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Forest disturbance and seasonal food availability influence a conditional seed dispersal mutualism

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ABSTRACT

The interaction between granivorous scatter-hoarding mammals and plants is a conditional mutualism: scatter-hoarders consume seeds (acting as predators), but the movement of seed by scatter-hoarders may contribute to dispersal (acting as mutualists). Understanding the ecological factors that shape this relationship is highly relevant in anthropogenically disturbed tropical forests where large-bodied frugivores are extirpated. In such forests, large-seeded trees that once depended on these frugivores for dispersal may now only have scatter-hoarders as prospective dispersers. We studied *Carapa oreophila* (Meliaceae) in an Afromontane forest, to test the hypotheses that the proportion of seeds immediately consumed or hoarded (dispersed) would vary over a disturbance gradient. Temporal replication also afforded exploration of how habitat effects might vary with food availability. Using a Bayesian framework, we demonstrate that seeds were more likely to be hoarded in less disturbed forest, irrespective of temporal variation in food abundance. In contrast, forest disturbance only appeared to increase seed predation in temporal replicates that coincided with sustained food availability. These results highlight the potential variability in the dynamics between plants and scatter-hoarders over fine temporal scales, elucidating possible ecological scenarios where scatter-hoarders might act as mutualists (contributing positively to plant recruitment). Our study also fills important knowledge gaps about the importance of scatter-hoarders as dispersers in tropical forests depleted of large-bodied frugivores, particularly in Africa where scatter-hoarding mutualisms have not been extensively studied.

Key words: Afrotropics; *Carapa oreophila*; granivorous scatter-hoarding mammals; large-seeded trees; Nigeria; plant-animal interactions; seed dispersal; tropical montane forests.

SCATTER-HOARDING, WHEREBY SEEDS ARE COLLECTED FROM THE FOREST FLOOR AND DEPOSITED IN SHALLOW CACHES, is a common behavior among rodents as a means of exploiting seasonal food abundance (Vander Wall *et al.* 2005, Forget *et al.* 2002). While the purpose of scatter-hoarding to the mammal is for consumption of seeds at a later date (when resources are scarce), seeds in forgotten caches may escape being eaten and establish as seedlings (Jansen *et al.* 2012). Such seeds potentially receive two major benefits over seeds deposited directly onto the forest floor. Firstly, cached seeds may be in a more suitable germination environment, which will increase the probability of seedling establishment (Vander Wall 2010, Hirsch *et al.* 2012). Secondly, scatter-hoarders may act as secondary dispersers of seeds, moving them beyond the destinations achieved by primary modes of dispersal, for example, gravity or frugivorous animals (Forget *et al.* 1998, Brewer 2001).

On discovery of seeds, the decision made by scatter-hoarding rodents to either immediately consume them, remove them to another site and immediately consume them, or remove them to another site and store them for later consumption, is ecologically contingent (Augaasen *et al.* 2010, Vander Wall & Beck 2012, Wang *et al.* 2013). Seed characteristics and abundance influence behavior. Highly nutritious and palatable seeds are more likely to be targets of immediate consumption than seeds that provide low nutrient value, are unpalatable, or difficult to handle (Wang & Chen 2009, Aliyu *et al.* 2014, Vander Wall 2010). Moreover, if seed availability is high, a greater proportion of seeds discovered by scatter-hoarders are likely to be hoarded because more seeds are available than are required to satiate the scatter-hoarding community (Vander Wall & Beck 2012, Augaasen *et al.* 2010, Jansen *et al.* 2004). Consequently, the fate of seeds discovered by scatter-hoarding mammals may vary with season (Augaasen *et al.* 2010). This interaction is mutualistic when the benefit of seed dispersal is outweighed by the cost of seed predation (Theimer 2005), and hence, the ecological contingency of this interaction deems it a conditional mutualism (Theimer 2005, Jorge & Howe 2009).

