



Differentiation and seasonality in suitable microsites of seed dispersal by an assemblage of omnivorous mammals

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ABSTRACT

In endozoochorous seed dispersal, the ecological characteristics of each disperser determine the quantitative and qualitative aspects of the dispersal mechanism. To understand the role of different frugivores in multispecies seed dispersal networks, it is necessary to focus on the community structure and investigate where in the landscape seed deposition occurs. The aim of this research was to assess the quantitative and qualitative aspects of a mammalian endozoochorous seed dispersal network in a temperate forest ecosystem and identify the seasonal dispersal niche of each member of the assemblage. We hypothesized that differences among dispersers and seasons would occur in (H1) the proportion of scats that contain seeds, seed abundance in scats, and the number of seed species dispersed per scat, and in (H2) the probability of dispersing seeds to suitable microsites for germination of each species and seed abundance. We also hypothesized (H3) that the microhabitat variables of deposition sites would vary among dispersers, and (H4) that complementary structures would occur in terms of dispersers, dispersed species, and deposition sites. From summer (June–August) to autumn (September–November) in 2003 and 2004, we collected scats of five mammalian frugivorous species and recorded eight microhabitat variables at each deposition site in central Japan. We recorded the presence and number of seeds in scats and identified all seed at the species level. We considered a deposition site as suitable when the habitat type (interior forest, treefall gap, forest edge, and outside the forest) at a deposition site matched the microhabitat required for the dispersed species to germinate and survive as seedlings. A total of 341 scats containing seeds of 16 fleshy-fruited species were collected. Among these, 213 (62.5 %) scats were dispersed to suitable habitats (summer: 68.8 %, autumn: 54.8 %). We found that the seed abundance in the scat varied among dispersers and was higher in autumn (H1–2). The probability of dispersing seeds to suitable microsites switched among dispersers from summer to autumn (H2). The distinctive microhabitat variables and variation in microhabitat at deposition sites differed among dispersers across seasons (H3). Disperser-plant and disperser-deposition site networks were specialized and modular in structure compared to random networks during both seasons, but there was a less nested structure in summer compared to autumn (H4). The five mammal species showed differences and

Abbreviation: SDS, Seed Dispersal to Suitable microsites.

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seasonality in seed dispersal niches. Because of these differences, these mammal species may play redundant and complementary roles in the seed dispersal network.

1. Introduction

Seed dispersal is a critical ecosystem process that affects plant population dynamics and community structures through sexual reproduction (Howe and Miriti, 2004; Jordano et al., 2007). The germination and establishment of dispersed seeds depend on both quantitative (e.g., number of seeds deposited per species) (Jordano and Schupp, 2000) and qualitative factors (e.g., environmental conditions at the deposition site) (Schupp et al., 2010, 2017). Environmental conditions include vegetation cover (García et al., 2005; Verheyen and Hermy, 2004), the abundance of leaf litter (Kolb and Barsch, 2010), and soil biogeochemistry (Messaoud and Houle, 2006). Other factors also affect the quality of seed dispersal; for example, mouth and gut treatment of endozoochorous dispersal agents (Traveset, 1998), and pre- and post-dispersal seed predation (Hulme, 1998).

A large proportion of dispersed seeds are transported by animals, especially in tropic and temperate regions (Howe, 1986; Dalsgaard et al., 2017). Additionally, in plant species that rely on endozoochory (i.e. seed dispersal via ingestion by vertebrates) for seed dispersal, deposition may be more deterministic than for plants that rely on abiotic factors (e.g., wind) for seed transport. In endozoochory, both quantitative and qualitative aspects of the dispersal mechanism are constrained by the ecological characteristics of the dispersal agent (e.g., body size, diet, habitat selection) (e.g. Russo et al., 2006). Dispersal agents also mediate seed dispersal spatial patterns, including the dispersal kernel (the probability density of the dispersal of a species as a function of the distance) (González-Varo et al., 2013; Garrote et al., 2022) and the seed shadow (the spatial distribution of dispersed seeds around their source) (Fedriani et al., 2010; Garrote et al., 2022). Dispersal agents can also direct deposition to specific sites or environments (García-Cervigón et al., 2018; Steyaert et al., 2018; García-Rodríguez and Selva, 2021; Arnberg et al., 2022), and coexisting dispersers may play complementary roles in seed dispersal networks (Escribano-Avila et al., 2014).

Multiple plant species can be dispersed by multiple dispersal agents (Howe and Smallwood, 1982; Jordano, 1987). In nested seed dispersal network structures, generalist dispersers form the core of the network and disperse the bulk of the seeds and species, whereas specialists disperse subsets of the species dispersed by the generalists (Bascompte et al., 2003). Nested structures increase network stability and can buffer the network against the loss of specialists. Networks with high modularity are composed of subsets of disperser–dispersed interactions (Mello et al., 2011). Although species within a network module play somewhat redundant roles within networks and ecosystems, modules are complementary (Sarmiento et al., 2014). Both modular and nested structures can minimize interspecific competition and facilitate species coexistence and biodiversity (Bastolla et al., 2009; Allesina and Tang, 2012). This, investigating network structure will enable us to understand the contributions of dispersers to persistence, stability, and diversity in multispecies seed dispersal systems. Identifying key players and interactions in seed dispersal networks is important for ecosystem conservation and management (Vizentin-Bugoni et al., 2021).

Different frugivores may play distinct roles within a community as a result of their quantitative (e.g. seed number) and qualitative (e.g. deposition in suitable site) differences in seed dispersal (Willson and Whelan, 1990; García-Rodríguez et al., 2022). Traditionally, quantitative components of endozoochorous dispersal networks have been considered a better proxy for seed dispersal than qualitative components. Consequently, many studies have investigated the quantitative components of endozoochorous dispersal networks (e.g., Vázquez et al., 2005), and relatively few studies have linked seed dispersal to deposition sites and interacting species (Jordano and Schupp, 2000; Niederhauser and Matlack, 2017; García-Cervigón et al., 2018). In addition, to what extent dispersal agents vary quantitatively and qualitatively in terms of seed dispersal to suitable microsites (hereafter referred to as “SDS” from Seed Dispersal Suitable microsites) remains largely unknown (Schupp et al., 2010; but see Rumeu et al., 2020).

Here, our objective was to assess both the quantitative and potentially qualitative aspects of a mammalian endozoochorous seed dispersal network in a temperate forest ecosystem, and to identify the dispersal niche of each member of the disperser assemblage. We did not test seed germination and seedling survival, but the ‘qualitative’ component of our study could be an essential intermediate step to achieve plant recruitment. We also aimed to identify the seasonal differences for the quantitative and qualitative aspects, as well as for the dispersal niche, because plant phenology, disperser behavior, and consequently, seed dispersal effectiveness change according to season (García-Cervigón et al., 2018; González-Varo et al., 2019). We examined four hypotheses: (1) The probability of dispersing the seeds of fleshy fruits (H1a), the seed abundance (H1b), and the seed species richness (H1c) vary among five potential dispersal agents (Asiatic black bear, *Ursus thibetanus*; Japanese macaque, *Macaca fuscata*; Japanese marten, *Martes melampus*; raccoon dog, *Nyctereutes procyonoides*; and Japanese badger, *Meles anakuma*) and between seasons. (2) The probability of dispersing seeds to suitable microsites (H2a) and seed abundance at these microsites (H2b) vary among dispersal agents and between seasons. (3) The microhabitat variables (e.g., canopy openness, soil hardness, and vegetation cover) at different deposition sites vary among dispersal agents (H3). (4) Complementary structures occur in seed dispersal networks in the study area in terms of dispersers, dispersed species, and deposition sites suitable for regeneration of the dispersed plant species (H4).

