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Re-caching behaviour of rodents improves seed dispersal effectiveness: Evidence from seedling establishment

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ABSTRACT

Long-distance seed dispersal is disproportionately important for recruitment, range expansion and gene flow in plant populations. The re-caching of seeds by rodents is considered a mechanism of long-distance seed dispersal. The effect of re-caching on dispersal distance is well studied. However, how re-caching by rodents affects seedling establishment remains unclear. To assess the role of re-caching by rodents on seedling establishment, we tracked a large number of seeds and investigated the seed dispersal and seedling establishment of two large-seeded tree species (*Scleropyrum wallichianum* and *Garcinia xanthochymus*) in a tropical forest. We found that rodents scatter hoarded 48.9–71.3% of the released seeds, and a total of 23.8–36.6% of the initial caches of both species experienced re-caching up to 2 or 3 times. Re-caching was correlated with farther dispersal and a higher probability of seedling establishment for both species. In addition, re-caching contributed to medium and long-distance seed dispersal, with 17.2% and 18.5% of seedlings located > 50 m from parent trees for *G. xanthochymus* and *S. wallichianum*, respectively, and 3.4% of seedlings of *G. xanthochymus* located > 100 m from parent trees. Our results suggested that re-caching by rodents can promote seed dispersal effectiveness and contribute to effective long-distance seed dispersal.

1. Introduction

Seed dispersal by scatter-hoarding animals plays a significant role in seedling recruitment, the coexistence of plants, and the structure and function of forest ecosystems (Howe and Smallwood, 1982; Vander Wall, 1990, 2001; Jansen et al., 2014; Garzon-Lopez et al., 2015). Scatter-hoarding animals are considered highly effective dispersal agents because they frequently dig up and re-cache (re-disperse) seeds into favourable sites where seed dispersal success is high (Hirsch et al., 2012a). The re-caching of seeds during seed dispersal by rodents is a widespread phenomenon in diverse forest ecosystems (Vander Wall and Joyner, 1998; Perea et al., 2011; Jansen et al., 2012; Wang et al., 2014). Previous studies suggested that re-caching by scatter-hoarding rodents had significant ecological implications for both plants and rodents, i.e., due to increase seed dispersal distance (Vander Wall and Joyner, 1998; Perea et al., 2011), reduced negative density-dependent pilfering by competitors (Munoz and Bonal, 2011; Hirsch et al., 2012a), and provided highly effective long-distance seed dispersal for large-seeded fruiting trees as a substitute for dispersal by extinct megafaunal dispersal agents (Jansen et al., 2012).

Previously, scatter-hoarding rodents were generally considered short-distance dispersers, as the dispersal distance produced by scatter-hoarding rodents was usually less than 25 m (Vander Wall, 1990). However, some recent studies have suggested that re-caching by rodents can be a mechanism of long-distance dispersal for plants. For example, Jansen et al. (2012) found that the re-caching of seeds by Central American agoutis (*Dasyprocta punctata*) accounted for an estimated 35% of seeds that were dispersed > 100 m, which was often used as a threshold for long-distance seed dispersal (Russo and Augspurger, 2004; Jordano et al., 2007; Jansen et al., 2012). The result that re-caching by rodents can increase dispersal distance is consistent among studies (Vander Wall and Joyner, 1998; Perea et al., 2011; Wang et al., 2014). However, how the re-caching of seeds affects dispersal success is unclear. The main reason may be that it is notoriously difficult to track

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seed movements and seed fates; therefore, few studies have been able to analyse the impact of the re-caching of seeds on seedling establishment.

Theoretically, the re-caching of seeds may have both beneficial and detrimental effects on seedling establishment. On the one hand, re-caching by rodents may increase the chance of seeds being deposited in habitats that are suitable for seed and seedling survival. Hirsch et al. (2012a) found in Barro Colorado Island that re-caching by rodents could directly move seeds to locations where the density of conspecific adults was low. Thus, re-caching is likely to reduce negative density-dependent pilfering by competitors and improve the rates of seed survival and seedling establishment (Munoz and Bonal, 2011). On the other hand, re-caching may decrease the likelihood of successful establishment if seeds are moved away from suitable microsites or are disturbed during the germination process, i.e., radicle pruning or embryo removal by rodents during re-caching (Jansen et al., 2006; Xiao et al., 2009). In addition, re-caching may enhance the spatial memory of rodents regarding cached seeds (Smulders et al., 2010; Hirsch et al., 2013), and the re-cached seeds may be more likely to be retrieved and ultimately consumed. Therefore, re-caching is likely to be detrimental to seed survival and seedling establishment (Perea et al., 2011).

