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Fine-scale spatiotemporal variation in seed-rodent interactions: A potential contribution to species coexistence

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ABSTRACT

Seed predation and dispersal by rodents plays an important role in seedling establishment and forest regeneration. Spatiotemporal variation in seed availability at fine scales is ubiquitous in the forest because of the different spatial locations and fruiting phenology among tree species, which may further lead to spatiotemporal variation in seed-rodent interactions. However, previous research has generally treated such variation as random effects among experimental replicates and provides few relevant explanations. Therefore, in this study, we directly tested the spatiotemporal variation in seed predation and dispersal at a fine-scale by manipulating a dynamic pattern of seed availability, releasing different species of seeds into the forest at 10 m intervals in space and 6 day intervals in time. In total, we tracked the dispersal and predation of 40,500 seeds belonging to 45 tree species in a subtropical forest in southwest China for three consecutive years. Our results provide strong evidence that fine-scale spatiotemporal variation in seed dispersal and predation by rodents always exists, although the overall intensity of seed harvest and removal significantly differs among experimental years and plots. Furthermore, the fine-scale spatiotemporal effect differs among plant species, indicating that the spatiotemporal effect may be species specific. Consequently, any specific seed may have the probability to survive or be dispersed as long as it appears at a specific site and time. Our findings further suggest that the fine-scale spatiotemporal variation in seed-rodent interactions may contribute to species coexistence in the forest, at least at the seed stage. Generally, we expect that similar fine-scale spatiotemporal variations occur in other plant-animal interactions, such as herbivory and pollination. Incorporating fine-scale spatiotemporal variation into future plant-animal studies may help us to gain a better understanding of species coexistence and biodiversity maintenance.

1. Introduction

Seed predation and dispersal by animals, especially rodents, is a key ecological process that plays an important role in seedling establishment and forest regeneration (Briggs et al. 2009, Zeng et al. 2019). Different species of seeds usually differ greatly in innate seed traits, such as seed size, nutrient content, and physical and chemical defenses, all of which significantly influence rodent foraging decisions (Vander Wall 2010, Lichti et al. 2017). Thus, rodents often show a consistent hierarchical preference among species of seeds during their foraging processes, for example, eating smaller-sized and low-fat-content seeds *in situ* while removing and caching larger-sized and higher fat content seeds (Xiao et al. 2006a, Wang and Chen 2009, Lichti et al. 2017). In forests, many tree species coexist and often overlap in fruiting time, supplying a large amount of seeds during the fruiting season (Takahashi et al. 2011, Yang et al. 2020). In such cases, some species of seeds may continually experience more predation and receive fewer dispersal services than other species because of the consistent interspecific variation in seed traits. This unequal seed predation and dispersal among species may further translate into a consequently interspecific variation in seedling establishments, thereby changing the species composition.

This prediction is based on the assumption that rodents encounter all the seeds in the forest at the same time and in the same place, and that making the optimal choice among a large number of seeds requires little time and energy, both of which may not really exist in nature. Usually, diverse species of trees spread into different positions in the forest,

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which further leads to spatial variation in both seed abundance and composition of seed species at fine scales because of 1) large variation in seed production and seed traits among both interspecific and intraspecific trees (Shimada et al. 2015, Wang and Ives 2017), and 2) differences in tree species compositions at a small scale, which may consequently lead to variation in the relative frequency of seeds among species (Condit et al. 2000, Garzon-Lopez et al. 2015). Furthermore, the fruiting time peak often varies greatly among species and among individuals within species, even though their fruiting periods show significant overlaps (Takahashi et al. 2011, Li et al. 2012, Sunyer et al. 2014). In this manner, the spatiotemporal variation in seeds available in the forest may further lead to the fact that rodents often make their foraging selection among seeds in a subset of the whole forest at a specific spatiotemporal point. As a consequence, seeds of a given species may face different fates (e.g., ignored versus harvested, and eaten *in situ* versus removed) depending not only on the seed trait themselves (Wang and Chen 2009, Lichti et al. 2017) but also the situation near them, for example, total seed availability (Xiao et al. 2013, Wang 2020a), relative frequency of seeds between the target species and its neighboring species (Garzon-Lopez et al. 2015, Yang et al. 2020), and the contrast of seed traits between target seeds and their neighboring seeds (Wang 2020b).