Firstly, we checked not only the differences among the dispersal agents but also the presence of seasonality as a quantitative component (H1) and a qualitative component (H2). Then, we verified the qualitative components of the dispersal agents for each season from the similarities and differences in the microhabitat of deposition sites (H3) and weighted network structure, accounting for seed abundance (H4).

2. Materials and methods

2.1. Study system

The study was conducted in the Okutama mountains, approximately 100 km west of Tokyo, Japan. This region has a Pacific climate, with heavy rainfall in summer and little snow in winter. The mean annual precipitation is 1586 mm, mean snowfall ranges from 2 to 4 cm, and the mean annual temperature is 11.8 °C, ranging from 0.6 °C in January to 24.2 °C in August (Tokyo Environmental Office, 2000). Natural forests cover 41.3 % of the total mountainous area, and conifer plantations (*Cryptomeria japonica* or *Chamaecyparis obtuse*) cover 50.3 % (S. Koike, unpublished data). The natural forests are dominated by *Castanea crenata* and *Quercus serrata* in the lower mountain zone (400–500 m above sea level [a.s.l.]); by *Quercus crispula*, *C. crenata*, and *Fagus crenata* in the middle zone (500–1500 m a.s.l.); and by *Abies homolepis* and *Tsuga diversifolia* in the upper zone (1500–1800 m a.s.l.).

Five medium- to large-sized mammalian frugivores are present in the study area: Asian black bear, Japanese macaque, Japanese marten, raccoon dog, and Japanese badger. Bears and macaques are large, frugivorous tree-climbing mammals that eat mainly fleshy fruits and nuts (Koike and Masaki, 2019). Martens are medium-sized, tree-climbing, mainly frugivorous mammals that consume fleshy fruits, invertebrates, and small vertebrates (Koike and Masaki, 2019). Raccoon dogs and badgers are medium-sized omnivores that forage mostly on the ground (Koike and Masaki, 2019).

At least 16 native fleshy-fruited species are dispersed by these frugivores in the study region (Koike et al., 2008). During surveys, we excluded scats that contained seeds of *Diospyros kaki*, which is a cultivated species in the area. For details about the fleshy-fruited species, see Table S1 (Supporting Information).

2.2. Scat collection

From May 2003 to April 2005, we conducted surveys twice a month along three transects (12.6 km in length of total transect) that were established at the onset of the scat collection study (Koike et al., 2008). Transect 1 extended from 498 to 1515 m a.s.l., transect 2 from 787 to 1210 m a.s.l., and transect 3 from 680 to 1230 m a.s.l. We conducted the survey four seasons, but we did not use the data from winter and spring because we found few scats that contained seeds in that period (1 bear and 5 marten scats in spring; 15 marten and 4 raccoon dog scats in winter; Koike et al., 2008). We collected all detected scats from the five focal mammals along the transects. Each scat sample was washed through a series of sieves (2.0-, 1.0-, and 0.5-mm meshes), and the presence of seeds was recorded (0, 1) for each scat. Each seed was identified to the species level, following Satake et al. (1989), and ‘spp.’ was used for seeds that could only be identified to genus level. Subsequently, we recorded the number of plant species per scat (species richness) and counted the number of intact seeds per scat and per plant species (seed abundance) (see Koike et al., 2008 for details).

2.3. Microhabitat variables

We recorded a set of microhabitat variables known to affect the germination and survival of seedlings (Gross-Camp and Kaplan, 2005; Wenny, 2000) at scat deposition sites and at control sites. The control sites were randomly distributed in a buffer zone around each transect. The size of the buffer zone was based on the maximum-measured home range size of the bear, the largest mammalian frugivore in the study area (46 km², 100 % minimum convex polygon estimation; Ohdachi et al., 2009). We sampled control data from 200 randomly selected points in summer and 100 points in autumn. At each seed deposition site and control site, we measured eight microhabitat variables: (1) canopy openness (%), (2) amount of leaf litter (number of leaves), (3) number of trees (woody plants with roots thicker than 1 cm) within a radius of 2.5 m (discrete number), (4) number of shrubs (woody plants with root thickness <1 cm) within a 1 m radius (discrete number), (5) vegetation cover (all vegetation, assessed at 1-m height) within a 0.5 m radius (%), (6) slope (degree), (7) soil hardness (kg/cm²), and (8) altitude (m a.s.l.). We took hemispherical photographs and used LIA for Win32 image analysis software (Yamamoto, 2004) to calculate the canopy openness at each site. We measured the amount of leaf litter by counting the number of leaves that were pierced by a metal stake that was pierced into the soil (Wenny, 2000). We also qualitatively classified the habitat type at each seed deposition site and control sites into (1) interior forest (“inter”); (2) outside the forest (e.g., clear-cut areas and forest roads, “out”); (3) treefall gap (“gap”); or (4) forest edge (interface between forested and nonforested areas, “edge”) (Fig. S1, Supporting Information).

2.4. Statistical analysis

We conducted the analyses for H1 and H2 with the datasets for both seasons together, and the analyses for H3 and H4 with the datasets for summer (June–August) and autumn (September–November) separately. All statistical analyses were conducted in the R 3.6.1 software environment (R Core Team, 2019).

2.4.1. Probability of dispersing seeds of fleshy fruits (H1a), seed abundance (H1b), and number of fleshy-fruited species (H1c)

We used logistic regression models to assess whether the probability that a scat would contain seeds (yes = 1, no = 0) differed among the focal mammals and seasons (H1a). We used negative binomial regression models to assess if the number of seeds per scat differed among focal mammals and seasons (H1b), with the number of seeds per scat as the response variable. We opted for a negative binomial model here (dispersion parameter for negative binomial model = 1.157) because the Poisson regression model with this structure was overdispersed (dispersion ratio = 1202.4, $P < 0.001$ at overdispersion test for Poisson regression model). We used a

Poisson regression model to determine whether the number of seed species per scat varied among the focal mammals and seasons (H1c). For all models for H1, we set the mammalian species, the season, and interaction term of the mammalian species and season as the explanatory variables. We used the MASS package for the negative binomial regression model fitting (Venables and Ripley, 2002). To compare the candidate models (mammal, season, and mammal \times season) to null models, we used the second-order Akaike information criterion (AICc) and selected the model with lower AICc as the most parsimonious model.