The role of re-caching in seed dispersal success is complex. Inconsistent patterns (both beneficial and detrimental effects) have been observed in previous studies by tracking seed survival. Perea et al. (2011) found that high numbers of movements decreased the probability of seed survival. In contrast, Hirsch et al. (2012a) found that the density of conspecific adults declined progressively as seeds were moved more often; hence, high numbers of movements may facilitate seed survival. However, these conclusions were usually made based on seed survival rather than on seedling establishment, which is a better indicator of seed dispersal success. In fact, seed survival cannot be equated with seedling establishment because the progression from seed to seedling is uncertain and can be influenced by various factors (Schupp et al., 2010). Accordingly, studies undertaken to explore how re-caching affects the success of seed dispersal using seedling establishment as a metric are required to understand the influence that this type of transportation has on seedling recruitment.

In the present study, we investigated the seed dispersal of two large-seeded trees (*Scleropyrum wallichianum* and *Garcinia xanthochymus*) by scatter-hoarding rodents in the Xishuangbanna tropical forest, Yunnan, southwest China. The interaction between the two trees and scatter-hoarding rodents was an ideal model because a large proportion of the cached seeds of the two species are likely to experience re-caching by rodents and establish large quantities of seedlings after dispersal. We aimed to assess the effects of re-caching of seeds by scatter-hoarding rodents on seed dispersal effectiveness. Seed dispersal effectiveness has been quantified as the quantitative component (the number of seeds dispersed by a dispersal agent) multiplied by the qualitative component (the probability of a dispersed seed survives to establish seedling and produces a new adult; Briggs et al., 2009; Schupp et al., 2010). In this study, we mainly focused on the effects of re-caching on seed dispersal distance and the probability of a cached seed survives to establish seedling, both of which are important parameters influencing the ultimate seed dispersal effectiveness (Briggs et al., 2009; Schupp et al., 2010).

2. Materials and methods

2.1. Study site and species

The present study was conducted in tropical forests located within the Mengla and Menglun Nature Reserves, Xishuangbanna, Yunnan Province, China. Two stands were selected for the field experiments. Stand 1 was a tropical seasonal rainforest in the 20-ha Xishuangbanna forest dynamics plot, located in Mengla Nature Reserve (21°36′ N, 101°34′ E, elevation: 709–869 m), which is dominated by *Shorea wantianshuea, Sloanea tomentosa, Pometia tomentosa, Pittosporum kerrii, Garcinia cowa, Mezzettiopsis creaghii, Saprosma ternatum,* and *Leea compactiflora* (Lan et al., 2008); this stand was used to study the seed dispersal of *G. xanthochymus*. Stand 2 was a tropical montane evergreen broad-leaved forest near the 1-ha Xishuangbanna forest dynamics plot located in Menglun Nature Reserve (21°50′ N, 101°12′ E, elevation: 780 m), which is dominated by *Castanopsis echinocarpa*, *Aporosa yunnanensis*, *Olea rosea*, *Lithocarpus truncates* and *Schima wallichii* (Zhang and Cao, 1995); this stand was used to release and track tagged seeds of *S. wallichianum*.

Both tree species are widely distributed in South and Southeast Asia and are common in the Xishuangbanna tropical forest (Wu, 1987). *G. xanthochymus* produces large, rounded fruits with 1–4 seeds per fruit. The fruit mass is 86 ± 5.9 g (mean ± SD, $n = 50$), and the seed mass is 4.4 ± 1.0 g ($n = 100$). The thickness of the endocarp is similar to that of thin paper and is difficult to measure. The seed endosperms have high fat (28.3%) and starch (38.2%) contents (seed nutrient composition were tested by the Cereal Quality Supervision and Testing Centre, Ministry of Agriculture, China), and the fruits mature from August to November. *S. wallichianum* produces rounded fruits with a single seed per fruit. The fruit mass is 40.9 ± 7.0 g (mean ± SD, $n = 30$), the seed mass is 4.7 ± 0.7 g ($n = 100$), and the thickness of the endocarp is 1.9 ± 0.3 mm. The seed endosperms have high fat (66.8%) and protein (18.7%) contents, and the fruits mature from August to September.

