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Factors influencing repeated seed movements by scatter-hoarding rodents in an alpine forest

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Scatter-hoarding rodents are effective dispersal agents for many plant species. Several studies have shown that rodents repeatedly re-cache seeds. The re-caching process often has a significant impact on final seedling establishment, but the factors determining its occurrence are poorly understood. In this study, we followed the fate of 3564 artificial seeds that varied in size, nutrient content and tannin content. Seeds cached closer to their original releasing plots were more likely to be re-cached, and to a further distance. Larger seeds were more likely to be re-cached than smaller ones, while nutrient and tannin content had little effect. Most plant species that depend on scatter-hoarding rodents for seed dispersal bear relatively large seeds, and large seeds are usually more likely to be dispersed and to establish seedlings, suggesting that the caching preferences of scatter-hoarding rodents may have played an important role in the evolution of large seeds.

Scatter-hoarding rodents are known to store large quantities of intact seeds in the soil in many separate caches where germination of neglected seeds is probable, and thus play a crucial role in the seed dispersal of many plant species^{1,2}. Many studies have only investigated the initial fate of experimental seeds without considering successive fates over time^{3–5}. However, several studies have shown that rodents often excavate and re-cache seeds more than once^{6–13}. For example, Perea et al.¹¹ found that seventy percent of the seeds were re-dispersed from their initial caches, with up to five successive dispersal movements. Jansen et al.⁹ found agoutis continued to move and re-cache the buried seeds, up to 36 times. Several studies have demonstrated that this successive re-caching process has significant ecological implications, increasing seed dispersal distance¹¹, providing directed dispersal¹³, and even providing a substitute for the extinct megafaunal dispersal agents of some large-seeded tropical species⁹.

Why are seeds often repeatedly excavated and re-cached? Essentially, there are two possible mechanisms: cache management by owners and cache pilferage by thieves, who then add the seeds to their own reserves. Some studies have suggested that this re-caching behaviour is a way for the owners to monitor cache theft and seed condition, as well as enhance spatial memory of cache locations^{14–17}. The rapid-sequestering hypothesis is an alternative explanation for cache management by the owner, i.e., rodents initially cache seeds close to the seed sources to maximize harvest rates during flushes of seed production, and subsequently they redistribute their initial caches further from the seed sources to reduce the cache density to make them less available to the thieves^{18,19}.

Based on a unique combination of radio-tracking of seeds, individual tagging of rodents and camera monitoring of caches, Jansen and his colleagues suggested that cache pilferage may be the major driver of re-caching⁹. In this light, a relevant question would be: what factors enhance cache theft? Logically, at least two factors may do so. One is the level of competition, i.e. the rates of cache pilferage were positively related to the abundance ratio of rodents to seeds^{8,20,21}. The other factor is the value of the seed cached, which is usually indicated by the seed traits. For example, seeds with large size or more energy content may be more easily detected and pilfered because they emit stronger odors^{22,23}. Furthermore, it is possible that the motivation of potential thieves to locate and steal caches increases with seed value (e.g. larger size or more energy content) because of the greater reward per unit search time. Some studies have indicated that several seed traits (e.g. seed size and tannin content) might be related to the seed re-caching process^{8,24}. However, few studies have directly examined how varied seed traits affect this important process.

In this study, we conducted all the experiments during the same year of average food abundance and rodent density, in order to keep the same level of competition. We developed a series of experiments using artificial seeds to test the effect of each single seed trait (i.e. seed size, nutrient or tannin content) on repeated seed movement by varying single traits experimentally, while keeping other traits constant. By detecting the fates of 3564 artificial



seeds with univariate seed traits, we aimed to address the following predictions: 1) Seeds with larger size and higher nutrient or tannin content are more likely to be re-cached; 2) Seeds cached closer to their original releasing plots are more likely to be re-cached.

Results

During our live-trapping census, we obtained seventeen rodents from the night traps, but none from the day traps. Among the seventeen rodents, ten were *Apodemus latronum* (56.3%) and seven were *Apodemus chevrieri* (37.5%).