Diverse species of rodents also coexist in the forest, and they often occupy different niches and vary in the activity range (Dueser and Shuggart Jr. 1979, Roll et al. 2006). They may also differ in body mass, physiological needs, and foraging preferences (Munoz and Bonal 2008, Cao et al. 2018). Even within the same rodent species, different foraging preferences may occur among individuals, possibly because of variations in body size, foraging experience, gender, or personality (Wang and Chen 2011, Zwolak 2018, Schirmer et al. 2019). Therefore, the spatiotemporal variation in rodent abundances and species composition may lead to significant differences in seed fate in space and time. Furthermore, other factors, such as differences in microhabitats (e.g., the spatial pattern of shelter shrubs or canopy gaps) (Iida 2006, Wang and Corlett 2017), real-time temperature (Orrock and Danielson 2009), and the phase of the moon (Perea et al. 2011), that affect rodent foraging behavior may also contribute to a spatiotemporal variation in seed dispersal and predation patterns.

As previously mentioned, large variations in seed predation and dispersal may occur in both space and time. Numerous studies have focused on this question at relatively large scales, such as years and seasons (Wang and Chen 2012, Zhang et al. 2021), forests (Zeng et al. 2019), and even large latitudinal and elevation gradients at continental and global scales (Hargreaves et al. 2019). However, few studies have directly tested the spatiotemporal variation in seed predation and dispersal at fine scales, even though they have different ecological significance and are affected by different factors compared to large spatiotemporal scales. Despite this, we can still find some evidence that such fine-scale spatiotemporal variation may always occur. For example, seed predation and dispersal by rodents often show large variation among experiment days and sample sites within the same forest (Wang and Chen 2008, Cao et al. 2016, Wang 2020a). However, most studies usually treat such variation as random effects among experimental replicates and provide few relevant explanations. Therefore, in this study, to obtain a more comprehensive understanding of seed predation and dispersal variation at fine spatiotemporal scales, we manipulated a fine-scale dynamic pattern of seed availability by releasing different species of seeds into the forest at a 10 m interval in space and a 6 day interval in time. In total, we tracked the dispersal and predation of 40,500 seeds belonging to 45 tree species in a subtropical forest in southwest China for three consecutive years. The aim of this study was to answer the following questions: 1) Do seed predation and dispersal by rodents vary at a fine spatiotemporal scale? 2) If so, is the fine-scale spatiotemporal variation similar among seed species?

2. Material and methods

2.1. Study site

The field experiments were conducted for three consecutive years (2017 – 2019) in a subtropical evergreen broadleaf forest in the Ailao Mountains, Yunnan Province, southwestern China (24°32′N, 101°01′E, altitude 2045 m). The mean annual temperature is 11.7 °C, and the annual precipitation is 1923.1 mm, much of which occurs during the wet season (from May to October). The dominant tree species is the *Fagaceae* species, including *Castanopsis wattii*, *Lithocarpus xylocarpus,* and *Lithocarpus hancei*. A mast seeding phenomenon occurred in 2019 for these three *Fagaceae* species, in which many more seeds were produced in the forest than were in 2017 and 2018 (unpublished seed rain data). Small rodents were primarily responsible for the seed predation and dispersal of our experimental seeds, with the dominant species being *Niviventer confucianus*, *Apodemus ilex*, and *Niviventer excelsior*. According to our live-trap surveys, rodent abundance differed annually. For example, the trap success rates were 6.5% and 12.2% (n = 245 trap days) in 2017 and 2018, respectively.

2.2. Study species

To guarantee a sufficient species sample size, seeds of 45 tree species were purchased from the Seed and Seedling Company of Yunnan for use in our experiments: 28 species in 2017, 30 species in 2018, and 32 species in 2019, wherein 14 species were used in all three years. The experimental seeds were not collected from the studied plots. However, this did not bias our target question (i.e., variation in seed dispersal and predation by rodents at fine spatiotemporal scale) because 1) of the 45 tree species, 38 were distributed widely in our study area or nearby regions (<200 km), while the remaining seven species were introduced species and have been widely used for afforestation for decades in the study area or nearby regions. Therefore, the rodents in our study plots were not unfamiliar with the experimental seeds. 2) It is a common method to use seeds from outside the studied plots to study seed-rodent interaction, for example, examining the effects of mast seeding of sympatric species on seed dispersal by rodents (Lichti et al. 2014, Yu et al. 2020), the effects of seed traits on rodent foraging behavior (Zhang et al. 2018), and comparisons of seed-rodent interactions among forests (Dittel and Vander Wall 2018, Yang et al. 2018). 3) Rodents make foraging decisions mainly based on seed traits (Vander Wall 2010), and have the ability to identify tiny differences among seeds, regardless of whether they are local or introduced species, even among artificial seeds made of clay and peanut powder (Wang and Chen 2009, Gong et al. 2015, unpublished data of artificial seed experiment collected in the same forest).