2.4.2. Seed dispersal to suitable microhabitats: probability of occurrence (H2a) and seed abundance (H2b)

To test the second hypothesis, we identified ‘potential regeneration habitats’ for all dispersed species (Table S1, Supporting Information). For all species in each collected scat, we recorded whether the seeds in the scat were deposited in a suitable habitat (1 = suitable, 0 = unsuitable) for regeneration. Because ecological niches at different stages in the life cycle of a plant species can be different, we defined ‘potential regeneration habitats’ as the microhabitats where seeds would possibly germinate and seedlings would survive for a few years. We decided to classify habitats as suitable (1) or unsuitable (0), omitting intermediate scenarios, because we simplified the contribution by dispersal agents to SDS, although suitability has gradient and complexity. In determining whether the seed was deposited in a suitable microhabitat when scats contained seeds multiple plant species, we assigned a binary value to each combination of plant species and deposition site habitat. For example, if a scat from one deposition site contained seeds from two plant species, the scat appeared twice in our dataset, with different information regarding the dispersed species name and the number of seeds. We defined matched combinations in the following cases: scats including plant species whose regeneration habitat was “edge” were deposited under “gap” and vice versa, because the treefall gap and forest edge are similar microhabitats.

We used logistic regression to assess whether the probability of seed being dispersed to suitable sites differed among dispersers and seasons (H2a). We also used negative binomial regression to evaluate whether the number of seeds per plant species per scat deposited in a suitable habitat varied among the focal dispersers and seasons (H2b). For all models for H2, we set the mammalian species, the season, and the interaction term of mammalian species and season as the explanatory variables. We used the AICc to compare the candidate models (mammal, season, and mammal \times season) to null models, and selected the model with lower AICc as the most parsimonious model.

2.4.3. Seed deposition site differentiation: microsite characteristics (H3)

We evaluated to what extent the microhabitat at the deposition sites differed from that at random sites and among dispersers (H3) using logistic regression and principal component analysis (PCA). We included only suitable deposition sites in the analyses and used logistic regression to compare suitable deposition site characteristics (coded as 1) with characteristics of random sites (coded as 0) separately for each disperser. As explanatory variables, we used eight microhabitat variables. We randomly selected one control site for each deposition site of each mammal. We evaluated multicollinearity among the explanatory variables by calculating the variance inflation factor (VIF) using the car package (Fox et al., 2012). Explanatory variables with VIF > 10 were systematically removed from the dataset until all potential explanatory variables had VIF < 10. Thus, the candidate models (5 mammals \times 2 seasons) had different sets of explanatory variables with VIF < 10. We calculated all possible combinations of explanatory variables in each candidate model. We used the MuMIn package for model selection (Bartoń *et al.*, 2019) and considered the model with Δ AICc < 2 and the lowest degrees of freedom as the most parsimonious model.

We conducted PCA to explore to what extent the microhabitat characteristics at the seed deposition sites differed among dispersers. PCA reduces the dimensionality of datasets and increases their interpretability with a minimum loss of information. In this analysis, each deposition site of SDS and control site was expressed as ordines in relation to eight microhabitat variables. Hence, it allowed us to differentiate the site characteristics between the control sites and the deposition sites in terms of SDS among different dispersers and to identify the microhabitat variables that explained the observed variation. We interpreted the PCA results on the basis of the three dimensions that accounted for more than 50 % of the variance of the data.

2.4.4. Seed deposition site differentiation: dispersal networks (H4)

We built a bipartite network to characterize the seed dispersal interactions between the mammalian species and the habitat types, and between the mammalian species and the plant species, for each season using bipartite network analyses (Dormann et al., 2009). In these networks, the number of seeds per species dispersed to each habitat type was represented proportionally to the total number of seeds for each dispersed plant species. The width of the links was scaled relative to the number of interactions between each disperser species–microhabitat or disperser species–dispersed species pair. We used the bipartite package (Dormann et al., 2009) in R to calculate the network metrics: H_2' , nestedness, and modularity. H_2' is a specialization index at the network level based on the deviation between the realized and expected number of interactions that the species experience (Blüthgen et al., 2006). Here, specialization indicates how each disperser interacts with specific plant species or deposition sites and with respect to other dispersers. A low degree of specialization indicates that dispersers interact with similar plant species or deposition sites. The metric ranges from 0 to 1, with values closer to 1 indicating a higher degree of specialization. We used the WNODF (weighted nestedness metric based on overlap and decreasing fill) metric in the weighted network (Almeida-Neto and Ulrich, 2011) to measure nestedness. Nestedness can be described as the tendency for nodes to interact with subsets of the interaction partners of better-connected nodes. Here, nestedness means that generalist dispersers interact with several specialist plant species or deposition sites. WNODF ranges from 0 (not nested) to 100 (completely nested). Modularity indicates the degree to which a subset of dispersers (i.e., modules) share the same plant species or deposition sites with other modules or dispersers. To evaluate the network modularity, we used the QuanBiMo algorithm, which calculates modularity by the likelihood and simulated annealing Monte Carlo approach (Dormann and Strauss, 2014). Modularity ranges from 0 to 1, and high values indicate more modular structures. We generated 1000 null networks using the algorithm

implemented by Vázquez et al. (2007) to test whether the observed network structure differed from a random structure. We estimated the statistical significance of the network metrics using the Z score (Dormann and Strauss, 2014), which indicates the number of standard deviations by which the observed metrics differ from those of random networks. Here, $|Z \text{ score}| > 2$, and higher values indicate significantly higher specialization, nestedness, or modularity than expected. We used the bipartite package (Dormann et al., 2017) to calculate the network metrics and for visualization.

3. Results

We collected 341 scats that contained plant seeds (bear: $n = 103$; macaque: $n = 52$; marten: $n = 92$; raccoon dog: $n = 45$; badger: $n = 49$) and 125 scats that did not contain seeds (bear: $n = 50$; macaque: $n = 18$; marten: $n = 20$; raccoon dog: $n = 16$; badger: $n = 21$) (Table S2, Supporting Information). For scats that contained seed, the mean \pm SD (median) number of seeds per scat was 1240.5 ± 2342 (620) for bear, 758.9 ± 1676 (121) for macaque, 236.9 ± 429.8 (58) for marten, 390.4 ± 556.9 (142) for raccoon dog, and 394.2 ± 641.8 (118) for badger. For scats with seeds, the mean number of dispersed species per scat was 1.5 ± 0.6 for bear, 1.2 ± 0.4 for macaque, 1.3 ± 0.4 for marten, 1.4 ± 0.5 for raccoon dog, and 1.5 ± 0.5 for badger. During both seasons, bears, raccoon dogs, and badgers defecated most scats with seeds in interior forests (75.6–100%; Table S2, Supporting Information). Macaques during summer and martens during both seasons commonly deposited scats with seeds in interior forests and treefall gaps (36.0–42.9%; Table S2, Supporting Information). However, macaques during autumn defecated predominantly in treefall gaps (87.5%; Table S2, Supporting Information).

3.1. Proportion of scats with seeds (H1a)

The proportion of scats containing seeds differed among dispersers only during autumn ($P < 0.05$ for interactive term between mammal and autumn; Fig. S2a and Table S3, Supporting Information). The probability of dispersing seeds by bears in autumn (60% [95% CI: 49–70%]) was significantly lower compared to other dispersers, especially macaques (83% [65–93%]) and martens (87% [75–94%]) (Fig. S2a, Supporting Information).