Most of the experimental seeds were harvested from the release points within the first three days after placement (96.9%, $N = 3564$). At the end of the experiment, we found 1333 primary caches, 209 secondary caches, 19 tertiary caches and 2 quaternary caches (Fig. 1). On average, higher-order caches (i.e. 2nd and 3rd) were located further from the release points than were primary caches: seed size experiment- 13.6 ± 1.6 m (mean \pm s.e.) and 12.3 ± 1.8 m vs. 6.9 ± 0.4 m (Linear mixed-effects model, $t = 6.683$, $P < 0.001$), nutrient content experiment- 19.5 ± 1.6 m and 34.4 ± 3.5 m vs. 10.3 ± 0.5 m ($t = 10.184$, $P < 0.001$), and tannin content experiment- 14.1 ± 1.0 m and 20.2 ± 3.9 m vs. 8.5 ± 0.3 m ($t = 7.565$, $P < 0.001$). Primary caching distance was positively related to seed size (Pearson's product-moment correlation, $R^2 = 0.975$, $P < 0.001$) and nutrient content ($R^2 = 0.782$, $P = 0.004$), while negatively related to both hydrolysable ($R^2 = 0.865$, $P < 0.001$) and condensed tannin content ($R^2 = 0.824$, $P = 0.002$)²⁵. Secondary caching distance (i.e. the distance from the release point to the secondary caches) was positively related to seed size ($R^2 = 0.957$, $P < 0.001$) and negatively related to hydrolysable tannin content ($R^2 = 0.809$, $P = 0.002$), but not significantly related to nutrient content ($R^2 = 0.279$, $P = 0.179$) or condensed tannin content ($R^2 = 0.451$, $P = 0.099$) (Fig. 2).

Seed dispersal distance increased significantly for successive movements. From primary to secondary caches it increased by 9.6 ± 1.5 m in the seed size experiment (Paired t-test, $t_{59} = 6.493$, $P < 0.0001$, two-tailed), 9.6 ± 1.4 m in the nutrient experiment ($t_{48} = 6.986$, $P < 0.0001$), and 8.1 ± 0.9 m in the tannin experiment ($t_{99} = 8.901$, $P < 0.0001$). From secondary to tertiary caches it increased by 4.8 ± 1.3 m in the seed size experiment ($t_7 = 3.556$, $P = 0.009$), 17.0 ± 4.1 m in the nutrient content experiment ($t_4 = 4.192$, $P = 0.013$), and 10.0 ± 2.4 m in the tannin content experiment ($t_5 = 4.204$, $P = 0.008$) (Fig. 3).

The likelihood of seeds being excavated from primary caches and re-cached decreased with distance from the release point in the tannin content experiment (Generalized linear mixed model, $Z = -3.131$, $P = 0.002$), but not in the seed size experiment ($Z = -0.117$, $P = 0.907$) or the nutrient content experiment ($Z = 1.039$, $P = 0.299$) (Fig. 3). The likelihood of seeds being excavated from primary caches and re-cached increased with seed size ($Z = 3.929$, $P < 0.001$), but not with nutrient content ($Z = 1.007$, $P = 0.314$) or tannin content ($Z = -0.931$, $P = 0.352$). No interactions between primary cache distance and seed size, nutrient content or tannin content were found to affect the likelihood of primary cached seeds being re-cached ($Z = -1.496$, $P = 0.135$; $Z = -1.052$, $P = 0.293$; $Z = 0.714$, $P = 0.475$; respectively) (Table 1).

Discussion

The removal of seeds further from parent plants when re-caching brings a significant fitness advantage to seed dispersal^{9,13}. In this study, a large proportion of seeds from the primary caches were excavated by rodents and dispersed for a second time, reaching up to four successive dispersal movements. Seed dispersal distances increased significantly for successive movements, with the maximum distance up to 77.3 m.