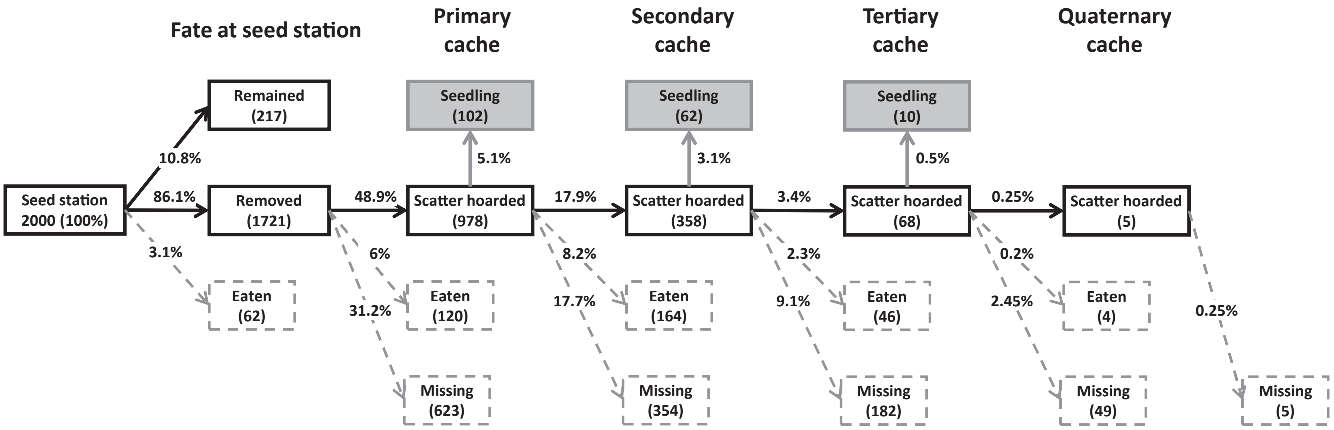
In the past, both species may have relied on dispersal by some large animals, i.e., macaques, elephants, or water monitors (Corlett, 1996, 1998; Lucas and Corlett, 1998; Corlett, 2017). However, large animals are rarely seen at the study sites owing to extensive human disturbances, such as hunting and deforestation (Liu and Slik, 2014). Scatter-hoarding animals have become the most important seed dispersers for the two tree species (Cao et al., 2011; Wang, 2013), and they provide substitutes for the extinct megafaunal dispersal agents. Two scatter-hoarding rodent species, *Niviventer confucianus* and *Maxomys surifer*, are the dominant seed dispersers in our study forests (Appendix S1) (Cao et al., 2016; Cao et al., 2017; Wang et al., 2018).

2.2. Seed releasing and tracking

We tagged and tracked seeds of *G. xanthochymus* in November 2009 and November 2011 and seeds of *S. wallichianum* in August 2007 and August 2008. Ten fruiting trees of *G. xanthochymus* and six fruiting trees of *S. wallichianum* were selected for seed releasing and tracking experiments in two years. Two hundred tagged seeds were placed under each of the fruiting trees, which were spaced 50–100 m from each other (a total of 2000 seeds for *G. xanthochymus* and 1200 seeds for *S. wallichianum*). For each focal tree, we established 4 seed stations in 4 directions within 2 m of the trunks of the trees and placed 50 tagged seeds on the ground at each station. Seeds were marked by attaching a small coded plastic tag (2.5 * 3.6 cm) to each seed by a thin steel thread (diameter, 0.2 mm; Zhang and Wang, 2001; Xiao et al., 2006). The steel thread was attached to seeds by drilling a 0.5-mm diameter hole through the cotyledons. When rodents buried the tagged seeds beneath leaf litter or in the soil, the tags were exposed on the surface, making them easy to relocate. Tagging has a negligible effect on seed removal (Xiao et al., 2006) and germination of the seeds of both species used in the present study (L. Cao and Z. Wang, personal observation).