3.2. Seed abundance per scat (H1b)

During summer, the number of seeds per scat was significantly larger for bears than for the other mammals (bear: 1117.5 [879.6–1419.8]; macaque: 196.1 [138.8–277.0]; marten: 74.6 [57.5–96.7]; raccoon dog: 315.4 [224.7–442.7]; badger: 130.3 [87.4–194.3]; Fig. S2b and Table S3, Supporting Information). During autumn, the number of seeds per scat was higher compared to summer for all mammals (Fig. S2b and Table S3, Supporting Information).

3.3. Number of fleshy-fruited species per scat (H1c)

The number of species per scat did not differ among dispersers or between seasons because the null model was selected as the most

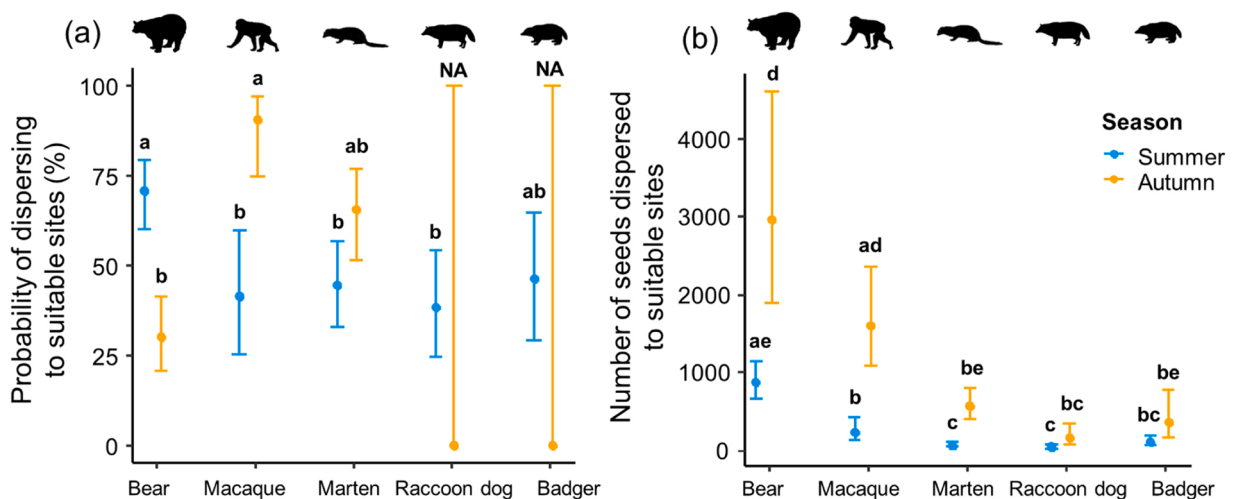


Fig. 1. (a) Estimated probability of dispersing seeds to suitable sites and (b) number of seeds dispersed to suitable sites by mammalian dispersers in summer and autumn. Dots indicate means and whiskers indicate 95% confidence intervals of (a) probability of dispersing seeds to suitable sites (b) and the number of seeds dispersed to suitable sites. The groups of dispersers in each season with the same letter show no significant difference, whereas the groups with different letters show significant differences. Significance is based on 95% confidence interval of the calculated predicted estimates.

parsimonious model (Table S3, Supporting Information).

3.4. Seed dispersal to suitable microhabitat: probability of occurrence (H2a)

In summer, bears deposited seeds in suitable microhabitats more often than any other species (bear: 71 % [60–79 %]; macaque: 41 % [25–60 %]; marten: 44 % [33–57 %]; raccoon dog: 38 % [25–54 %]; badger: 46 % [29–65 %]; Fig. 1a). During autumn, macaques dispersed the highest proportion of scats to suitable sites (macaque: 91 % [75–97 %]; marten: 65 % [52–77 %]; bear: 30 % [21–42 %]; Fig. 1a), and raccoon dogs and badgers did not disperse seeds to suitable habitats during that season.

3.5. Seed dispersal to suitable microhabitats: seed abundance (H2b)

During summer, the number of seeds per plant species per scat dispersed to suitable regeneration microhabitats was significantly larger for bears compared to the other mammals (bear: 875.4 [669.4–1144.6]; macaque: 238.7 [130.9–435.1]; marten: 67.6 [45.5–100.3]; raccoon dog: 47.4 [27.6–81.4]; badger: 105.9 [59.4–188.7]; Fig. 1b and Table S4, Supporting Information). The number of seeds dispersed to suitable sites was higher in autumn than in summer for all mammals (Fig. 1b and Table S4, Supporting Information). During autumn, the number of seeds dispersed to suitable microsites did not differ significantly between bears and macaques, but was significantly lower for marten (bear: 2963.5 [1903.4–4613.9]; macaque: 1601.9 [1089.3–2355.7]; marten: 562.5 [393.9–803.4]; Fig. 1b and Table S4, Supporting Information).

3.6. Seed deposition site differentiation: microsite characteristics (H3)

Habitat characteristics of suitable microhabitat varied among dispersers (Table 1), and the combination of variables describing suitable microhabitat varied between seasons for each disperser (Table 1). For bears, the probability of seed deposition to suitable sites increased with increasing tree density and altitude, and was more likely to occur in less steep terrain and at sites with relatively little litter ($P < 0.05$; Table 1). During autumn, canopy openness and number of trees had a positive effect ($P < 0.05$; Table 1) on the probability of deposition in a suitable site, whereas slope steepness had a negative effect ($P < 0.05$; Table 1). For macaques during summer, soil hardness and the amount of litter negatively affected the probability of deposition into a suitable site ($P < 0.05$; Table 1), and litter amount was the only variable affecting this probability during autumn ($P < 0.05$; Table 1). For marten during summer, canopy openness had a positive effect ($P < 0.05$; Table 1), but litter amount and soil hardness had negative effects ($P < 0.05$; Table 1). During autumn, litter amount and slope negatively affected the probability for deposition in suitable habitat for marten ($P < 0.05$; Table 1). For raccoon dog during summer, vegetation cover had a positive effect ($P < 0.05$; Table 1), but soil hardness had a negative effect ($P < 0.05$; Table 1). For badger during summer, slope had a negative effect ($P < 0.05$; Table 1) on deposition in suitable habitat. We did not observe SDS by raccoon dog and badger during autumn.

Table 1
Differences in microhabitat characteristics of seed dispersal to suitable deposition sites by frugivorous mammals.