Our tannin experiment indicated that current caching distance might be a major factor that influenced the re-caching process. Seeds with current caches closer to the original releasing plots were

more likely to be re-cached, and to further distances. These results are consistent with the rapid-sequestering hypothesis^{18,19}. Most of the experimental seeds (98.6%, $n = 1620$) were harvested from the release points within the first three days after placement and successive re-caching reduced the cache densities and presumably decreased the probability of pilferage. However, we did not record which animal made the original cache, so we could not tell if the re-caching was by the same individual. Cache pilferage by conspecific or heterospecific scatter-hoarders could give the same results, because pilferers are more likely to find and pilfer seeds that are closer, as higher seed density could improve foraging ability^{1,26}. Furthermore, the tagging method used in our study might encourage pilfering behavior by providing an obvious indicator of a cached seed and making it easy for naïve rodents to locate caches^{27,28}; and this may make it less likely that many of these re-caching events involved recovery by the original cache owner.

However, current caching distance was found to have little effect on the re-caching process in both the seed size and nutrient experiments. In the nutrient experiment, seeds at primary caches, whether they were re-cached or not, were already dispersed relatively far away from the seed releasing plots (9.8 ± 1.1 m and 10.4 ± 0.5 m, respectively) (Fig. 3), perhaps reducing the likelihood of selective re-caching; while in the seed size experiment, the overwhelming effect of seed size on the re-caching process might attenuate the effects of distance; similar overwhelming effects of seed size were also found during the primary caching process when rodents initially encountered a seed²⁵.

In our study, seed size was positively related to re-caching probability and similar results were also found in some other studies^{8,10}. Seed size usually directly indicates seed quality and may be much easier to assess than other seed traits (e.g. nutrient or tannin content). Furthermore, it is logical that a larger amount of cached food supply may be more likely to be relocated by rodents than a smaller one (either by smell or using visual clues), and/or may increase the motivation of potential thieves to locate and steal caches because of the greater reward per unit search time. Nutrient and tannin content of seeds had no effect on the re-caching process, although both factors significantly influenced the primary caching process at the rodents' initial encounter with a seed^{25,29}. After the initial foraging decision at the seed releasing plots, certain seeds were chosen to be scatter-cached by rodents based on several criteria, while others were either ignored or eaten *in situ*^{25,29}; thus the variations in nutrient and tannin content among the cached seeds would be too limited to affect rodent re-caching decisions.

However, in the wild, nutrient quality (e.g. lipid reserves) and tannin content of seed are sometimes correlated with the germination delay, i.e. lipid and tannin-rich seeds sprouted later than those with less lipid and tannin, the former and later being used as long- and short-term term reserve for animals, respectively^{30,31}. Independently of nutrient type, seed dormancy (especially in the temperate regions) might be also be an important factor, and it is well known in the literature that sprouting affects the chance of germinating seeds being re-cached, with the result that non-germinating seeds are more likely to be re-cached than germinated ones³¹⁻³³. Some studies found that the germ can be excised (pruning) when re-caching occurs, which prevents germination and allows the conservation of the food supply by reducing the perishability of seed reserves during the establishment phase¹⁶. Thus, finally, seed size, nutrient content, tannin content and timing of germination might be interacting factors that determine whether or not seeds are re-cached. However, it is impossible to test the timing of germination when using artificial seeds; furthermore, using peanut powder (lipid-rich) to make artificial seeds likely affected re-caching compared to using other materials, e.g. flour powder (sugar-rich). A very interesting comparison would be the fate of artificial seeds made out of two contrasting components (lipid vs. sugar), although it will still be impossible to monitor how factors such as rapid (for sugar-rich