The tagged seeds were surveyed at weeks 1 (only for *G. xanthochymus*), 2, 3 (only for *G. xanthochymus*), 4, 6, 8, 12, and 16 after seed placement and then in March/May, July, September, and December of the following 1 to 3 years (some *S. wallichianum* seeds survived in caches for more than 3 years before germination and seedling establishment). We spent 1–7 days (depending on the number of seeds removed) searching for the removed seeds in one stand for each survey. For each survey, 3 people searched the entire area independently but concurrently. We intensively searched the area within an 80-m (for *S. wallichianum*) or 100-m (for *G. xanthochymus*) radius around each tree to retrieve the removed seeds and record the seed fates. When we found

(a) *Garcinia xanthochymus*



(b) *Scleropyrum wallichianum*

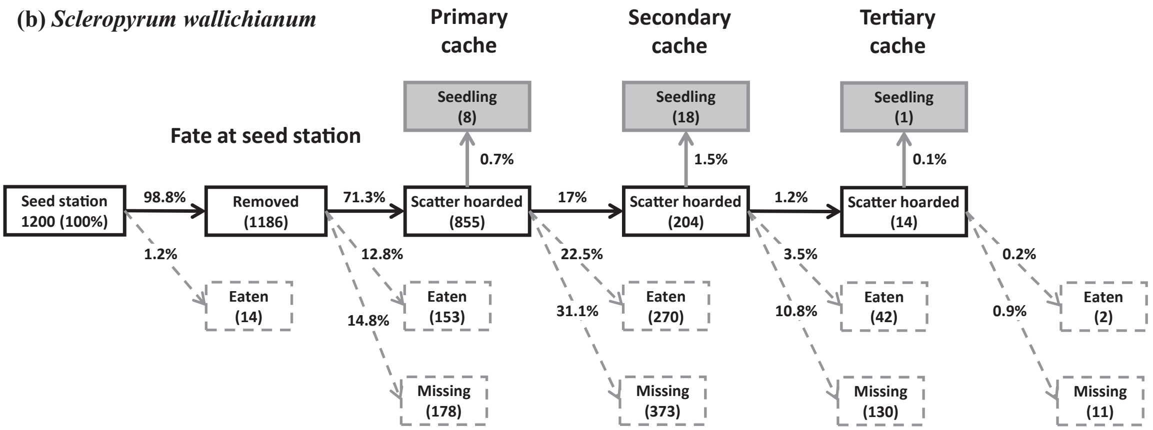


Fig. 1. Seed fate pathways of the released seeds of (a) *Garcinia xanthochymus* and (b) *Scleropyrum wallichianum* during seed dispersal. The percentages given here are cumulative.

that the dispersal distance of some seeds approached the maximum search radius, the search radius was increased to 120 or 150 m until we could not retrieve any more seeds within the area. Our tagging and searching methods allowed us to relocate 68.8% (*G. xanthochymus*) and 85.2% (*S. wallichianum*) of the released seeds.

The seed fates at each station were categorized as intact, predated, or removed, and those removed from seed stations were categorized as scatter hoarded, predated, missing, or established seedlings. We also recorded the dispersal distances of cached seeds from the parent tree. Cached seeds were marked using a numbered bamboo stick 20 cm away from caches for later relocation. On subsequent visits, we checked the cached seeds until they were recovered (eaten and removed) by animals. If a marked cache was removed, then the area around the cache was extensively searched to relocate the seeds. When seeds in primary caches or higher-order caches (i.e., secondary caches that were hoarded after primary caching, Fig. 1) were removed and found in other caching sites, we also recorded the seed fate and dispersal distance.

2.3. Data analysis

A generalized linear mixed model (GLMM) was applied to analyse the difference of seed recovery (eaten and removed) or seedling establishment between the primary caches and re-cached seeds. Seed recovery or seedling establishment was modelled as a binomial variable with a logit link (1 for success and 0 for failure), while the different caching stages (primary caches vs. re-cached seeds) were treated as a fixed categorical variable. Years and parent trees were treated as random variables.

Because some of the seeds could not be tracked finally, and the missing seeds outside of the search area likely caused a biased estimate in our study, thus we analyzed the seedling establishment of cached seeds while the missing seeds were either included or excluded.

The Cox regression model was applied to compare the difference among the survival time (the time a seed remained in the same cache) of the primary caches (t1), secondary caches (t2) and the cumulative survival time (sum of the survival time of a seed in all the caches, i.e. t1 + t2 + …) of re-cached seeds. The mean ultimate dispersal distance of re-cached seeds was estimated by Kaplan-Meier survival analysis, while treating distance as time (Hirsch et al., 2012b; Jansen et al., 2012), as many seeds could not be finally tracked and the ultimate dispersal distance was usually underestimated. Missing seeds were included as observations censored at the last recorded distance. Then, the Cox regression model was applied to compare the difference among the dispersal distance (treated as time) of primary caches, observed ultimate dispersal distance of re-cached seeds (the last recorded distance) and the estimated ultimate dispersal distance of re-cached seeds (the last recorded distance, while missing seeds are treated as observations censored). Similarly, the Cox regression model was also applied to compare the difference in the dispersal distance between seedlings that established from primary caches and re-cached seeds. Years and parent trees were treated as random variables when analysing the differences of survival time and dispersal distance.