2.3. Seed dispersal experiment

In this study, three 50 m × 50 m plots (>150 m apart) were established in the forest. The plots were assumed to be spatially independent because seeds are usually dispersed<30 m in this forest (Lang and Wang 2016, unpublished data of artificial seed experiments). In each plot, 36 seed release points were located in a 6 × 6 grid, which had 10 m between the points. In 2017, 12,600 seeds (450 seeds × 28 species) were selected and weighed individually. Each seed was drilled with a 0.6 mm hole at the base and connected to a plastic tag (3.5 cm long and 2.5 cm wide) by a 15 cm long steel thread, and each tag was uniquely numbered for individual seed identification using the methods of Xiao et al. (2006b) and Wang and Ives (2017) with a slight modification. Seeds were released into the forest 15 consecutive times every 6 days at the end of the fruiting season to stagger the possible effects of local seed production, with 840 seeds being released each time (10 seeds × 28 species × 3 plots). For each release, 28 points were randomly selected from each plot, and one species was randomly assigned to one point, after which 10 seeds of the selected species were released at the point along a circle (approximately 30 cm in diameter) with the tags pointing outward. The same procedure was followed to release 13,500 seeds in 2018 (450 seeds × 30 species) and 14,400 seeds in 2019 (450 seeds × 32 species).

The overwinter fate of each tagged seed was checked in May of the following year. Previous studies in the same forest have indicated that seeds are usually dispersed by rodents within<30 m (Lang and Wang 2016, unpublished data). Therefore, we searched the areas with a radius of 30 m around each point, and performed a further search haphazardly beyond this area to relocate as many of the dispersed seeds as possible. Following the step-wise decision-making concept in scatter-hoarding rodents (Wang et al. 2013), seed fates were first divided into two categories: ignored (i.e., seeds that were left intact at their original release points) versus harvested by rodents. The harvested seeds were further divided into seeds eaten *in situ* (i.e., seeds that were entirely or partially consumed at their original release points with the tags and fragments left on the ground) and seeds removed by rodents, which included seeds cached (i.e., seeds buried in the soil or deposited intact on the ground after being removed), seeds eaten after being transported, and missing seeds (i.e., seeds that were not found within our search area).

2.4. Data analysis

All statistical analyses were conducted using R (version 4.0.1). First, we analyzed the overall seed fate pattern, for which all 40,500 seeds released in the three years were combined. A generalized linear mixed model (GLMM) was used to analyze the effect of the year (defined as a factor) and plot (defined as a factor) on seed harvest (whether a seed at the releasing point would be harvested or ignored by rodents) and seed removal (whether a harvested seed would be removed or eaten *in situ* by rodents), with a binomial error distribution and logit link function (function glmer, package "*lme4*"). The ID number of each seed nested in species, release point, and seed release day were considered as random effects. Wald χ^2 statistics were used to test the effects of fixed factors (function Anova, package "*car*").

To analyze the fine-scale spatiotemporal variation in seed harvest and seed removal, the data for each plot in each year were analyzed separately. A zero-inflated GLMM was used to analyze the effect of seed release point (defined as factor) and seed release day (defined as date) on seed harvest and seed removal, with a binomial error distribution and logit link function (function glmmadmb, package "*glmmADMB*"), and all the species were analyzed together, in which seed ID nested in species was considered as a random effect. Then, a GLMM was used to test the effect of seed release point and seed release day on seed harvest and seed removal for each species separately, wherein seed ID was considered as a random effect. Because the same test was repeated for each species, the false discovery rate was used to adjust the p-values to avoid a type I error (function 'p.adjust' in package '*stats*').

To test whether the spatiotemporal variation of each single species showed a similar pattern to the overall spatiotemporal variation of the combined dataset, a Spearman's rank correlation was used to test the relationship of seed harvest (or seed removal) with the specific species and combined datasets at the same seed release points (or seed release days). A positive relationship indicated that the target species had a similar pattern to the overall spatiotemporal variation; otherwise, no consistent effect existed. The data for each plot for each year were analyzed separately. Similarly, the p-values were adjusted accordingly.