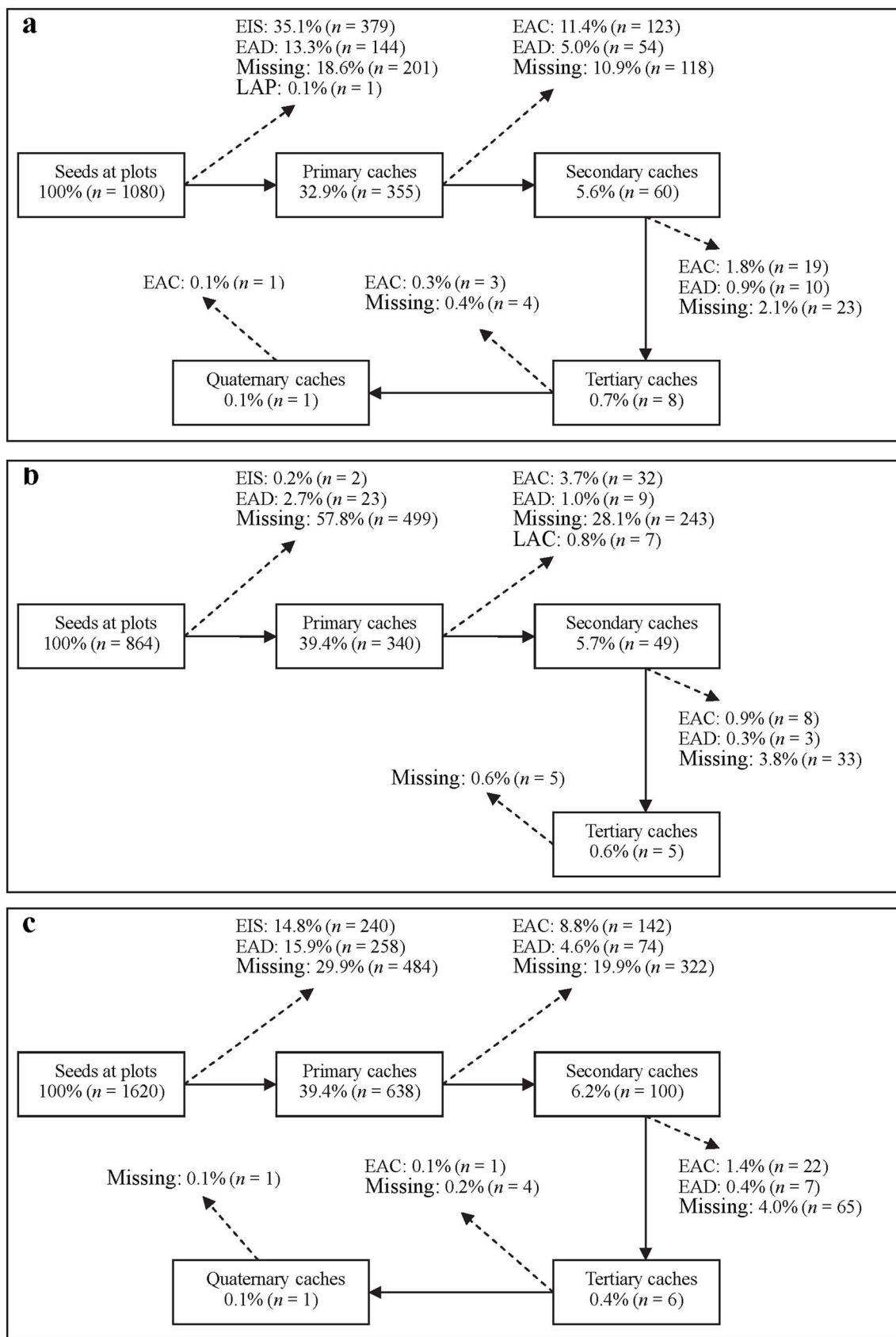


Figure 1 | Diagram of seed fates, showing the percentages and numbers of seeds for each fate category during the re-caching process by scatter-hoarding rodents (EIS, eaten in situ; EAD, eaten after dispersed; LAP, left at plots; EAC, eaten at current caches; LAC, left at current caches). (a): seed size experiment: seeds with different size; (b): nutrient experiment: seeds with different nutrient content; (c): tannin experiment: seeds with different tannin content.

