

Can Scatterhoarding Rodents Assume the Role of Effective Large Seed Dispersers in a Fragmented Afromontane Forest?

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Abstract

Anthropogenic pressure has led to fragmentation of tropical forests and defaunation of local animal communities (particularly large-bodied vertebrates). Loss of large frugivore species may be highly detrimental to fruiting species that produce large-sized seeds. This is because in their absence there might be a lack of frugivore species that can efficiently disperse their seed. Here, the dispersal of *Carapa oreophila* Kenfack (Meliaceae) is addressed in the context of Ngel Nyaki a fragmented Afromontane forest in north eastern Nigeria. The *C. oreophila* suffers from human-driven degradation and has lost large-bodied frugivores. To test for the effect of habitat (Core = "COR", Edge = "EDG" and Fragment = "FRG") on seed fate, in each habitat two 100m-long transects (100 m apart with five 1×1 m² quadrats placed along its length, 25 m apart) were set up to examine how many seeds were: (a) consumed (predation); (b) covered under forest floor litter away from the plot (cached) or dug into the soil (buried); or (c) removed but not locatable (fate unknown, i.e. missing). In the highly degraded riparian fragments, where resources are scarce, rodents act more as seed predators than dispersers, consuming the majority of seed, whilst in forest, there was a greater propensity to hoard. Furthermore, it was deduced that rodents are more likely to disperse seed in the middle of *C. oreophila*'s fruiting season when the abundance of seed is greater. Results therefore suggest that the benefit *C. oreophila* receive from scatterhoarding rodents as substitute dispersers at Ngel Nyaki is dependent on the habitat; these effects thus modulate the role of rodents as predators or dispersers.

Keywords: Fragmentation; Afromontane; large seed; frugivores; Scatterhoarding rodents.

Introduction

Scatterhoarding by rodents, whereby seeds are collected during periods of abundance and stored in caches with one or few for later consumption (Vander Wall 1990), has the potential to disperse seeds great distances and deposit them in sites suitable for germination (Vander Wall 1990; Jansen et al. 2012). Seed characteristics such as size, nutrient content (Jansen et al. 2004; Vander Wall 2010) tannin levels (Wang & Chen 2011), and palatability (Feer & Forget 2002; Aliyu et al. 2014) can contribute toward a rodent's choice to either consume a seed immediately or stock-pile it for later consumption. Such manipulation of a scatterhoarder's behaviour is believed to be under selection (Vander Wall 2010), and opposing selective pressures from different granivore taxa

may shape seed trait variation in a plant's population (Siepielski et al. 2010).

The ecological context in which the rodent-plant relationship occurs might also play an important role in determining the role scatterhoarders assume (Theimer 2005). Fragmentation and degradation of forest may drive a scatterhoarder's behaviour from acting predominantly as a mutualist that disperses seed to an antagonist that consumes the majority of seed. Jorge and Howe (2009) demonstrated the ratio of predation to hoarding increased, and the distance of seed moved decreased, from continuous forest to intensely fragmented forest in the Amazon. In a Nigerian montane forest, Aliyu et al. (2014) observed a similar pattern between continuous and degraded forest fragments. They also demonstrated that palatability of seeds can

influence a scatterhoarder's decision to cache or consume a seed, in that seeds of the more palatable species *Pouteria altissima* were consumed more readily versus *Garcinia smeathmanii* (which had a greater propensity to be hoarded). Research on seed fate suggests that seeds in the forest edge may also suffer higher rates of removal and predation compared to the forest interior (Pinto et al. 2009).

Carapa (Meliaceae) is a Pantropical genus native to central and southern South America and the West Indies. However, its centre of origin is in West Africa (Kenfack 2008, 2011) where it occurs in lowland to montane forest: e.g. 2,600 m a.s.l. in Rwanda (Nyiramana et al. 2011) and 2,400 m a.s.l. in Nigeria (Chapman & Chapman 2001). It is an economically important genus (Forget & Jansen 2007) valued for its timber and oil which is extracted from its extremely large, lipid-rich seeds (Gueye et al. 2010; Weber et al. 2010; Prophiro et al. 2012). Fruit traits of this genus suggest adaptation and coevolution toward mega-fauna, in that trees produce large fruits with several chambers containing large seeds (Jordano 1995). In the Neotropics, *Carapa* spp. are now dispersed almost exclusively by scatterhoarding rodents (Jansen et al. 2004).