Model		Variable	Mean	SE	Z value	P value	AICc
Summer	Bear	Intercept	-1.859	1.956	-0.951	0.342	120.26
		Altitude	0.002	0.001	2.059	0.040	
		Canopy openness	0.326	0.169	1.927	0.054	
		Litter amount	-0.205	0.090	-2.280	0.023	
		Slope	-0.300	0.055	-5.428	< 0.001	
		Number of trees	1.167	0.255	4.572	< 0.001	
Autumn	Bear	Intercept	-7.216	3.842	-1.878	0.060	30.68
		Canopy openness	1.103	0.367	3.006	0.003	
		Number of trees	1.246	0.582	2.141	0.032	
		Slope	-0.206	0.085	-2.417	0.016	
		Soil hardness	14.965	6.245	2.396	0.017	
Summer	Macaque	Soil hardness	-0.427	0.188	-2.268	0.023	29.298
		Litter amount	-0.567	0.272	-2.090	0.037	
		Intercept	9.732	2.508	3.881	< 0.001	
Autumn	Macaque	Litter amount	-0.834	0.197	-4.240	< 0.001	51.57
		Intercept	2.775	2.501	1.110	0.267	
Summer	Marten	Canopy openness	0.684	0.249	2.751	0.006	36.72
		Litter amount	-0.353	0.171	-2.056	0.040	
		Soil hardness	-0.210	0.092	-2.278	0.023	
		Intercept	12.818	3.757	3.411	< 0.001	
Autumn	Marten	Litter amount	-0.520	0.145	-3.579	< 0.001	33.60
		Slope	-0.424	0.156	-2.717	0.007	
		Intercept	4.674	2.542	1.839	0.066	
Summer	Raccoon dog	Vegetation cover	0.066	0.028	2.352	0.019	25.74
		Soil hardness	-0.347	0.129	-2.701	0.007	
		Intercept	3.856	1.538	2.508	0.012	
Summer	Badger	Slope	-0.310	0.109	-2.842	0.004	36.05

Only the most parsimonious models, from all possible combinations of explanatory variables are represented in the table. Bold fonts indicate significant variables at an $\alpha = 0.05$ level.

The first three PCA dimensions explained 53.0 % (PC1: 23.8 %; PC2: 15 %; PC3: 14.2 %) and 63.1 % (PC1: 34.6 %; PC2: 15.3 %; PC3: 13.1 %) of the variance in the microhabitat characteristics at suitable sites during summer and autumn, respectively (Fig. 2). During summer (Fig. 2a–b), the first dimension was characterized by high loadings of litter amount (loading value -0.58) and soil hardness (-0.52). The second dimension was characterized by the high loadings of the number of trees (-0.58) and canopy openness (0.51). The third dimension had high loadings of number of shrubs (-0.58) and vegetation cover (-0.63). During autumn (Fig. 2c–d), the first dimension had high loadings of litter amount (0.53), soil hardness (0.50), and canopy openness (-0.49); the second dimension had high loadings of the number of trees (-0.71) and vegetation cover (0.53); and the third dimension had a high loading of altitude (-0.82). During both seasons, control sites were associated with harder soils, steeper slopes, and more litter compared to the deposition sites of all dispersers (Fig. 2). The microhabitats of suitable deposition sites of bears in summer mostly overlapped with those of control sites and the microhabitats of the deposition sites of other dispersers (Fig. 2a–b) compared to autumn (Fig. 2c–d). The suitable deposition sites of macaque and marten varied greatly and overlapped relatively little with those of other species during both seasons (Fig. 2). During summer, raccoon dog and badger deposition sites were clustered by microsite characteristics compared to control sites and deposition sites of other dispersers (Fig. 2).

3.7. Seed deposition site differentiation: dispersal networks (H4)

We made tripartite networks to show the differences in the structures of networks among dispersers, dispersed plants and deposition sites (Fig. 3). During summer, bears mainly dispersed seeds of species of the interior forests (proportion of seeds dispersed: 74.4

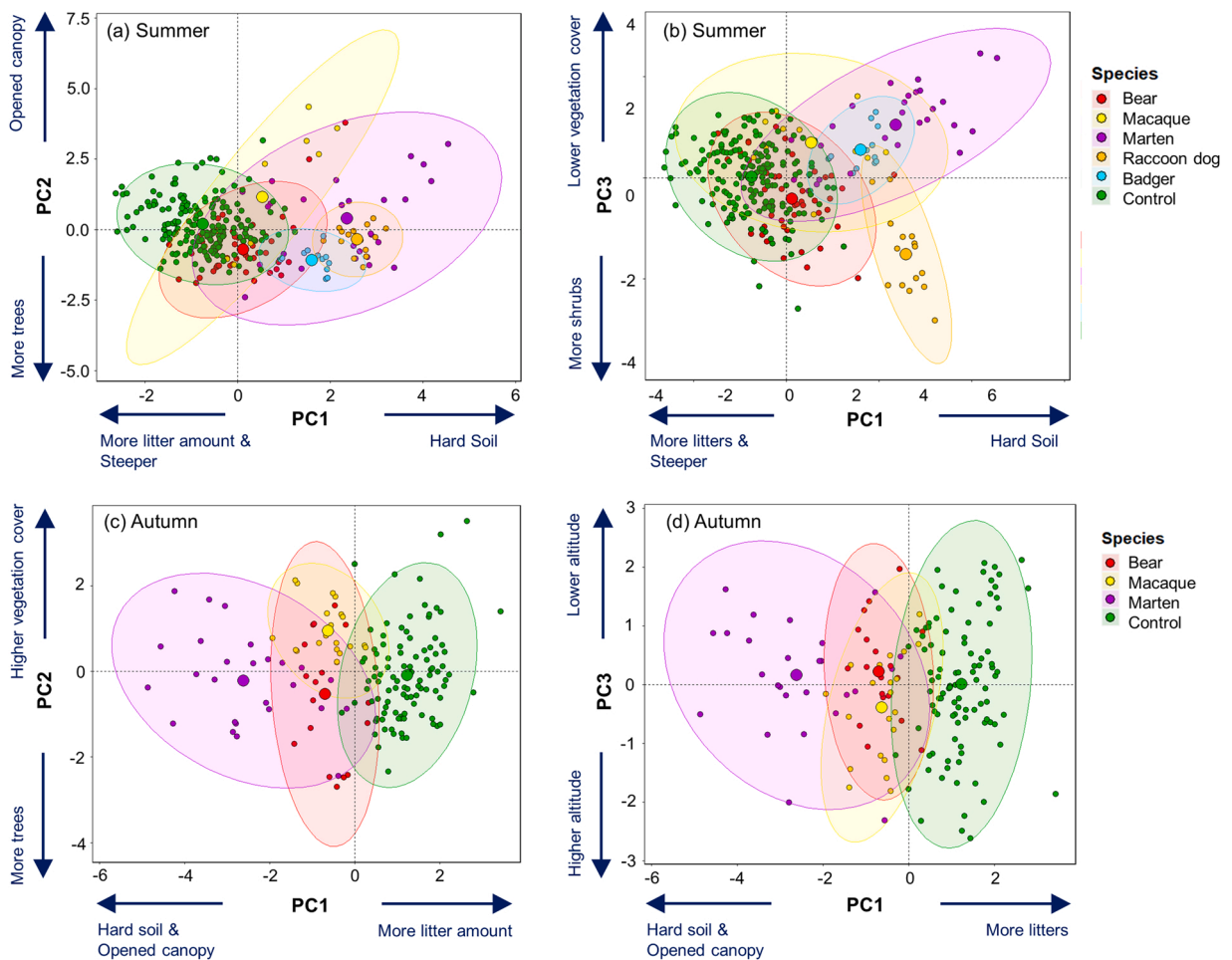


Fig. 2. Principal component analysis showing variation in microhabitat variables at scat deposition sites at suitable regeneration sites by mammalian dispersers in (a, b) summer and (c, d) autumn, and in control sites. The PCA scores of each scat site and control site are shown as points. Distance between points correspond to the degree of similarity between the microhabitats of the scat deposition sites of the five mammalian species and the control sites. Dispersers and control sites are represented in color coded ellipses. Raccoon dogs and badgers are not included in the autumn charts because they appeared not to disperse seeds to suitable habitats during autumn.