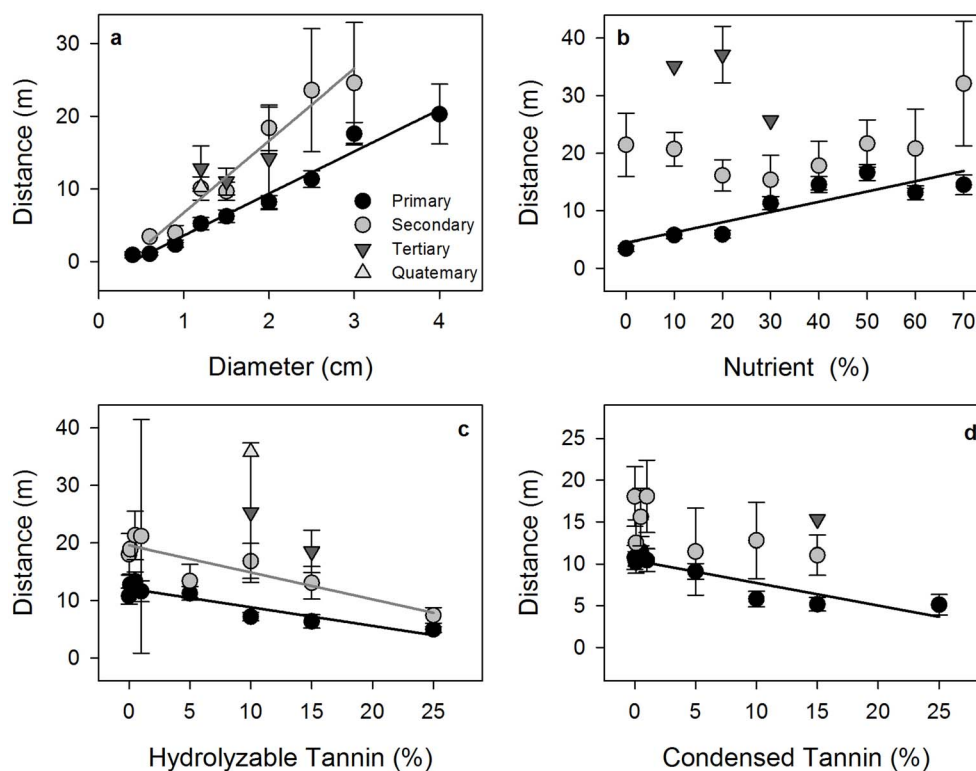


Figure 2 | Relationship between dispersal distance (mean \pm s.e.) of cached seeds and seed traits. Linear regression models were used to test for significance of the relationships. (a) Positive relationships were found between dispersal distance and seed size for both primary (Pearson's product-moment correlation, $R^2 = 0.975$, $P < 0.001$) and secondary cached seeds ($R^2 = 0.957$, $P < 0.001$). (b) Positive relationships were found between dispersal distance and nutrient content for primary cached seeds ($R^2 = 0.782$, $P = 0.004$) but not for secondary cached ones ($R^2 = 0.279$, $P = 0.179$). (c) Negative relationships were found between dispersal distance and hydrolysable tannin content for both primary ($R^2 = 0.865$, $P < 0.001$) and secondary cached seeds ($R^2 = 0.809$, $P = 0.002$). (d) Negative relationships were found between dispersal distance and condensed tannin content for both primary cached seeds ($R^2 = 0.824$, $P = 0.002$) but not for secondary cached ones ($R^2 = 0.451$, $P = 0.099$).

seeds) or delayed (lipid-rich) germination determine scatter-hoarding rodent decisions to re-cache primarily cached seeds. For that, it would be important to use wild seed species with different attributes, seed size and nutrient composition, and to monitor them during the establishment period during the fall through spring in future studies.