3. Results

3.1. General pattern of seed harvest and seed removal

In total, 40,500 seeds were released during the study period, of which 24,189 (59.7%) were harvested by rodents. Seeds were more likely to be harvested in 2018 (71.2%) than in either 2017 or 2019 (63.0% and 46.1%, respectively) ($\chi^2 = 2822.57$, $p < 0.001$) (Fig. 1A). Seed harvest also differed among plots, with more seeds harvested in plots II and III than in plot I ($\chi^2 = 51.92$, $p < 0.001$) (Fig. 1A). Of the 24,189 harvested seeds, 39.4% were removed from their release points, while the remaining 60.6% were eaten *in situ*. The proportion of seed removal was also different between both years and plots, for which the results show that more seeds were removed in 2018 (54.2%, n = 9608) and 2017 (42.2%, n = 7939) than in 2019 (14.7%, n = 6642) ($\chi^2 = 1385.19$, $p < 0.001$). Further, more seeds were removed in plots I and II than in plot III ($\chi^2 = 128.92$, $p < 0.001$) (Fig. 1B). Moreover, significant interactive effects were detected between the year and plot for both the seed harvest ($\chi^2 = 25.72$, $p < 0.001$) and seed removal ($\chi^2 = 294.89$, $p < 0.001$) (Fig. 1).

3.2. Fine-scale spatiotemporal variation in seed harvest

Of the 12,600 seeds released in 2017, 7939 (63.0%) were harvested by rodents. The proportion of harvested seeds differed greatly among the 36 seed release points in all three plots (GLMM, all p values < 0.001; Table 1), in which the ranges were 38.0% – 90.0%, 30.8% – 98.9%, and 32.3% – 85.8%, respectively, for plots I, II, and III (Fig. 2A – C). The

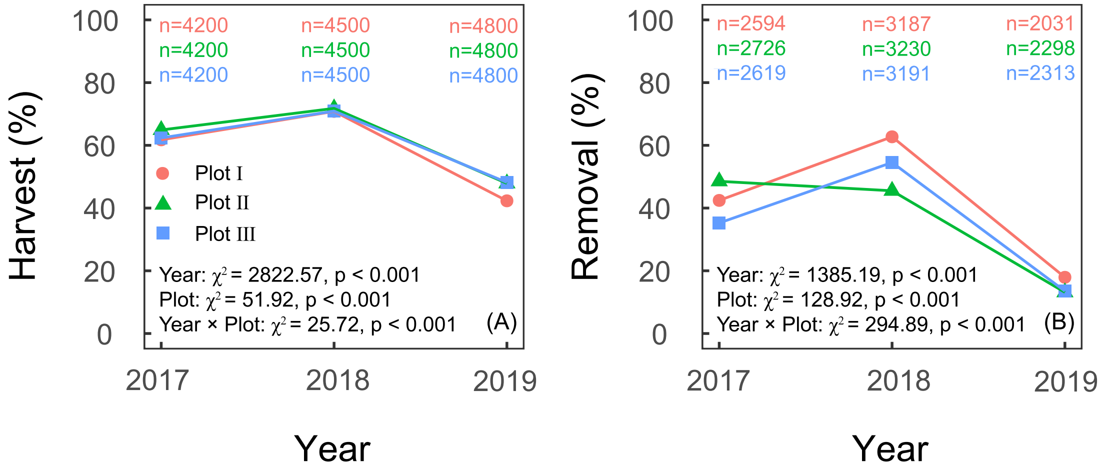

Fig. 1. Variation in (A) seed harvest and (B) seed removal among years and plots. A generalized linear mixed model (GLMM) was used to analyze the effect of year (defined as factor) and plot (defined as factor) on seed harvest and seed removal, wherein the ID number of each seed nested in species, release point, and release day were considered as random effects. Wald χ^2 statistics were used to test the effects of fixed factors (function Anova, package "*car*"). Numbers denote the sample sizes, which are the number of seeds analyzed in the models.

Table 1
Fine-scale spatiotemporal variation in seed harvest and seed removal. A zero-inflated generalized linear mixed model (GLMM) was used to analyze the effect of seed release point (defined as factor) and release day (defined as date) on seed harvest and seed removal using a binomial error distribution and logit link function (function glmmadmb, package "*glmmADMB*"). All species were analyzed together, wherein the seed ID nested in species was considered a random effect. Wald χ^2 statistics were used to test the effects of the fixed factors (function Anova, package "*car*").