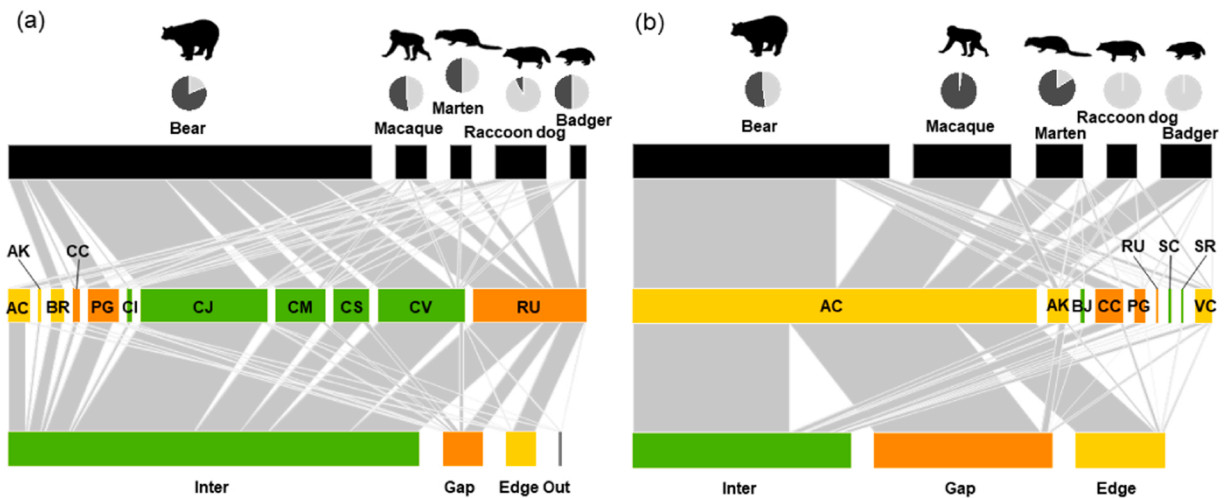


Fig. 3. Weighted tripartite network structure for mammalian dispersers, fleshy-fruited species, and deposition site type in (a) summer and (b) autumn. The top nodes show the five mammalian species acting as seed dispersal agents. The colored middle and bottom nodes correspond to dispersed seed species colored by three regeneration site types and four microhabitat types of the scat deposition sites, respectively. Abbreviations: “inter,” interior forest; “gap,” treefall gap; “edge,” forest edge; “out,” outside the forest. Because these networks were created from seed-based data, the width of each link indicates the seed number dispersed by the corresponding mammal. The pie charts at the top show the proportion of seeds that each mammalian species dispersed to suitable regeneration sites for the plant species. See Table S1 for names of dispersed species.

%). Macaque and raccoon dogs frequently transported seeds of treefall gap species (macaque: 73.5 %; raccoon dog: 53.9 %). Marten and badgers dispersed seeds of interior forest species (marten: 37.8 %; badger: 50.3 %) as well as treefall gap species (marten: 47.0 %; badger: 49.7 %). During autumn, all mammalian species mostly dispersed seeds of treefall gap species (bear: 84.9 %; macaque: 99.4 %; marten: 96.4 %; raccoon dog: 98.9 %; badger: 96.7 %). During summer, more seeds of interior forest species were deposited at suitable sites (94.3 %) by all mammalian species compared to other plant species (gap: 12.8 %; edge: 31.9 %). During autumn, a high proportion of interior forest species seeds were dispersed to suitable sites (78.4 %), and more treefall gap species seeds were dispersed in autumn than in summer (59.3 %). The proportion of seeds dispersed in suitable sites declined for forest edge species (8.7 %) during autumn.

The seed dispersal network between dispersers and deposition sites was significantly more specialized (Z score = 22.940; Table 2) and modular (Z score = 18.107; Table 2) compared to random networks. During autumn, the bipartite network of dispersers–deposition sites was significantly more specialized (Z score = 3.596; Table 2) and modular (Z score = 4.116; Table 2) than random networks. In summer, however, the network of dispersers–deposition sites had significantly lower nestedness than random networks (Z score = -2.689; Table 2), whereas in autumn, the network was not significantly different from random networks (Z score = -1.388; Table 2). The seed dispersal network of disperser–dispersed plant was significantly more specialized and modular in summer (Z score_{H2'} = 36.075; Z score_{Modularity} = 40.356; Table 2) and autumn (Z score_{H2'} = 16.081; Z score_{Modularity} = 15.116; Table 2) compared to random networks. Like the disperser–deposition site network, the disperser–dispersed plant network showed significantly

Table 2
Metrics of networks of seeds dispersed to suitable sites by frugivorous mammals.

Network type	Network metric	Observed network	Random network	Z score
Mammal–Deposition site	Summer			
	H_2'	0.199	0.026	22.940
	wNODF	43.750	73.301	-2.689
Mammal–Deposition site	Autumn			
	H_2'	0.455	0.197	3.596
	wNODF	33.333	54.479	-1.388
Mammal–Fleshy-fruited species	Summer			
	H_2'	0.260	0.024	36.075
	wNODF	43.846	71.593	-5.654
Mammal–Fleshy-fruited species	Autumn			
	H_2'	0.103	0.014	16.081
	wNODF	59.316	70.744	-1.943
	Modularity	0.064	0.009	15.116

|Z score| > 2 indicates observed network significantly higher specialization, nestedness, or modularity than random network.

lower nestedness than random networks in summer (Z score = -5.654 ; Table 2). However, the network did not significantly differ from random networks in autumn (Z score = -1.943 ; Table 2).

We found two modules in dispersers–deposition sites and dispersers–dispersed plants. During summer, bears, raccoon dogs, and badgers mainly dispersed seeds of interior forest species to suitable sites (Fig. 4a,c), whereas macaques and martens predominantly dispersed seeds of species of treefall gap and forest edge to suitable sites (Fig. 4a,c). During autumn, bears predominantly dispersed species of the interior forest and treefall gap to the interior forest or forest edge as suitable sites (Fig. 4b,d). Macaques mostly dispersed species of forest edge to treefall gap as suitable sites (Fig. 4b,d). Although martens mostly dispersed species of forest edge to forest edge as suitable sites (Fig. 4d), they partly dispersed interior forest species to suitable sites, thus they were included in the same module as