All analyses were conducted in R 3.5.2 (R Core Team 2018) and associated packages; the GLMM were constructed with *lme4* and the Cox regression model was constructed with *survival*; Tukey's test was applied for post hoc pair-wise comparisons with *lsmeans*.

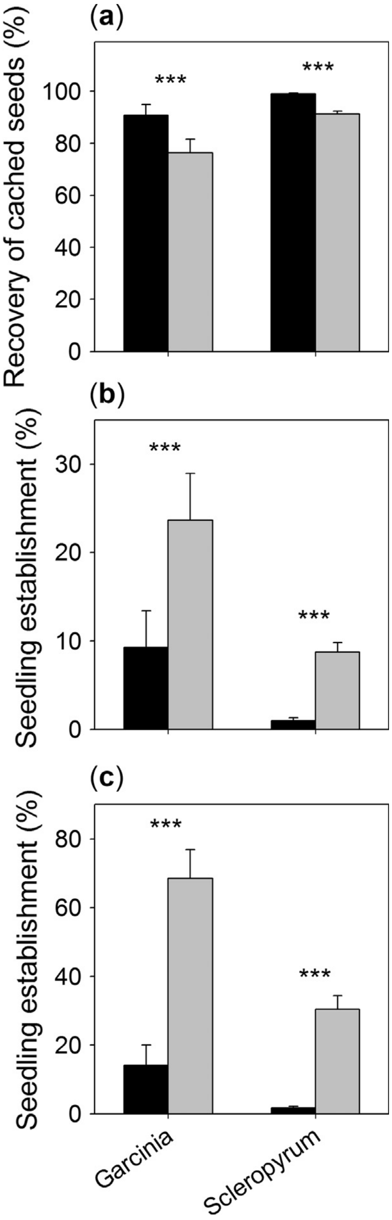


Fig. 2. The difference in (a) seed recovery and (b, c) seedling establishment between primary caches (black bar) and re-cached seeds (light grey bar) for *Garcinia xanthochymus* and *Scleropyrum wallichianum*. (b) Missing seeds were included; (c) missing seeds were excluded for analysis. ***$P < 0.001$.

3. Results

For *G. xanthochymus*, rodents removed 86.1% of the released seeds from parent trees and scatter hoarded 48.9% (978 seeds, primary caches) of the seeds (Fig. 1a). Most cached seeds were excavated, and many of these seeds were re-cached, with 358 seeds found in secondary caches, 68 seeds in tertiary caches, and 5 seeds in quaternary caches (Fig. 1a). Finally, a total of 102, 62, 10, and 0 cached seeds in primary, secondary, tertiary, and quaternary caches, respectively, became established seedlings (Fig. 1a). For *S. wallichianum*, rodents removed 98.8% of the released seeds from parent trees and scatter hoarded 71.3% (855, primary caches) of the seeds (Fig. 1b). We found 204 seeds in secondary caches and 14 seeds in tertiary caches (Fig. 1b). In total, 8, 18, and 1 cached seeds in primary, secondary, and tertiary caches, respectively, became established seedlings (Fig. 1b).

Seeds in the primary caches were more likely to be recovered (including seeds both eaten and removed) than re-cached seeds for both species (*G. xanthochymus*, $z = 6.7$, $P < 0.001$; *S. wallichianum*, $z = 5.6$, $P < 0.001$; Fig. 2a). The probability of seedling establishment from primary caches was significantly lower than that from re-cached seeds, for both species (missing seeds were included; *G. xanthochymus*, $z = -6.7$, $P < 0.001$; *S. wallichianum*, $z = -5.6$, $P < 0.001$; Fig. 2b), and we found a similar pattern when the missing seeds were excluded for analysis (*G. xanthochymus*, $z = -10.1$, $P < 0.001$; *S. wallichianum*, $z = -7.2$, $P < 0.001$; Fig. 2c).