The level of competition may also be an important factor influencing the seed re-caching process, as it has been found to be positively related to the rates of cache pilferage^{8,20,21}. However, we did not test the competition level as our study was conducted in one year across a small scale, when both food abundance and rodent populations were average. In our study, we checked seed fates 11 times after release, and the length of the census intervals increased during the study. It is possible that seeds were moved multiple times within an interval, and Jansen et al.⁹ even found that seeds were re-cached twice in a single day. This may be the reason that there were only few scattered occurrences of 3rd and 4th levels of re-caching in our study, because the repeated re-caching process was found to increase the probability of seed consumption by rodent¹¹. Furthermore, more than half the seeds (56.2%, $n = 3564$) were missing with their fate unknown in our study, and were omitted from the analyses. Some of these missing seeds might have been dispersed beyond our search radius (≈ 20 m). Hirsch et al.³⁴ suggested that these incomplete data sets may bias the dispersal results, especially the seed dispersal kernel, because long-distance dispersal events were the least likely to be observed, and they also developed a 'censored tail reconstruction' method to provide unbiased estimates of long distance movements. However, it is still difficult to assess the repeated movements of missing seeds as they were not tracked.

In this study, we used artificial seeds to separate the effects of seed size, nutrients and tannin content on the seed re-caching process.

The likelihood of seeds being re-cached increased with seed size, but not with nutrient content or tannin content. Furthermore, seed size also demonstrated a much more consistent and overwhelming effect than nutrient and tannin content on the primary foraging decision at the rodents' initial encounter with a seed²⁵. Most plant species that depend on scatter-hoarding rodents for seed dispersal bear relatively large seeds^{8–11,35,36}. Larger seeds usually have a much greater chance of being scatter-cached while small ones have a greater chance of being eaten^{8,12,37,38}. Meanwhile, large seeds were often more likely to produce seedlings³⁹. We therefore believe that the foraging preference for large seeds by scatter-hoarding rodents may have played an important role in the evolution of large seeds in these taxa^{40,41}.

Methods

Ethics statement. This study was carried out in strict accordance with the Guide for the Care and Use of Laboratory Animals of China. The protocol was approved by the Administrative Panel on the Ethics of Animal Experiments of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (Permit Number: XTBG2007-004). We signed a contract (No. 20070017) with the Shangri-La Alpine Botanical Garden in 2007, and the contract included the permissions to access the study site and conduct this study.

Study site. The experiment was conducted during September to November in 2007, in a natural forest at the Shangri-La Alpine Botanical Garden (27°54' N, 99°38' E, altitude 3456 m), Yunnan province, southwestern China, where *Pinus densata* is the dominant tree species and the Sichuan field mouse (*Apodemus latronum*) and Chevri's field mouse (*Apodemus chevrieri*) are the two most abundant seed predators/dispersers²⁵. Both rodent species have similar body sizes and foraging behaviour given the artificial seeds⁴².

Experiment design. The experimental data analyzed here was collected during September to November in 2007. The full description of the experiment design and the results of the primary seed fate from the release points have been already reported by Wang and Chen²⁵. We used three univariate series of artificial seeds from