Habitat effects may also be important in modulating the conditionality of secondary dispersal mutualisms. In several studies, forest disturbance and degradation have been shown as key drivers in shifting the balance from mutualistic to predatory roles by scatter-hoarding mammals. Jorge and Howe (2009) demonstrated that increasing fragmentation of forests increases seed predation by Neotropical scatter-hoarding mammals because smaller forests have reduced food availability. Forest edges, which are more disturbed than forest interiors, and have different plant composition, may also experience higher ratios of consumption to hoarding and declines in the distance seeds are moved by mammals (Chauvet & Forget 2005, Forget & Cuijpers 2008, Aliyu *et al.* 2014, Forget *et al.* 1999). However, the impact of disturbance on rodent behavior in regard to the between seed dispersal and consumption varies across plant species (Holl & Lulow 1997, Aliyu *et al.* 2014), thus requiring species-specific assessment of how habitat effects modulate conditional scatter-hoarding mutualisms with plants.

The potential benefits of secondary dispersal by scatter-hoarding mammals may be greatest in locales where frugivorous animal dispersal agents have become scarce or locally extirpated (Jansen *et al.* 2012, Cramer *et al.* 2007, Babweteera 2009, Babweteera *et al.* 2007, Babweteera & Brown 2010, Thia *et al.* 2016). This is especially true in tropical and sub-tropical forests where large-bodied frugivores are often the target of the bush meat trade (Ripple *et al.* 2016) and are most susceptible to anthropogenically driven habitat disturbance and degradation (Babweteera & Brown 2010, Thornton *et al.* 2012). Concurrently, large-seeded trees are highly dependent on large frugivores for dispersal (Cramer *et al.* 2007, Babweteera 2009, Babweteera *et al.* 2007); hence, it is

vital to ascertain how much scatter-hoarders contribute to seed dispersal as this might strongly impact tree recruitment dynamics.

While scatter-hoarding by mammals has been studied extensively in the Neotropics (*e.g.*, Forget 1990, Forget *et al.* 1999, Jansen *et al.* 2004, 2012, Forget & Cuijpers 2008, Pinto *et al.* 2009, Haugaasen *et al.* 2010), relatively little is known about scatter-hoarding in Africa. While some recent studies have emerged from African forests (Nyiramana *et al.* 2011, Aliyu *et al.* 2014, Rosin & Poulsen 2017, Moupela *et al.* 2014), there remain critical gaps in our knowledge about the importance of scatter-hoarders to the recruitment dynamics of African forest trees, not to mention how these dynamics change under different ecological conditions. Addressing these gaps is particularly imperative where anthropogenic disturbance is rapidly changing ecosystems.

To this end, we use *Carapa oreophila* Kenfack sp. nov. (Meliaceae) (Kenfack 2011) as a model to assess the role of granivorous mammals as dispersers of large-seeded Afrotropical trees and to investigate the conditionality of scatter-hoarding behavior in disturbed forests. The big, heavy fruit and seeds of *C. oreophila* suggests that it is adapted to dispersal by very large frugivores (Guimaraes Jr. *et al.* 2008), possibly elephants (Debroux 1998). However, at our study site, Ngel Nyaki Forest Reserve (Nigeria), elephants have been locally extinct since at least the 1940s (Thia 2014), and we have never observed any primary frugivore dispersers for *C. oreophila*. We know from personal observations (camera traps) that two species of rodents, the African giant pouched rat (*Cricetomys sp.*) and the African brush-tailed porcupine (*Atherurus africanus*), are the major consumers of *C. oreophila* seeds in Ngel Nyaki forest. Both these rodents are known to scatter-hoard and previous studies at Ngel Nyaki (Dutton *et al.* 2014, Aliyu *et al.* 2014) and forests elsewhere in Africa (Nyiramana *et al.* 2011, Rosin & Poulsen 2017) indicate that they may contribute to dispersal of *Carapa* and other large-seeded species. All aforementioned ecological features of *C. oreophila*, and the ease of collecting substantial numbers of seeds during peak fruiting season, make it an ideal species to study secondary dispersal by scatter-hoarding rodents. We investigated how the immediate fates of the large nutrient rich *C. oreophila* seeds were influenced by forest disturbance (habitat: core, edge, or forest fragment) and different periods during the fruiting season (food abundance) at Ngel Nyaki. Our study therefore assesses how different ecological factors interact to influence a scatter-hoarder's initial decision to hoard or consume discovered seeds. At Ngel Nyaki, greater disturbance through anthropogenic effects causes ecological degradation, and the diversity and abundance of large-seeded trees is lower in disturbed forest. We therefore hypothesized that the proportion of seeds hoarded versus consumed would correlate with disturbance; we predicted that increased disturbance from core, to edge, to forest fragment, would show decreasing propensity for rodents to hoard, and an increase in immediate consumption, of *C. oreophila* seeds. Additionally, we considered how habitat effects