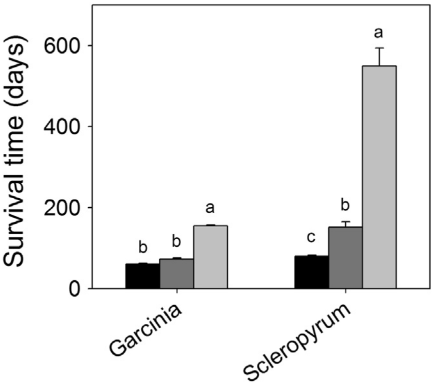


Fig. 3. Comparison of the survival time among primary caches (black bars), secondary caches (light grey bar) and the estimated cumulative survival time of re-cached seeds (dark grey bar) for *Garcinia xanthochymus* and *Scleropyrum wallichianum*. Different letters indicate significant differences among groups ($P < 0.05$).

Seed survival time in primary caches was significantly shorter than that in secondary caches for *S. wallichianum* (Tukey's test, $z = -7.6$, $P < 0.001$; Fig. 3), but not for *G. xanthochymus* (Tukey's test, $z = -1.5$, $P = 0.279$; Fig. 3). The estimated cumulative survival time of re-cached seeds was about 2.5 and 6.8 times longer than the survival time of primary caches for *G. xanthochymus* and *S. wallichianum* (Fig. 3), respectively.

The mean dispersal distance of re-cached seeds were significantly farther than that of primary caches for both species (*G. xanthochymus*, Tukey's test, $z = 10.8$, $P < 0.001$; *S. wallichianum*, Tukey's test, $z = 12.9$, $P < 0.001$), although the observed dispersal distance of re-cached seeds may be largely underestimated (Fig. 4a). For primary caches, only 14.9% (146 of 978) and 3.6% (31 of 855) of seeds were dispersed > 50 m for *G. xanthochymus* and *S. wallichianum*, respectively, while no seeds were dispersed > 100 m for either species. Compared with the estimated densities of ultimate dispersal distances for the primary caches, those for re-cached seeds had long right tails for both species (Fig. 5). A total of 43.9% (157 of 358) and 19.1% (39 of 204) of re-cached seeds were dispersed > 50 m, and 3.9% (14 of 358) and 0.5% (1 of 204) were dispersed > 100 m for *G. xanthochymus* and *S. wallichianum*, respectively. The farthest dispersal reached 180 and 108 m from the parent trees for *G. xanthochymus* and *S. wallichianum*, respectively. Moreover, the observed dispersal distance of re-cached seeds may have been significantly underestimated (Fig. 4a).

Similarly, the mean dispersal distance of seedlings that established from re-cached seeds was farther than that from primary caches for both *G. xanthochymus* (Wald test, $\chi^2 = 44.6$, $df = 1$, $P < 0.001$; Fig. 4b) and *S. wallichianum* (marginal significant, $\chi^2 = 2.4$, $df = 1$, $P = 0.1$; Fig. 4b), respectively. Long right tails were also observed in the estimated densities of dispersal distances for the seedlings that established from the re-cached seeds (Fig. 5). Of the seedlings that established from primary caches, only 3.9% (4 of 102) and 12.5% (1 of 8) distributed > 50 m away from parent trees for *G. xanthochymus* and *S. wallichianum*, respectively; and no seedlings distributed > 100 m away for either species. However, of the seedlings that established from re-cached seeds, 36.1% (26 of 72) and 21.1% (4 of 19) were distributed > 50 m away for *G. xanthochymus* and *S. wallichianum*,

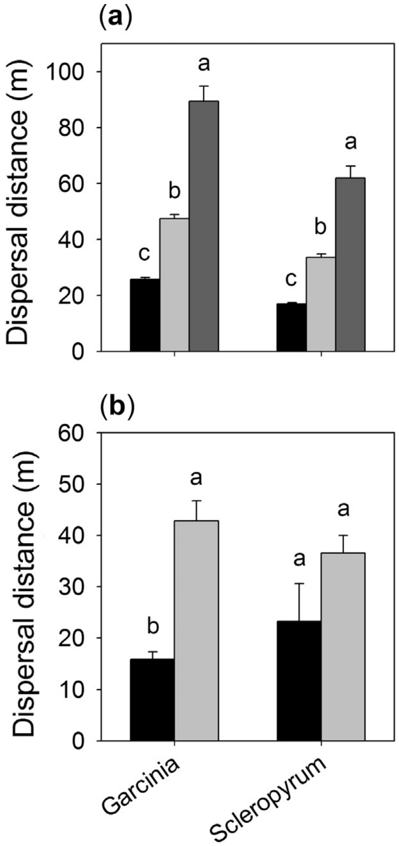


Fig. 4. (a) The difference among the observed dispersal distance of primary caches (black bar) and re-cached seeds (light grey bar), and the estimated dispersal distance of re-cached seeds (dark grey bar) for *Garcinia xanthochymus* and *Scleropyrum wallichianum*; and (b) the difference in the dispersal distance between seedlings established from primary caches (black bar) and that from re-cached seeds (light grey bar).