Carapa spp. evolved in Africa and all the 16 African species have large seeds (>20 mm in diameter) (Kenfack 2011) and may have evolved for dispersal by mega-fauna (Blake et al. 2009), so that recent mega-faunal mammal declines in Africa (Hawthorne 2000; Blake et al. 2009) could pose a potential threat to the regeneration ecology of *Carapa* in Africa. While it would appear African *Carapa* meet the criteria to be considered a potential victim of mega-faunal fruit syndrome, empirical evidence to directly support this is lacking. Elephants in montane West Africa are known to consume many large fruits including *Carapa* (Theuerkauf et al. 2000). However, the observation that seedlings of *C. grandiflora* were found throughout the Kilum-Ijim Forest (Cameroon Highlands, north-west Cameroon; where elephants went extinct approximately 100 years ago and are apparently dispersed by rodents) (Maisels et al. 2001) suggests that *Carapa* may be adapted, but not completely reliant on mega-faunal dispersal. The overall aim of this study was to explore the fate of *C. oreophila* seeds deposited onto the floor

of the three Ngel Nyaki forest habitats (Core = "COR", Edge = "EDG" and Fragment = "FRG") in order to determine whether or not *C. oreophila* is being dispersed at Ngel Nyaki in the absence of any mega-fauna. From previous studies and observations in Ngel Nyaki (camera trap images), it is known that the most important (and possibly sole) disperser of large seed (>20 mm) in Ngel Nyaki is the African pouched rat *Cricetomys* sp. Nov (Olayemi et al. 2012). Camera trap observations by Nyiramana et al. (2011) for *C. grandiflora* also supported this genus as the singular secondary disperser of *C. grandiflora* in Rwanda.

The main objective of this study was to: determine how forest fragmentation and degradation affects the fate of *C. oreophila* seeds in the absence of mega-fauna.

The hypothesis tested was: seeds in degraded/fragmented habitats will have a higher probability of being predated than in core forest because of reduced seed availability in forest fragments (Nyiramana et al., 2011; Aliyu et al., 2014).

Materials and Methods

Study site:

The study was conducted within Ngel Nyaki Forest Reserve on the Mambilla Plateau, in Taraba State, Nigeria (7° 5'N, 11° 3'E). The reserve covers a total area of 4600ha and includes 750ha of almost continuous mid-altitude sub-montane forest at 1400–1600m elevation (Chapman & Chapman 2001). This forest is embedded within a savannah-grassland landscape of *Sporobolus* grasses (Chapman & Chapman 2001; Beck & Chapman 2008; Adanu et al. 2010). The mean annual rainfall is 1800mm (Nigerian Montane Forest Project, NMFP, rainfall data) and the mean monthly maximum and minimum temperatures for the wet and dry seasons are 26 and 13°C, and 23 and 16°C, respectively (Matthesius et al. 2011). The reserve is officially protected by the Taraba State Forest Service and the presence of NMFP researchers also has a positive influence on reducing poaching. However, local Fulani pastoralists and their cattle still remain on the reserve land, and their cows enter the forested areas, trampling and eating seedlings and compacting soil (Chapman &

Chapman 2001). Additionally, the grassland is annually burnt towards the beginning of rainy season to encourage new growth; fires encroach into the forest edge, opening it up and encouraging the growth of light demanding lianas and grasses. Outside the main Ngel Nyaki Forest are small riparian forests. The small riparian forests also presumably suffer from cattle browsing, trampling, fire encroachment, as well as the removal of poles for fence posts and fuel by the local Fulani families.

Study species

Carapa oreophila is an Endemic tree to Cameroon and the Eastern Nigerian highlands (Chapman & Chapman 2001). It is distributed in Montane regions at altitudes ranging from 1100–2500m above sea level. *Carapa oreophila* is common within the Ngel Nyaki forest particularly in more humid west-facing slopes and close to streams (Aliyu unpubl. data). It is less common in the riparian fragments. It is possible the large fruit measuring 14 x 10 cm and weighing 185 gm has evolved to be consumed and dispersed by large mammals such as elephants (Blake *et al.* 2009), which are locally extinct. Seeds measuring 4 x 3 cm and weighing 15 gm are now more likely dependant on rodents for secondary dispersal as observed among members of same genus in the Neotropics.