		2017		2018		2019	
Plot	Fixed effect	χ^2	*P*	χ^2	*P*	χ^2	*P*
	Harvested vs. Ignored.						
Plot I	Point	280.09	< 0.001	7.91×10^3	< 0.001	42.87	0.171
	Time	16.60	< 0.001	188.73	< 0.001	0.39	0.535
	Time × Point	243.06	< 0.001	5.78×10^4	< 0.001	40.42	0.244
Plot II	Point	114.64	< 0.001	424.03	< 0.001	290.20	< 0.001
	Time	0.07	0.786	26.99	< 0.001	13.80	< 0.001
	Time × Point	112.95	< 0.001	276.90	< 0.001	293.94	< 0.001
Plot III	Point	75.67	< 0.001	70.18	< 0.001	65.96	0.001
	Time	0.07	0.797	6.29×10^3	< 0.001	2.37	0.124
	Time × Point	50.85	0.042	52.28	0.031	58.62	0.008
	Removed vs. Eaten *in situ*.						
Plot I	Point	104.70	< 0.001	64.37	0.002	7.68×10^4	< 0.001
	Time	7.31	0.007	3.02	0.083	1.28×10^5	< 0.001
	Time × Point	101.86	< 0.001	51.84	0.034	5.62×10^4	< 0.001
Plot II	Point	277.57	< 0.001	251.92	< 0.001	44.47	0.131
	Time	18.64	< 0.001	5.74	0.017	0.70	0.404
	Time × Point	230.79	< 0.001	211.28	< 0.001	42.07	0.192
Plot III	Point	502.75	< 0.001	157.45	< 0.001	103.81	< 0.001
	Time	12.21	< 0.001	12.57	< 0.001	0.13	0.717
	Time × Point	150.99	< 0.001	95.30	< 0.001	60.94	0.004

proportion differed among the 15 seed release days in plot I ($p < 0.001$) but not in plots II and III (Table 1), exhibiting ranges of 53.6% – 71.1%, 58.6% – 71.8%, and 58.2% – 67.5%, respectively (Fig. 3A). Furthermore, a significant interaction was detected between space and time in all three plots (Table 1). When analyzing each of the 28 species separately, only a few species showed significant variation in seed harvest among release points (3, 1, and 1 species in plots I, II, and III, respectively) and release days (4, 2, and 1 species in plots I, II, and III, respectively) (Supporting Information, Tables A1-A3). In addition, few correlations between the seed harvest proportion of each species and the combined dataset were detected either among the seed release points or among the seed release days (Supporting Information, Tables A1-A3), indicating that the spatiotemporal effects on seed harvest did not follow a consistent rule among species.

Of the 13,500 seeds released in 2018, 9608 (71.2%) were harvested by rodents. The proportion of harvested seeds differed greatly among both release points and release days in all three plots (all p values < 0.001; Table 1), revealing ranges of 47.3% – 100%, 43.3% – 100%, and 25.0% – 100% among release points (Fig. 2G–I) and 60.3% – 82.7%, 63.3% – 81.7%, and 61.7% – 84.0% among release days for plots I, II, and III, respectively (Fig. 3B). Significant interactions were detected between space and time in all three plots (Table 1). When analyzing each of the 30 species separately, only a few species showed significant variation in seed harvest in space (2, 2, and 1 species in plots I, II, and III, respectively) and time (5, 5, and 0 species in plots I, II, and III, respectively) (Supporting Information, Tables A4-A6). Furthermore, when analyzing the correlations of the seed harvest proportion between each species and the combined dataset among release points or release days, only a few species showed a positive correlation among release days (6, 5, and 1 species in plots I, II, and III, respectively) (Supporting Information, Tables A4-A6).

Of the 14,400 seeds released in 2019, 6642 (46.1%) were harvested by rodents. The proportion of harvested seeds differed among release points in plots II and III (both p values < 0.001) but not in plot I ($p = 0.171$) (Table 1), exhibiting ranges of 24.2% – 78.3%, 21.7% – 85.0%, and 21.8% – 61.7%, respectively (Fig. 2M–O). The seed harvest proportion differed among the seed release days in plot II ($p < 0.001$) but not in plots I ($p = 0.535$) and III ($p = 0.124$) (Table 1), with ranges of 41.9% – 56.6%, 35.3% – 49.7%, and 43.4% – 52.8%, respectively (Fig. 3C). Significant interactions were detected between space and time in plots II ($p < 0.001$) and III ($p = 0.008$) but not in plot I ($p = 0.244$) (Table 1). When analyzing each species separately, only a few species showed significant variation in seed harvest in space (3, 9, and 7 species in plots I, II, and III, respectively) and time (4, 6, and 7 species in plots I, II, and III, respectively) (Supporting Information, Tables A7-A9). Furthermore, few correlations between the seed harvest proportion of each species and the combined dataset were detected either among release points or among release days (Supporting Information, Tables A7-A9).