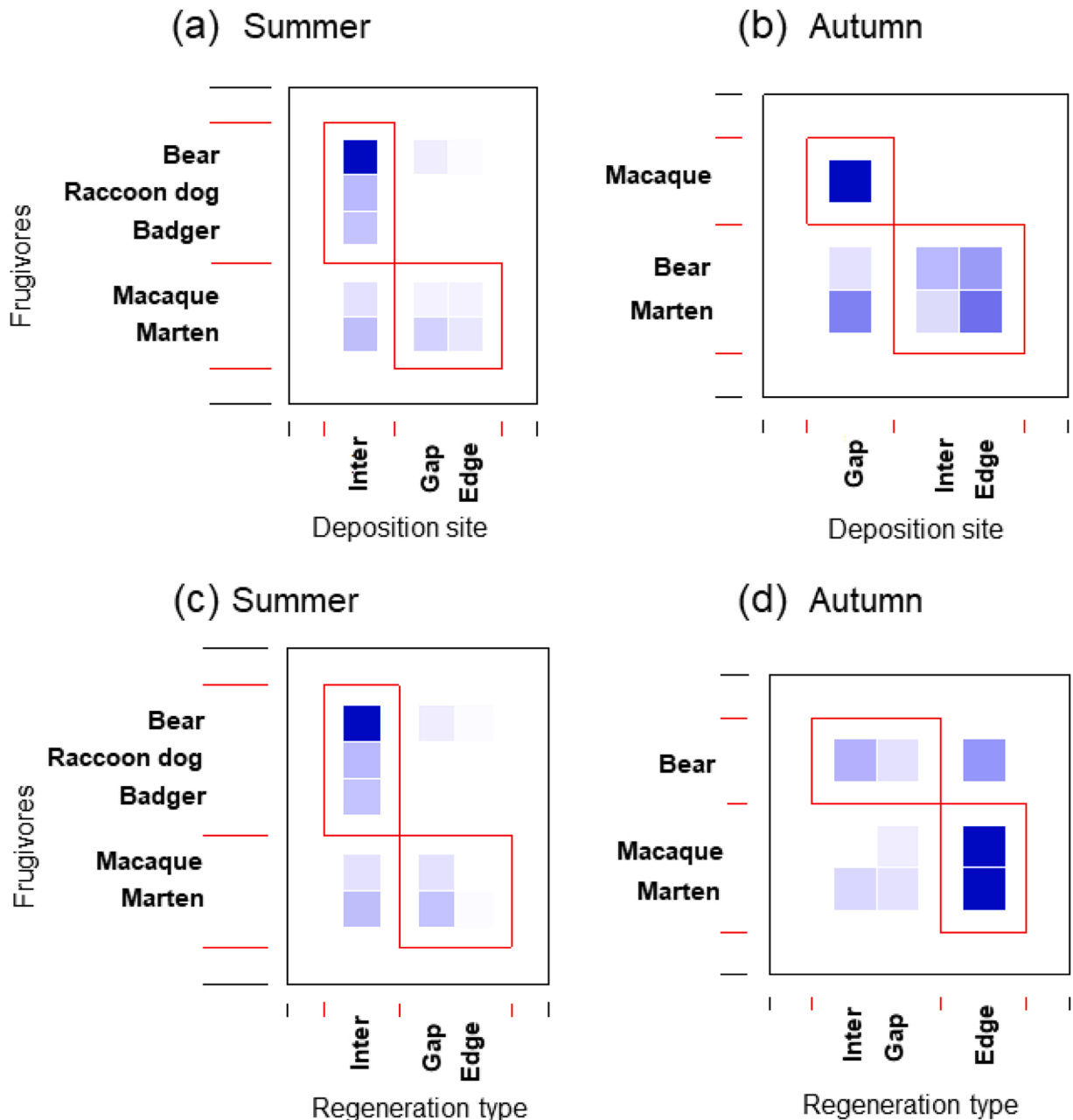


Fig. 4. Modular structure of mammalian dispersers–deposition site type networks in (a) summer and (b) autumn and mammalian dispersers–fleshy-fruited species networks in (c) summer and (d) autumn. Darker blue squares indicate that mammalian species dispersed more seeds to suitable regeneration habitats or more seeds of fleshy-fruited species to suitable sites for each regeneration type. Red boxes delineate the two modules. Modules were identified by the QuanBiMo algorithm. Abbreviations: “inter,” interior forest; “gap,” treefall gap; “edge,” forest edge. Raccoon dogs and badgers are not included in the autumn charts because they did not disperse seeds to suitable habitats.

bears (Fig. 4b).

4. Discussion

Our results show that not only quantitative but also qualitative components of endozoochorous seed dispersal vary among dispersers and between seasons. Most studies on frugivory and seed dispersal in temperate regions have traditionally focused on birds (e.g. Herrera and Jordano, 1981; García et al., 2018; Ohkawara et al., 2022), and information regarding the role of mammals as seed dispersers remains limited (but see García-Cervigón et al., 2018; García-Rodríguez et al., 2022). Because the quantitative component of seed dispersal is considered a good proxy of the total effectiveness of frugivores, most studies have systematically ignored factors affecting the qualitative component of seed dispersal, such as differences in the characteristics of deposition sites among different frugivores. Our study could help fill these gaps of knowledge. Moreover, seasonality is shown to be important for both quantitative and qualitative components (García-Cervigón et al., 2018; González-Varo et al., 2019; García-Rodríguez et al., 2022). The animal assemblages indicate that seasonal dynamics are driven by flowering or fruiting phenology, and result in a turnover of interactions (Morente-López et al., 2018; Dehling et al., 2021). Plant–animal mutualisms in temperate zones with high seasonal variability show dynamic interactions, and our study evaluated differentiation in dispersal niches of dispersal agents while accounting for seasonality.

4.1. Difference among seed dispersal agents across seasons in the quantitative component

We found that the probability of fleshy-fruit seed dispersal was similar among different dispersal agents during summer but not during autumn, when the probability that bears would disperse seeds declined (H1). This is probably because Asian black bears consume mostly hard mast during autumn to store fat for hibernation (Koike, 2010). The number of seeds dispersed per scat differed substantially among dispersal agents and seasons. Bears dispersed the largest number of seeds per scat during both summer and autumn, probably as a direct consequence of their large body size and food intake compared to the other studied dispersers (body mass of bear: 58.3 ± 16.0 kg (mean \pm SD); macaque: 9.8 ± 1.8 kg; marten: 1.1 ± 0.2 kg; raccoon dog: 3.5 ± 0.4 kg; badger: 10.2 ± 0.7 kg; unpublished data).

4.2. Differences among seed dispersal agents across seasons in the qualitative component

The probability of SDS varied among dispersers and between seasons (H2). During summer, the probability was higher for bears because bears feed mainly on fruit species that regenerate in interior forest habitats (e.g., *Cerasus verecunda* and *C. jamasakura*; Koike, 2010). Macaques and martens often feed on fruits that regenerate in interior forest, as well as in treefall gaps and forest edges (e.g., *Rubus* spp.). However, the probability of these species dispersing the seeds to such regeneration sites was found to be low in this study. Macaques and martens consume leaves and invertebrates as well as fruit (Ohdachi et al., 2009); thus, they likely forage across various habitats, and deposition sites do not necessarily correspond to regeneration sites. Raccoon dogs and badgers forage for fruits such as *Actinidia* spp. in interior forest, treefall gap, and forest edge, but their deposition sites are located predominantly within forests (Ohdachi et al., 2009), which may reduce the probability of seeds being deposited in a suitable habitat for regeneration. During autumn, macaques and martens forage mainly on fruits of species such as *Akebia*, which grow in treefall gap and forest edge, and they appeared to use these open areas for scat deposition. Bears feed extensively on acorns, which occur predominantly in the interior forest, and occasionally forage on fleshy fruits that occur more in treefall gap and forest edges (Koike, 2010). Therefore, the contribution of bears to SDS decreased during autumn. The number of seeds dispersed in suitable sites differs among the mammal species and it may depend on the body size of the dispersal agent. Seed abundance of SDS was also higher in autumn than in summer for all mammalian species. This may be due to the increase in bearing of fruits with small seeds during autumn, and especially for macaque and marten, the shift of foraging on leaves and invertebrates to fleshy fruits.