The effect of habitat on seed fate

To test for the effect of habitat (COR, EDG and FRG) on seed fate, in each habitat two 100m-long transects (100 m apart with five 1x1 m² quadrats placed along its length, 25m apart) were set up to

examine how many seeds were: (a) consumed (predation); (b) covered under forest floor litter away from the plot (cached) or dug into the soil (buried); or (c) removed but not locatable (fate unknown, i.e. missing); NOTE: both caching and burial are considered as “hoarded” in this study, because *C. oreophila* being large seed distinguishing cached and buried seeds was difficult in Ngel Nyaki Forest. Each quadrat was divided into four 0.25m² plots, and five fresh *C. oreophila* seeds were placed in each plot one seed in the plot centre and one in each corner, *sensu* (Aliyu *et al.* 2014) (Figure 1). Deposition of seeds onto the forest floor was to simulate seed released from fruits after they had fallen onto the ground and split open, spilling seeds. A total of 800 seeds were used per habitat and 2,400 seeds in the entire experiment. Each seed was marked with a 1m-long white nylon thread following the method of Forget (1991) to aid in their location post-removal. Once set up, the experimental plots were evaluated for seed fate at two, five and 10th days. Seeds were discovered and rapidly removed by rodents from all plots irrespective of habitat or fruiting period. Removed seeds were searched for within a five metre (m) radius of plots, which was then extended to 10 m if all seeds were not accounted for. Predated seeds were identified by having been partially consumed or by the presence of a thread with no seed attached. When a seed was found hoarded a knot was made in the end of the thread in order to avoid recording it twice. All threads from missing or eaten seeds were removed (Forget 1996).

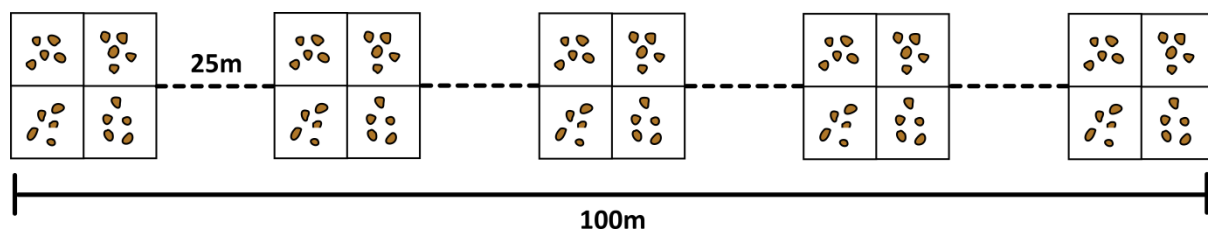


Figure 1: Experimental setup for *C. oreophila* seed removal, Five seeds were placed in one of four quadrats per plot.

The effect of seasonal variation on seed fate

To test for the effect of seasonality on seed fate the experiment was repeated four times during the fruiting season of 2022, from the very beginning of the season until there were insufficient seeds

available to run the experiment. Each experiment ran for 10 days and there were four periods (S) during the season: August 18–28 (S1); September 5–15 (S2), 18–28 (S3); and October 2–12 (S4). At the end of each 10th day run the experiment was

reset with fresh *C. oreophila* seeds, because seeds were removed rapidly within two to five days.

Analysis of seed fate Data

To determine the probability that a *C. oreophila* seed placed on the forest floor would be predated, hoarded (potentially dispersed), or go missing, in each of the four 10 day periods during the fruiting season of the species, and in the three different habitats (COR, EDG and FRG), Bayesian statistics (Ellison 2004) were employed. A mixed effects multinomial logistic effects model was used, similar to that in Aliyu *et al.* (2014). Since the analysis was concerned with the analysis of categorical response (for example seed fate could be categorized into predated, cached, buried and missing, we have used a mixed effects multinomial logistic regression model. we have chosen to implement it within the Bayesian framework both, because of the flexibility of the Bayesian approach, and because of the availability of the statistical software package WinBUGS (Spiegelhalter *et al.* 2002).