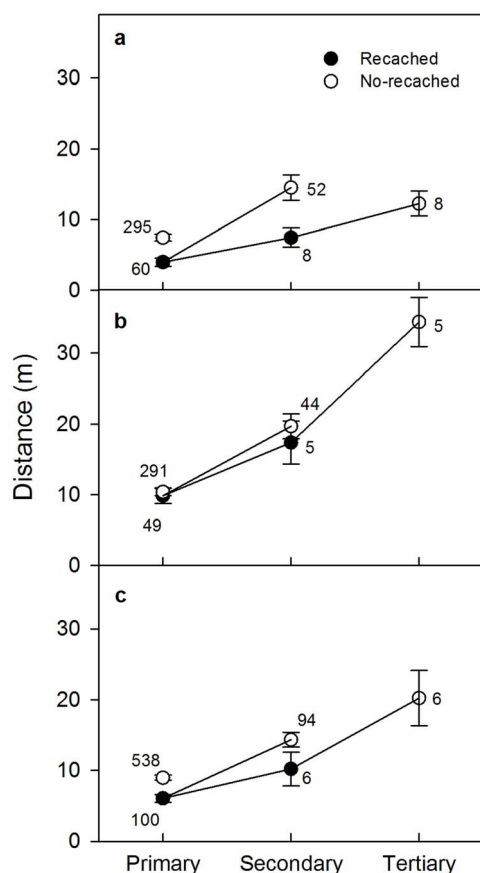


Figure 3 | Effects of current caching distance (mean \pm s.e.) on seed re-caching process. The likelihood of seeds being excavated from primary caches and re-cached decreased with distance from the release point in (c) tannin content experiment (Generalized linear mixed model, $Z = -3.131$, $P = 0.002$), but not in (a) seed size experiment ($Z = -0.117$, $P = 0.907$) nor (b) nutrient content experiment ($Z = 1.039$, $P = 0.299$); similar patterns were also found in the seeds from secondary caches (no statistical analysis were conducted because of the limited sample size). Seed dispersal distances increased significantly along re-caching processes (paired t-test, $P < 0.05$, two-tailed). Numbers besides the bars are the sample sizes.

clay, peanut powder and tannin to test the response of rodent foraging behaviour to three important seed traits: 1) Seed size - ten values: 0.2, 0.4, 0.6, 0.9, 1.2, 1.5, 2.0, 2.5, 3.0 and 4.0 cm in diameter (a total of $108 \times 10 = 1080$ seeds), with each seed consisting of 50% peanut powder and 50% clay; 2) Nutrient content - eight values, with the percentage of peanut powder: 0, 10, 20, 30, 40, 50, 60 and 70 (totaling $108 \times 8 = 864$ seeds), with each seed the same size (1.5 cm in diameter); 3) Tannin - seven

values of percentage of tannin: 0.1, 0.5, 1, 5, 10, 15, and 25, with each seed the same size (1.5 cm in diameter), consisting of 50% peanut powder. A different series was created for hydrolyzable and condensed tannins separately, with one control containing no tannin, giving a total of $108 \times 15 = 1620$ seeds. A 15 cm thin steel thread with a small red plastic tag (modified from the tin-tag method⁴³) was connected to each artificial seed so they were easy to relocate. Rodents in the forest are already familiar with our artificial seeds, since we have been conducting the artificial seed experiments for several consecutive years (from 2005). Furthermore, in our study area, tannin-rich seeds are quite common, and among the 11 local species analyzed, tannin concentrations ranged from 0 to 26.5% (mean $7.8\% \pm 2.9\%$), of which just one species had no tannin content⁴⁴. Our previous studies found that rodents in this forest were usually found to move seeds less than 20 m based on our previous studies^{12,25}, so we conducted a complete search within 20 m of each plot in all directions to relocate the removed seeds. We also conducted an extra search in a larger area in order to relocate as many of the seeds as possible. When we found a cache, we recorded whether the cached seeds were intact or eaten, and the exact location with a directional angle and the distance to their original seed sources. At subsequent visits, we checked all caches identified in the previous visit, until they were removed or eaten by rodents. If a marked cache was removed, then the area around the cache (radius of at least 20 m) was searched. Seed fates were grouped into the following categories: 1) left at plot, leaving intact at the original release plot; 2) eaten in situ/eaten at caches, leaving only plastic tags and seed fragments on the ground surface of the original release plot/current caches; 3) cached, buried intact in the soil or deposited intact on the soil surface; 4) eaten after dispersed, removed by the rodents from the original release plots/current caches before being eaten; 5) left at current caches, leaving intact at current caches until the end of the experiments; 6) missing, seeds that were not found within the search area, hence with an unknown fate.