The microhabitat characteristics of the deposition sites varied among the dispersal agents and between seasons, likely owing to species specific habitat selection and behavioral traits (Ohdachi et al., 2009). The seasonal changes may also reflect different spatial distributions of available food resources between summer and autumn. Bears and macaques substantially shared deposition site characteristics during both seasons. Marten dispersed seeds to various microhabitats, including ones with habitat characteristics different from those of sympatric dispersers. Raccoon dogs and badgers dispersed seeds in a limited range of microhabitats.

4.3. The network structure between disperser–deposition site and disperser–dispersed plant

We documented the existence of complementary structures (significant specialization and modularity, and low or no apparent nestedness) of seed dispersal networks between dispersers and the suitable microhabitats of deposition sites during summer and autumn. The results imply that the studied dispersers have specific functions in terms of SDS across the entire landscape. One possible explanation for the network structure might be seasonal temperature variations and seasonal partitioning of fruiting phenology in temperate regions such as our study area (Schleuning et al., 2014). These variations probably mediate diet and behavior in the seed disperser community, causing the seed dispersal network to have a modular structure. It is possible that the structure of our seed dispersal networks was due to the relatively low species (and microhabitat type) richness and low human impact, both of which are associated with a more nested, less modular seed dispersal network structure (see Sebastián-González et al., 2015). We detected that the number of modules was constant over the seasons but that the number of dispersal agents in each module varied by season and the relationships we focused on (i.e., dispersers–deposition sites or dispersers–dispersed plants). Therefore, there appeared to be some

division in the seed disperser roles in terms of SDS among the disperser agents in our study system. Despite the generalist feeding habits of all of the studied mammalian species, they dispersed seeds to different deposition sites (Fig. 3).

4.4. Seasonality and temporal effects on differences in microsite suitability

We detected the turnover of probability of SDS from summer (bear > badger > macaque, marten, and raccoon dog) to autumn (macaque and marten > bear > raccoon dog and badger). Macaques and martens dispersed more seeds in autumn. The two mammals may compensate for the decline of contribution to seed dispersal by the other mammals, especially bears, that can disperse the greatest number of seeds. Judging from this relationship, we can see some complementarity across seasons. Furthermore, bears, macaques, and martens turned over in two modules from summer (bear–‘inter’ vs. macaque and marten–‘gap’ and ‘edge’) to autumn (bear and marten–‘inter’ and ‘edge’ vs. macaque–‘gap’; Fig. 4a,b). However, the similarity of the microhabitat characteristics did not reflect the turnover (bear and macaque shared the microhabitat variation vs. marten had unique and high variation; Fig. 3). Therefore, we suggest that they may play different functional roles to disperse in finer scale habitats between seasons.

In central Japan, fruit abundance can exhibit a remarkable fluctuation across the years, with the number of fruiting plants and mature fruits fluctuating repeatedly every other year (Ohkawara et al., 2022). Although we collected the scats for two years, we pooled all the data for analysis because we did not have a sufficient sample size to evaluate the fluctuation across years. Thus, our results might be hiding some variability among years. We believe that the fruit abundance of some of the studied fleshy-fruit species (e.g., *Prunus grayana* and *Cornus controversa*) may have changed from year to year in our study area. The fluctuation of fruit abundance affected the behavior of dispersers and network structure (Ohkawara et al., 2022). In our study system, the fluctuation could alter the dispersed seed numbers and probability of being dispersed to suitable deposition sites.

4.5. Future work

In future work, integrated observation data, such as the regeneration rates of plant species, are needed to improve our understanding of deposition to suitable microsites. In addition, avian dispersers, which can be important dispersal agents in temperate forests, should be included (Herrera and Jordano, 1981). Birds can potentially disperse seeds to different microhabitats and act as “connectors” that bridge different deposition environments through long-distance dispersal, thereby linking different modules (Olesen et al., 2007) in network structures (Rumeu et al., 2020). However, bears and martens are also capable of long-distance seed dispersal (bear up to 22,000 m, Koike et al., 2011; marten up to 5000 m, Ohdachi et al., 2009), especially compared to macaques and raccoon dogs (macaque up to 1200 m, Ohdachi et al., 2009; raccoon dog up to 938 m, Mise et al., 2016; badger up to 1100 m; Koike et al., 2022). Connector species improve the survival of plant offspring by allowing the species to escape negative-density dependency effects (Jansen et al., 2008; Terborgh et al., 2008; Brodie et al., 2009). Long-distance seed dispersal may also affect plant demography by other means (e.g., by increasing gene flow among populations or triggering the colonization of new areas; Cain et al., 2000). Therefore, bears and martens could have quality components other than ones we focused on in this study. Furthermore, we did not analyze other seasons due to the sample size, but only few scats might be relevant for the demography of these species (González-Varo et al., 2019). In future work, it would be informative to also consider the contribution of such ‘minority depositions’ in the seed dispersal network.

5. Conclusions

The annual cycle and behavioral traits of dispersal agents and the seasonal and spatial variation in the availability of their foods mediate the entire endozoochory process, from foraging and seed intake to movement during digestion and eventual seed deposition (Nathan and Muller-Landau, 2000). In general, effective seed dispersers ingest large quantities of seeds that survive gut passage and deposit them at sites with good conditions for germination and establishment (Schupp et al., 2010, 2017). It remains a challenge to assess endozoochorous seed dispersal in complete assemblages of dispersers in ecosystems and to determine how they contribute to the dispersal of plant life across the entire landscape. Although the five mammal species included in this study are generalist frugivores, they have considerable differences in food habits and behavioral traits (e.g., home range size and placement, habitat selection, sociality, and activity patterns; Ohdachi et al., 2009). The differences in ecological characteristics between species (disperser and dispersed) can modulate the structure of endozoochorous seed dispersal networks and result in overlapping and complementary relationships for seed dispersal across landscapes (Sarmiento et al., 2014). The ecological consequences of the complementary modules we found would not necessarily extrapolate to other temperate regions. Human disturbances such as habitat loss and fragmentation decline biodiversity (Fahrig, 2003; Betts et al., 2017) and may reduce seed dispersal distances by more restricted mammal movement (Tucker et al., 2018, 2021). We urge to protect the temperate forests, where a high diversity of mammalian frugivores has been preserved, as the richness of mammalian seed dispersers and functional diversity decline in intensely degraded areas (Arévalo-Sandi et al., 2018). We suggest that conservation and management of mammalian frugivores is necessary to enhance their roles in endozoochorous seed dispersal.

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Authors' contributions

KT and SK conceived and designed the study and performed the field research, KT and SS analyzed the data, and KT, SS, TN, KY, and KS wrote the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02335](https://doi.org/10.1016/j.gecco.2022.e02335).

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