Observation of seed fate

Seed fate—the effect of habitat

Out of the 2,400 *C. oreophila* seeds used, about 50% of seed had been removed from all plots across all habitats after two days. By the 10th day 100% of seeds were removed from the EDG and FRG, and 98% from the COR. Of the total seeds removed, 65% (1,562) were recovered and 35% (823) were missing. Of all the removed seeds 886 (37%) were predated and 28.3% (676) were hoarded.

Habitat and season interaction effects on seed fate

Markedly fewer seeds were predated in all three habitats at the start of the fruiting season (S1) than later on, but this was particularly so in the EDG ($P= 0.999$) and FRG ($P\geq 0.999$). Seeds in the COR and EDG had a higher probability of being hoarded in the second fruiting period (S2) than either at the start of fruiting ($P= 0.999$) or towards the end of the season (S3 and S4; $P= 0.999$). While not as strong, the same trend was apparent in the FRG ($P= 0.827$). There was a particularly strong effect of fruiting period on the probability of seed going missing; in all three habitats a higher proportion of seeds was missing in the first period (S1) than in any of the later three periods ($P >0.999$). The interactive effect of habitat and season is depicted in Figure 2.

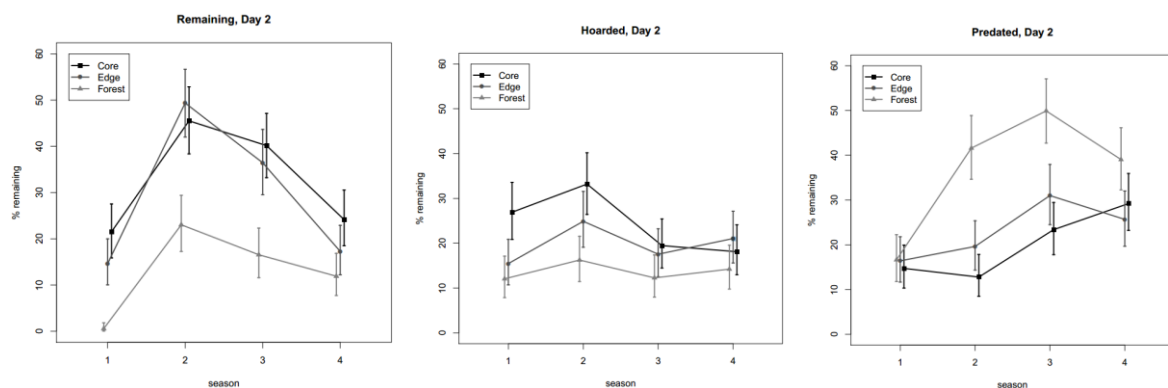


Figure 2: Interplay between seasonality and habitat on seed fate. Abundance of *C. oreophila* seed was greatest in the middle of the season (S2), lower during the start (S1), and end (S3/4). Percent of seeds remaining (left), predated (middle), and hoarded(right) for each of the habitats (“core”, “edge”, and “forest” fragments) are given.

Overall observation of the seed fates by days on average shows that the rates of seed predation consistently increased with fragmentation ($P =$

0.9604). The rates of hoarded seeds by rodents consistently decreased with fragmentation ($P =$

0.9864). The proportion of seeds missing increased from the COR to FRG ($P = 0.9898$); see Figure 2. The fate of seeds changed with variation in seasons in all habitats: after 10 days, higher proportion of

seeds was lost in the fragment than any of the other two habitats ($P = 0.9999$).