respectively, and 8.3% (6 of 72) were distributed > 100 m away for *G. xanthochymus*.

4. Discussion

Our results indicated that the re-caching of seeds by scatter-hoarding rodents significantly increased the dispersal distance and seedling establishment of cached seeds for both species. The cached seeds can also be stored for longer time after being excavated by rodents and re-cached from primary caches. Re-caching contributed a large proportion of seeds and seedlings distributed > 50 m away from parent trees, and a few seeds and seedlings attained a dispersal distance > 100 m, which is often used as the threshold for long-distance seed dispersal (Russo and Augspurger, 2004; Jordano et al., 2007; Jansen et al., 2012). Our results suggest that re-caching can be an effective strategy of cache management to prolong seed storage time for scatter-hoarding rodents and can contribute to effective long-distance seed dispersal in plants.

The results suggested that the re-caching of seeds by scatter-hoarding rodents significantly increased the dispersal distance, which was consistent with the findings of most previous studies (Vander Wall and Joyner, 1998; Perea et al., 2011; Wang et al., 2014). Re-caching or some farther dispersal is likely to reduce cache pilfering by competitors around parent trees (Munoz and Bonal, 2011; Hirsch et al., 2012a) and prolong seed storage time, and it may ultimately be beneficial to seedling establishment. Therefore, re-cached seeds are more likely to survive to establish seedlings when compared with primary caches for both species in this study. Frequent re-caching of seeds may also enhance the spatial memory of rodents regarding cached seeds (Hirsch et al., 2013) and may be detrimental to seedling establishment. Since few seeds were transported multiple times, we were unable to assess the impact of multiple movements on seedling establishment. We did not assess cache pilfering and the spatial memory of rodents in this study, so we cannot accurately analyse their impacts on the seedling establishment of cached seeds. However, whether the cache owners or thieves had re-cached or recovered the seeds, the re-caching of seeds by rodents did improve seed dispersal effectiveness for the plants. Furthermore, our results showed a consistent predation rate of seeds during the caching and re-caching processes for both species (Fig. S1), indicating that the re-caching did not reduce seed predation of cached seeds. This may infer that the higher probability of seedling establishment of re-cached seeds was not due to the lower seed predation, but because of the longer cumulative storage time and less likelihood of being recovered before germination.

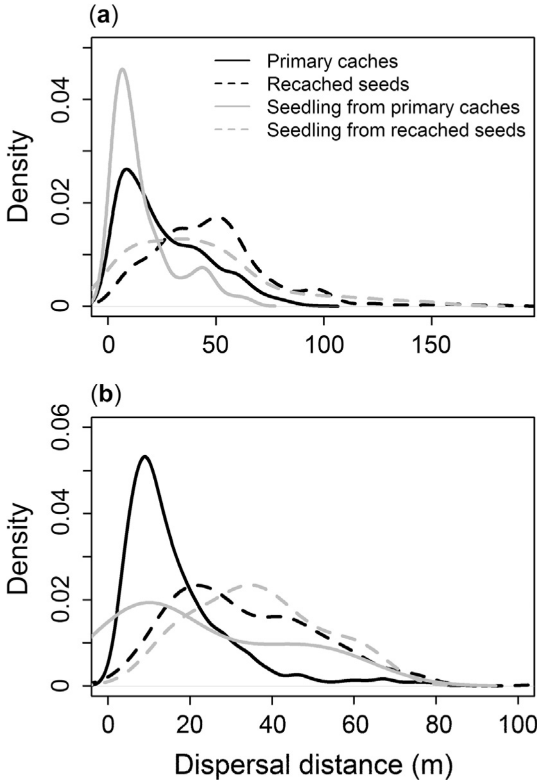


Fig. 5. The estimated kernel densities of dispersal distances of the primary caches, re-cached seeds, seedlings established from the primary caches and re-cached seeds for (a) *Garcinia xanthochymus* and (b) *Scleropyrum wallichianum*.