3.3. Fine-scale spatiotemporal variation in seed removal

Of the 7939 seeds harvested in 2017, 3347 (42.2%) were removed by rodents. The removal proportion differed greatly among release points and among release days in all the three plots (all p values < 0.01; Table 1), with ranges of 21.5% – 75.0%, 14.3% – 80.9%, and 10.3% – 79.5% among release points (Fig. 2D – F) and 28.1% – 52.2%, 37.3% – 62.8%, and 26.0% – 50.3% among release days in plots I, II, and III, respectively (Fig. 3D). Furthermore, a significant interaction was detected between space and time in each plot (Table 1). When analyzing each of the 28 species separately, only a few species showed significant variation in seed removal in space (0, 2, and 2 species in plots I, II, and III, respectively) and time (2, 1, and 2 species in plots I, II, and III, respectively) (Supporting Information, Tables A10-A12). In addition, when analyzing the correlations of seed removal proportion between each species and the combined dataset among release points or release days, only a few positive correlations were detected (Supporting Information, Tables A10-A12).

Of the 9608 seeds harvested in 2018, 5206 (54.2%) were removed by rodents. The proportion of seed removal differed among release points in all three plots (all p values < 0.01; Table 1), with ranges of 29.7% – 93.6%, 12.5% – 83.1%, and 19.6% – 100%, in plots I, II, and III, respectively (Fig. 2J – L). The seed removal proportion also differed among the 15 seed release days in plots II ($p = 0.017$) and III ($p < 0.001$), but not in Plot I ($p = 0.083$), with the ranges of 28.3% – 57.9%, 37.8% – 67.5%, and 51.1% – 67.5%, respectively (Fig. 3E). A significant interaction was detected between space and time for each plot (Table 1). When analyzing each of the 30 species separately, only a few species showed significant variation in seed removal in space (1, 1, and 2 species in plots I, II, and III, respectively) and time (1, 2, and 3 species in plots I,

Fig. 2. Variation in the proportion of seed harvest and removal by rodents among release points. The mean values (±standard deviation (SD)) of the 36 release points in each plot are shown at the top of the panels, and the maximum (in red squares) and minimum (in green squares) values in each plot are highlighted. A zero-inflated generalized linear mixed model (GLMM) was used to analyze the effect of release point on seed harvest and removal (please see Table 1 for detailed statistical values). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