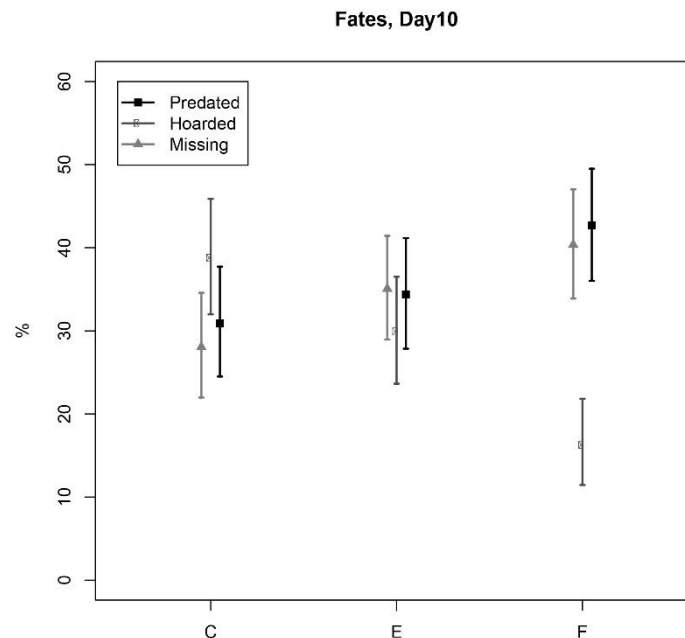


Figure 3: Percentages of seed predated, hoarded and missing after 10 days of seed placement on experimental plots in the three habitats.

Habitat and rodent interaction effects on seed fate

Markedly fewer seeds were predated in COR and EDG among the habitats (Figure 3), but this was particularly so in the COR ($P = 0.999$). In FRG predation rate was high ($P \geq 0.999$). Seeds in the COR and EDG had a higher probability of being hoarded compared to FRG ($P = 0.827$). There was a particularly strong effect of habitat on the probability of seed going missing; in all three habitats a higher proportion of seeds was missing in the fragment than in any of the habitat ($P > 0.999$).

Observations in this study suggest that habitat drive changes in the behaviour of scatterhoarding rodents. This impacts the role they play as mutualistic dispersers and shifts it to one of a predator. The observation further indicated that scatterhoarding rodents in Montane Afrotropical forest may have more of an impact on seed Core relative to Fragment and Edge counterparts.

and the borders of large forest patches, like Ngel Nyaki (Chapman *et al.* 2004; Adanu *et al.* 2010). It

was hypothesised that increasing degradation/fragmentation would lead to *C. oreophila* seeds in such sites having a higher probability of being predated than in continuous forest because of reduced seed availability. The density survey of *C. oreophila* adults showed relatively few adult trees in the EDG and even fewer in the FRG (Babale, Unpublished Data), and given the fragment forest around Ngel Nyaki contains few large-seeded tree species (Ihuma 2007), one might predict that any large seeds will exhibit high probabilities of predation (Ihuma 2007). What was surprising, though, was *C. oreophila* seed fate in the COR and EDG were not markedly different to each other. However, seed fates in the COR always differed more from the FRG than the EDG. Possible causes of these trends that require further testing could be the rodents may have larger home ranges in the EDG and travel farther to find food (Godsall *et al.* 2014) or there may be alternative food sources in the EDG. Rodent density may be lower in the EDG, for example because of a higher density of predators

(Asquith *et al.* 1997). Regardless, the results demonstrated a higher probability that rodents were predators of *C. oreophila* seed in the highly

Effect of season

The results of this study demonstrate that seasonality contributes to differences in immediate seed fate in *C. oreophila* at Ngel Nyaki. The general trend observed in all habitats was high removal rates in the early period of the season (S1), followed by dramatically lower rates of removal during the peak of the season (S2), ending with an increase in removal toward the end of the season as seeds became increasingly less abundant again (S3–S4). Removal of seed by rodents may be expected to decrease during episodes of abundance as predators become increasingly satiated (Theimer 2005; Xiao *et al.* 2005; Li & Zhang 2007), but studies suggest that local density of seeds can play an important role in removal rates as well (Hulme & Hunt 1999). Even though seed fates differed across habitats, the shape of the intra-seasonal trends was largely the same for each habitat.

Interestingly, the results of this study in the abundant fruiting year of 2022 were comparable to those of Jansen *et al.* (2004) and Forget (1996) during lean fruiting periods in each study. Jansen *et al.* (2004) reported 100% removal of *C. procera* within 10 days during lean years and Forget (1996) reported >90% removal over 20 days in the lean fruiting month of May. Of interest are the similarly high removal rates (>90% in six days) reported for *C. grandiflora* in the large expanse of montane forest in Rwanda during the lean fruiting years of 2008 and 2009 (Nyiramaana *et al.* 2011). It thus appears (from seed removal alone) that in the Ngel Nyaki's rich 2022 fruiting year, the probability of seeds being removed by rodents is very similar to that of lean fruiting years in lowland Neotropical forest and extensive expanses of montane forest in Rwanda.

