasive dispersal kernels might have difficulty identifying seeds at more remote sites (e.g. lower sensitivity of seedfall density to distance). However, we cannot rule out some physical or biological process being behind this finding. For example, the process by which cones (*Betula*) or infructescences (*Carpinus*) containing seeds fall under their mother trees might differ from that of seeds released with wings. In endozoochory, some frugivores deposit seeds primarily under designated roosting or feeding sites, causing aggregation of seeds (Sugiyama et al. 2018). To clarify the biological mechanism causing spatial uncertainty in seedfall near a mother tree, additional detailed studies of the seedfall process are required.

The simulation results suggest that spatial uncertainties in seed dispersal affect colonization processes within the community: even near a mother tree, sites may exist where the density of seedfall from the mother tree is lower than that from another tree growing far away (100 m, for example). Even near a mature *Betula* tree, where seedfall from that tree is more abundant than that of other species on average, our simulations showed that other species often had greater seedfall densities (Fig. 4). This finding implies that stochastic processes related to the aggregation of seed dispersal might enable competitively inferior species to succeed based on chance colonization of sites where low numbers of seeds of more competitive species are present.

Limitations of this study and recommendations for further study

Some caution is needed when interpreting the results of this study. First, the data for each species were collected in a single year and lacked temporal replication. Various temporal factors may affect the degree of aggregated dispersal, including annual variation in tree fecundity (Shibata et al. 2002), weather conditions such as wind speed (Sato et al. 2010), and the abundance and movement patterns of frugivorous animals (Naoe et al. 2018). Furthermore, the behavior of frugivores may be influenced by the patterns of seed production at a landscape scale (Koike et al. 2011, Morales et al. 2012, Tochigi et al. 2018). All of these temporal variables may cause year-to-year changes in seedfall distribution irrespective of dispersal mode (Schurr et al. 2008, Martínez and González-Taboada 2009, Koike et al. 2011, Wright et al. 2016, Yamazaki et al. 2016, Naoe et al. 2018). It is likely that the spatial uncertainty in seedfall shown in this study would also be observed in other years, but its potential effects on the

colonization process might differ quantitatively among years. Therefore, studies with temporal replication are necessary to confirm the findings of this study.

Second, the years and seedfall sampling designs differed between endozoochory and other dispersal modes. During the 20 years from 1988 to 2007, there were no apparent changes in the structure and composition of the forest in and around the plot (Masaki unpubl.), and thus the biological processes surrounding seed dispersal are unlikely to have changed. However, different patterns of seed trap distribution might have affected the results. Seedfall through endozoochory was investigated with a 14.1 m interval between sites, while other dispersal types used a 7.0 m interval. This difference might affect the evaluation of spatial aggregation patterns.

In future studies, topography should also be considered to more precisely evaluate seed dispersal patterns. Even with the same dispersal kernel, the realized horizontal dispersal distances from a tree living on a ridge are greater, and those from a tree living in a narrow valley bottom are shorter, as discussed above. Topography also influences the movement of vertebrates, resulting in unique spatial variation in endozoochorous seed dispersal patterns (Naoe et al. 2016). Three-dimensional analyses of dispersal patterns are necessary for future studies in real-world environments. Third, individual variation is important. Variation in seed dispersal patterns has been observed among conspecific individuals that use anemochory (Augspurger et al. 2016) and endozoochory, which is affected by the crop size of each individual tree (Morales et al. 2012). Such variation due to random effects of individuals must be quantified to evaluate its implications for forest community assembly.

Finally, assessment of later life history stages is essential. Following primary seed dispersal, secondary dispersal is likely, particularly for Fagaceae species in this forest (Iida 1996). However, the methodology used to evaluate this is not fully established except for large-seeded species (Martínez and González-Taboada 2009). Post-dispersal survivorship is also critical. For instance, *Quercus*, which is less fecund and has a shorter dispersal distance, has greater survival of seeds and seedlings than other species in the study forest (Nakashizuka et al. 1995), which may offset the numerical disadvantages associated with seed dispersal. At later stages, the spatial scale will be important. In this study, we evaluated variation in seedfall patterns by 0.5 m^2 seed traps. However, the space that a tree occupies as an adult often reaches 100 m^2 or more. Even when a species numerically overcomes another species in terms of seedfall in a 0.5 m^2 site, the surrounding sites may be colonized by another species, which may result in numerical superiority of the latter species at large scales. We must consider changes at relevant spatial scales throughout the long lifespan of trees; therefore, the outcomes of seed dispersal must be analyzed at various temporal and spatial scales. Simulation studies of population dynamics would be useful to determine the community-level consequences and to validate further the conclusions of this study.

Conclusion

This study hierarchically expanded a statistical model based on a dispersal kernel function by adding a gamma distribution with variable parameters. We confirmed that interspecific variation in seed dispersal distance depends on seed dispersal type, as shown in previous studies. In addition, we established that endogenic spatial aggregation and uncertainty in seedfall near conspecific mother trees occurs irrespective of dispersal mode. Our simulations suggest that this uncertainty could influence colonization dynamics in this temperate forest. However, various other factors may have influenced our findings such as annual variation, topography and long-term demographic processes. Evaluating the role of seed dispersal in colonization dynamics within forests remains a challenging but fruitful task.

Speculations

Aggregated distributions of seedfall have been reported in studies of tropical forests where endozoochory is more dominant (Sugiyama et al. 2018). It has often been hypothesized that this process could partly explain species coexistence in these regions (Schupp et al. 2002). However, the findings of this study suggest that a similar process could also occur in temperate forests where dispersal types other than endozoochory are prominent, possibly promoting coexistence by making colonization rates similar on average among species and equalizing species fitness (Adler et al. 2007), contributing in a limited way to the maintenance of species diversity in temperate forests. This mechanism of species coexistence does not conflict with other hypothesized processes. For example, distance- or density-dependent mechanisms are likely to occur at the study forest (Masaki et al. 1998, Masaki and Nakashizuka 2002, Shibata et al. 2010) as proposed by the Janzen–Connell hypothesis (Comita et al. 2014). Various mechanisms could work in harmony to allow species coexistence, varying in magnitude and relative importance among forests and along latitudinal gradients, potentially causing geological variation in species diversity.

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Supplementary material (available online as Appendix oik-06236 at <www.oikosjournal.org/appendix/oik-06236>). Appendix 1.