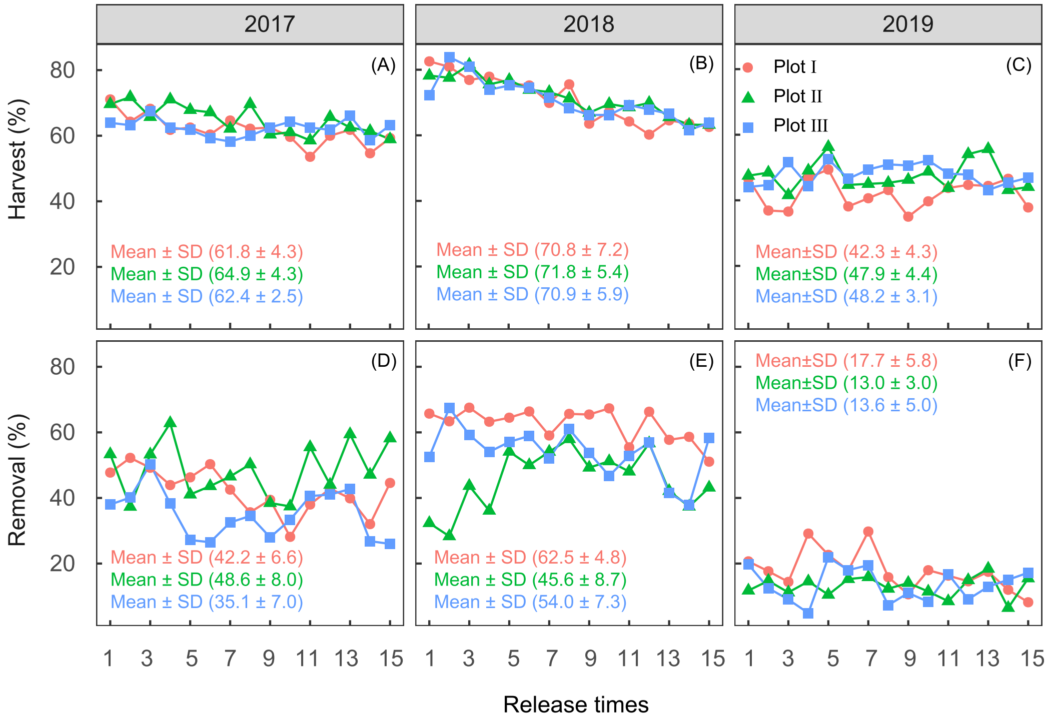

Fig. 3. Variation in the proportion of seed harvest and removal by rodents among release times. The mean values (±standard deviation (SD)) of the 15 release times of each plot are shown. A zero-inflated generalized linear mixed model (GLMM) was used to analyze the effect of release time on seed harvest and removal (see Table 1 for detailed statistical values).

II, and III, respectively) (Supporting information, Tables A13-A15). Furthermore, only a few positive correlations between the seed removal proportion of single species and the combined dataset were detected among the release points and release days (Supporting Information, Tables A13-A15).

Of the 6642 seeds harvested in 2019, 979 (14.7%) were removed by rodents. The removal proportion differed among the 36 seed releasing points in plots I and III (both p values < 0.001), but not in plot II ($p = 0.131$) (Table 1), revealing ranges of 0% – 67.9%, 2.7% – 45.9%, and 1.7% – 31.6%, respectively (Fig. 2P – R). The seed removal proportion also differed among release days in plot I ($p < 0.001$) but not in either plot II or plot III, exhibiting ranges of 8.2% – 29.8%, 6.5% – 18.4%, and 4.9% – 21.9%, respectively (Fig. 3F). Significant interactions were detected between space and time in plots I and III, but not in plot II (Table 1). When analyzing each species separately, no species showed any variation in seed removal in either space or time (Supporting Information, Tables A16-A18). Furthermore, only a few positive correlations between the seed removal proportion of a single species and the combined dataset were detected among the release points (2 species in plot I) and release days (1 species in plot III) (Supporting Information, Tables A16-A18).

4. Discussion

Our study provides strong evidence that fine-scale spatiotemporal variation in seed dispersal and predation by rodents exists, although the overall intensity of seed harvest and removal significantly differs among experimental plots and years. Furthermore, fine-scale spatiotemporal effects differ among plant species, indicating that the spatiotemporal effect may be species specific, which may further lead to interspecific variation in seed fate, thereby changing the species composition of seedlings.

In this study, the dynamic pattern of seed availability was created by arbitrarily releasing seeds at a fine scale of intervals in both space (i.e., 10 m intervals) and time (i.e., 6 day intervals). However, similar, or even stronger, fine-scale spatiotemporal variation in seed availability may exist in natural forests, because 1) any individual tree in the forest usually coexists with other homologous or heterologous trees at a fine scale, and their canopies often, more or less, overlap (Benavides et al. 2019, Zambrano et al. 2019); 2) trees often differ in seed production both among species and within the same species (Shibata et al. 2002, Wang and Ives 2017); 3) seed traits differ greatly among species, and even among trees within the same species (Gong et al. 2015, Shimada et al. 2015); and 4) the peak time of seed release or fruit ripening often varies among species and among individual trees of the same species, although their fruiting periods show significant overlap (Takahashi et al. 2011, Sunyer et al. 2014). Therefore, the ubiquitous fine-scale spatiotemporal variation in seed availability (including both seed quantity and quality) may explain, to a certain extent, the fine-scale variation in seed dispersal and predation patterns.