Such results do not bode well for secondary dispersal at Ngel Nyaki, because seedling survival is higher following predator satiation (Li & Zhang 2007; Vander Wall 2010), and if rodents at Ngel Nyaki are never satiated, they are less likely to act as dispersers. However seed removal alone is not necessarily a good predictor of seed fate (Xiao *et*

al. 2013), and it is thus important to consider what specifically happens to each seed. Averaged over the entire fruiting season, the proportion of removed seed predated in the COR (32%), was high compared with predation of *C. procera* in rich fruiting years (14%) and even lean years (23%) in French Guiana (Jansen *et al.* 2004). Such high immediate predation rates of *C. oreophila* in Ngel Nyaki, relative to the lowland Neotropics, again suggest seed limitation could constrain *C. oreophila* recruitment within this forest.

Taken together, the seed fate census in Ngel Nyaki's COR suggests a low probability of effective seed dispersal; even in rich fruiting years a high proportion of seed is rapidly removed from the plot and predated. Under these conditions it is highly likely that cached seeds will be removed and also ultimately predated (Jansen *et al.* 2004). By mid-August to October when this study was carried out, *C. oreophila* was one of the few large-seeded species fruiting in Ngel Nyaki. *Cricetomys* rats have shown to be strong seed predators of Ngel Nyaki's large-seeded and small-seeded trees: e.g. *P. altissima*, *Syzygium guineense*, *Trilepesium madagascariense* (Dutton *et al.*, 2014), and *A. noldeae* (pers. obsv.). Despite high numbers of *C. oreophila* individuals in the COR, it seems that they are not producing sufficient seeds to satiate the rodents at this time of year. Despite 2022 being a prolific year for *C. oreophila*, not all trees fruited and fruiting was asynchronous.

Predator satiation promotes seed survival (Vander Wall 2010) and may even be essential for effective dispersal by scatterhoarding rodents. For example, in a rich fruiting year, Jansen *et al.* (2004) found that the probability of *C. procera* seedlings establishing from caches was only 0.7% and this was 13 times the seedling establishment of cached seeds during lean years. While further research is required with greater emphasis on rodent density and total available resources, it appears that the fruiting phenology may be a disadvantage for *C. oreophila* in terms of secondary seed dispersal by rodents.

Fragmentation impacted seed fate in two major ways

Firstly, by creating a more rapid removal rate of seed, and secondly, lowering the probability of seeds being hoarded versus predated, relative to the forest habitats. The proportion of removed seed predated was markedly higher in the FRG. However, it is likely that most 'missing' seed in the FRG was taken down burrows and eaten, based on the observation of string trailing from burrow entrances which was record as predated seed (see Nyiramana *et al.* 2011). Fragments are also very small, such that strings would have been easier to detect than in the forest had they been hoarded. It was therefore assumed that missing seeds in the FRG were eaten is justified; whereas in core forest where seeds were abundant missing seeds were assumed to be cached farther than 10 m. Markedly higher predation in the FRG versus the forest is in agreement with findings of several other studies (Cordeiro *et al.* 2009; Jorge & Howe 2009) and is most likely to be a consequence of limited resources. As a consequence, we surmise that *C. oreophila* should be highly seed limited in the FRG and this is partially supported by the low density of juveniles observed in the fragment forest and that under these degraded habitat conditions, *Cricetomys* rats are even less likely to fulfil the role of mutualists and instead act as antagonists. Such behaviour may cause "local extinction" of seed populations in fragments (Hulme & Hunt 1999).

Conclusions

This study has produced valuable insights into the vulnerability of species that, until recently, may have been entirely dependent on mega-fauna such as elephants for primary dispersal. While in the Neotropics (and elsewhere where there has been a long history of mutualism between rodents and tree species). And rodents have selected for mast seeding (which leads to some seed dispersal), it may be that in the Afrotropics, where elephants (mega-fauna) are exhibiting major local extirpation, there is an ecological gap forming. Scatterhoarding rodents may thus represent a means of compensating for the loss of large-bodied frugivores in the Afrotropics as demonstrated in this study. However, trees species with large, nutritious seeds like *C. oreophila* may exhibit variable benefits from rodent secondary dispersal depending on the ecological context in

which the interaction between plant and animal occurs.

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