We found the estimated cumulative survival time of re-cached seeds differed greatly between the two species, with that 549.5 ± 44.6 days (mean ± SE) for *S. wallichianum*, which was about 3.5 times longer than that of *G. xanthochymus* (154.9 ± 2.2 days, Fig. 3). A possible explanation might be that the difference in the time over which a seed develops into a seedling between the two species (see Table S2). The time from seed release to seedling establishment of *S. wallichianum* seeds varied from 440 to 1155 days, with a mean of 703 ± 44.3 days, whereas the time for *G. xanthochymus* varied from 164 to 179 days, with a mean of 167 ± 0.5 days. The results suggested that rodents preferred to store long-term dormancy seeds for long periods. Different dormancy time may result in different pattern in the recovery and seedling establishment of cached seeds between the two plants. The long-term dormancy of *S. wallichianum* seeds gave the hoarders sufficient time to retrieve the cached seeds, whereas short dormancy cannot guarantee retrieval of the caches. Therefore, the established seedlings of *S. wallichianum* were more likely to come from the caches forgotten by rodents, whereas the established seedlings of *G. xanthochymus* may have been due to the short dormancy (compared with that of *S. wallichianum*) of the seeds rather than the seeds being forgotten. In the same way, compared with the primary caches, re-cached seeds of *S. wallichianum* held the relatively lower recovery rate because of their higher likelihood of being forgotten by rodents, thus may in turn promote seed survival and seedling establishment.

Re-cached seeds held a higher probability of seedling establishment than primary caches did; however, digging up and re-dispersing of primary caches may lead many seeds to be predated and few seeds being re-cached. In this case, the number of seedlings that established from re-cached seeds may not be necessarily greater than that from primary caches. We observed two different patterns, i.e., the number of seedlings that came from re-cached seeds was greater than that from primary caches for *S. wallichianum*, while *G. xanthochymus* showed an opposite pattern (Fig. 1). Furthermore, a great number of seeds were missing after recovery from primary caches, some of which may escape from predation and finally establish seedlings. Thus, the seedlings that came from re-cached seeds may have been underestimated.

Jansen et al. (2012) found that the seeds of a palm can be moved and re-cached up to 36 times by agoutis in response to heavy pilfering of caches. Because of the low pilfering in our study sites (Cao et al., 2018), neither of our studied species was moved many times. However, due to some longer survey interval in this study, the number of times that the seeds have been transported may have been underestimated. The long survival times in cache sites for both species (61 and 80.2 days in primary caches, Fig. 3) also suggested that cache pilfering was not severe in the present study. Therefore, the re-caching may be a strategy of hoarders for managing their cached seeds. However, some other factors, e.g., seed abundance in population or community, length of the seed-drop timing, rodent abundance or seed characteristics may affect the recovery or pilferage of cached seeds (Perea et al., 2011; 2016; Cao et al., 2017; Cao et al., 2018; Dittel and Vander Wall, 2018). In order to accurately understand the relationship between the survival times and the cache recovery and pilferage, further research is needed.

We found that large proportions of re-cached seeds and seedlings attained a dispersal distance > 50 m, and a few re-cached seeds and established seedlings attained a dispersal distance > 100 m from the parent trees for both species. The results suggest that rodents can provide effective medium and long-distance seed dispersal, which ensures that many seedlings can escape negative density-dependent effects around parent trees and colonize new habitats (Janzen, 1970; Connell, 1971). Rodents played a significant role in seed dispersal and seedling regeneration for large-seeded fruiting trees in our study, which is consistent with previous findings (Jansen et al., 2012). We expect that rodents will play an increasingly important role in heavily disturbed tropical forests, acting as substitutes for extinct megafaunal dispersal agents.

5. Conclusion

In conclusion, our study indicated that the re-caching of seeds by rodents can significantly increase seed dispersal distance and seedling establishment and contribute to effective long-distance seed dispersal in plants. Our study suggests that conclusions based on seedling establishment are important to understanding the complex processes of seed dispersal and plant regeneration. Thus, future studies of sites containing diverse taxa and ecosystems that are focused on seedling establishment during dispersal are encouraged to provide further information for comprehensive assessments of the role of re-caching in plant fitness and forest dynamics.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.04.044.

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