Six plots (2 m \times 2 m) > 50 m apart were set up in the forest to conduct the three univariate-trait experiments separately. At each plot, we located 9 subplots in 3×3 grids, with about 1 m between subplots. Each circular subplot was about 15 cm in diameter and the seeds were placed along the circle with the tags located outwards. Two seeds of each value of size (or nutrient or tannin content) were placed in each subplot. In total, 108 seeds of each kind were spread evenly over the six plots (2 seeds \times 9 subplots \times 6 plots). We checked the plots and recorded seed harvest (i.e. seeds eaten *in situ* or removed away from their releasing point) 11 times, i.e. the 1st, 2nd, 3rd, 4th, 6th, 8th, 12th, 16th, 20th, 28th and 36th day after seed placement. Rodents in this forest were usually found to move seeds less than 20 m based on our previous studies^{12,25}, so we conducted a complete search within 20 m of each plot in all directions to relocate the removed seeds. We also conducted an extra search in a larger area in order to relocate as many of the seeds as possible. When we found a cache, we recorded whether the cached seeds were intact or eaten, and the exact location with a directional angle and the distance to their original seed sources. At subsequent visits, we checked all caches identified in the previous visit, until they were removed or eaten by rodents. If a marked cache was removed, then the area around the cache (radius of at least 20 m) was searched. Seed fates were grouped into the following categories: 1) left at plot, leaving intact at the original release plot; 2) eaten in situ/eaten at caches, leaving only plastic tags and seed fragments on the ground surface of the original release plot/current caches; 3) cached, buried intact in the soil or deposited intact on the soil surface; 4) eaten after dispersed, removed by the rodents from the original release plots/current caches before being eaten; 5) left at current caches, leaving intact at current caches until the end of the experiments; 6) missing, seeds that were not found within the search area, hence with an unknown fate.

Survey for rodents' community. During the same period of seed placement, live-traps were baited with fresh peanuts to determine the key rodent species that were affecting seed predation/dispersal. In order to minimize the trapping effect on the rodent population in the plots where the artificial 'seeds' were released, the trapping plots were about 500 m away but in the same forest. Five transects were selected and five trap stations at an interval of 10 m were set along each of the five transects for six consecutive days and nights. At each trap station, two living traps were set together with their orientation reversed. Traps were checked every day at 7:30 am and 6:00 pm, and the numbers of captured rodents were recorded.

Data analysis. We performed several models according to different objectives, and plot was treated as a random effect. Generalized linear mixed model (package 'lme4') was used to analyze the effects of current dispersal distance and seed traits on seed fate, i.e. re-cached or not. Linear mixed-effects model (package 'nlme') was used to analyze the effects of seed trait and cache order on dispersal distance. Pearson's product-moment correlation was used to test for significance of the relationships between dispersal distance and seed trait. Paired t-tests were used to analyze whether a seed would be dispersed further along the re-caching process. All the analyses were performed in R (v. 2.15.0).

Table 1 | Summary of the generalized linear mixed model to test the effects of current dispersal distance and seed traits on seed fate (i.e. re-cached or not)

	Estimate \pm SE	Z-value	P-value
Seed size-Experiment			
Size	1.336 \pm 0.340	3.929	0.000
Distance	-0.012 \pm 0.102	-0.117	0.907
Size \times Distance	-0.073 \pm 0.049	-1.496	0.135
Nutrient content-Experiment			
Nutrient	1.308 \pm 1.300	1.007	0.314
Distance	0.048 \pm 0.047	1.039	0.299
Nutrient \times Distance	-0.122 \pm 0.116	-1.052	0.293
Tannin content-Experiment			
Tannin	-1.847 \pm 1.983	-0.931	0.352
Distance	-0.082 \pm 0.026	-3.131	0.002
Tannin \times Distance	0.185 \pm 0.259	0.714	0.475

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Author contributions

B.W. and J.C. designed the study. B.W. performed the experiments. B.W. analyzed the data. B.W., J.C. and R.T.C. wrote the manuscript.

Additional information

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