The spatiotemporal variation in seed predation and dispersal in our study could not be explained by the total number of seeds, total mass of seeds, number of species of seeds, or the Shannon diversity index of the seeds released, as few of these indicators were correlated with seed harvest or seed removal in any plot or year (Supporting Information, Fig. A1), indicating the presence of other potential factors. The neighboring effect is believed to influence seed-rodent interaction. This effect considers whether a specific species of seed would be harvested versus ignored or eaten *in situ* versus removed by rodents can be affected by the existence of neighboring seeds, and the relative frequency between them (Ostoja et al. 2013, Lichti et al. 2014). Furthermore, different species of neighboring seeds may lead to different results (Garzon-Lopez et al. 2015, Yang et al. 2020), possibly because of the contrasting seed traits between the focused and neighboring seeds (Wang 2020b). In this study, the species of seeds were randomly selected and released at certain times and points. Therefore, a spatiotemporal dynamic pattern of species composition of seeds occurred, which may consequently lead to a spatiotemporal variation in neighboring effects, potentially affecting the seed-rodent interaction.

Significant spatiotemporal effects on seed dispersal and predation were detected among some species, but not all species. Moreover, only a small proportion of positive correlations were detected between the proportion of seed harvest (or seed removal) of a single species and the combined dataset among both release points and release days (Supporting Information, Tables A1-A18), indicating that the spatiotemporal variation in seed-rodent interaction does not follow a consistent rule among plant species. Similar interspecific variation has been detected in many other seed-rodent interaction studies, for example, the effect of density on seed predation by rodents (Wang 2020a) and elevation patterns in seed removal by rodents (Thein et al. 2021). Interspecific variation in seed traits usually determines the degree of foraging preference of rodents among plant species, which may result in different responses to spatiotemporal effects among species. In this case, rodents would harvest the most preferred seeds but ignore the most non-preferred seeds regardless of when and where the seeds were released. Our results verified this prediction, as the species experiencing either extremely high or low seed predation showed little variation in both space and time (Supporting Information, Tables A1-A18). Meanwhile, for the species that experienced moderate seed predation, some species showed a significant spatiotemporal variation, while others did not, indicating that other factors may potentially influence the fine-scale spatiotemporal effects, such as differences in rodent abundance and species composition, variation in foraging preference, and range of activity among rodent species and individuals within the same species (Zwolak 2018; Schirmer et al. 2019). In addition, the microhabitat (e.g., shrubs, litter, and woody debris) can also affect rodent foraging behavior (Iida 2006, Wang and Corlett 2017). However, the microhabitat was relatively uniform within each of our plots, indicating that microhabitat may contribute little to our fine-scale spatiotemporal variation in seed-rodent interaction.

Our experiment was conducted for three consecutive years, which differed in both rodent and seed abundance. Fine-scale spatiotemporal variations in the seed-rodent interactions were detected in all years, although both the overall seed harvest and seed removal differed among years (63.0%, 71.2%, and 46.1% for seed harvest, and 42.2%, 54.2%, and 14.7% for seed removal in 2017, 2018, and 2019, respectively). Furthermore, in each year, the overall seed harvest and removal showed a certain amount of variation among the three plots (Fig. 1), although we did not test the differences in seeds and rodents among the plots. Therefore, we believe that fine-scale spatiotemporal variation in seed-rodent interactions has always existed, regardless of the differences in seed or rodent abundance. However, the intensity of this spatiotemporal variation did vary among years and plots (Table 1), indicating that variation in seed-rodent interaction at fine scales in both space and time may be a much more complex process than expected. Our experiment was conducted in a subtropical forest. However, we believe that such fine-scale spatiotemporal variation in seed-rodent interaction may also exist in other forests, especially in the tropics where a wide range of species co-exist.

Our findings suggest that the fine-scale spatiotemporal variation in seed-rodent interactions may contribute to the coexistence of multiple species of seeds in natural forests, which may further translate into a seedling recruitment stage and the biodiversity maintenance of the whole community. In fragmented and degraded forests, wherein the composition and abundance of both plants and rodents has changed dramatically, such fine-scale spatiotemporal variation may also change, which in turn affects natural regeneration. Therefore, we suggest that future forest management practices, such as thinning, restoration, and afforestation, should consider this possible effect.

5. Conclusions

Our results indicate a ubiquitous fine-scale spatiotemporal variation in seed-rodent interactions. As a consequence, any specific seed may have the probability to survive or be dispersed as long as it appears at a specific site and time. Generally, we expect that similar fine-scale spatiotemporal variation also occurs in other plant-animal interactions, such as herbivory and pollination. Incorporating this fine-scale spatiotemporal variation into future plant-animal studies may help us to gain a better understanding of species coexistence and biodiversity maintenance, thereby providing important implications for forest management and conservation.

6. Data archiving statement

All data used in the manuscript are available in the supplementary material.

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.

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Appendix A. Supplementary material

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