might change with temporal variation in food availability in the forest using phenological records. Our results provide evidence that decisions by rodents to immediately hoard or consume seed might have complex interactions with forest disturbance and temporal patterns of seed abundance.

METHODS

STUDY SITE.—The study was conducted within Ngel Nyaki Forest Reserve (<http://www.canterbury.ac.nz/afromontane/>) on the Mambilla Plateau, Taraba State, Nigeria (7°5'N, 11°3'E). The reserve covers a total area of 4600 ha and includes 750 ha of almost continuous mid-altitude sub-montane forest at 1400–1600 m elevation (Chapman & Chapman 2001). This forest is embedded within a grassland landscape of *Sporobolus* grasses, which have been introduced via cattle and form a largely monoculture matrix (Beck & Chapman 2008, Adanu *et al.* 2010). The mean annual rainfall is 1800 mm (Nigerian Montane Forest Project 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).

Three main habitat types are described in this study, *sensu* Aliyu *et al.* (2014): interior core forest (COR), edge forest (EDG; 100m into the main forest from the surrounding grassland), and small forest fragments (FRG) that are embedded in the grassland. Forest fragments are riparian, tightly hugging the borders of streams, and range from a few meters to tens-of-meters across. These habitats exist along a disturbance gradient: core forest is the least disturbed, edge forest is somewhat disturbed, and forest fragments are highly disturbed and degraded. The main causes of degradation to edge and forest fragments are burning of the grassland by local pastoralists and damage caused by cattle. Additionally, the abundance and diversity of large-seeded trees also decreases from core, to edge, to forest fragments (Aliyu 2014), suggesting that forest fragments are poor quality foraging habitats for scatter-hoarding rodents.

STUDY SPECIES.—*Carapa oreophila* is an endemic tree to Cameroon and the eastern Nigerian highlands (Kenfack 2011). It is distributed in montane regions at elevations ranging from 1100–2500 m above sea level. *Carapa oreophila* is common within the main Ngel Nyaki Forest but is less common in the forest fragments. Its fruit are large woody pods (approx. 130 × 100 mm), each containing up to four or five valves that hold about four shiny, smooth, large seeds: 41.38 ± 4.45 mm × 29.70 ± 3.34 mm × 34.33 ± 3.67 mm (mean ± standard deviation for length, width and height, respectively; *N* = 20 seeds). These seeds are without pulp and possess a hard seed coat. Such fruit and seed characteristics are adapted for consumption and dispersal by elephants, as evidenced by *Carapa* species seeds being recovered in elephant dung in Camerounese Dja Reserve, for instance (Debroux 1998: Table 3.3, pg. 84). Elephants, however, are locally extinct at our study site.

Fruiting of *C. oreophila* is mostly synchronous, with the peak of the fruiting season being towards the end of the rainy season in August, although individual trees can be found fruiting any time of the year (Nigerian Montane Forest Project phenology data, 2006–present). Based on known adult trees (>10 cm in diameter at breast height of 1.4 m) in our study area that occur along extensive, monthly-monitored phenology transects, it was estimated that the peak fruiting of *C. oreophila* in 2011 was from August–October (Fig. 1).

EXPERIMENTAL DESIGN.—Our study is concerned with the immediate seed fates of *C. oreophila* across a forest disturbance gradient (core < edge < fragment) and at different points during the peak fruiting season. Specifically, we recorded if seeds were either: (1) consumed, (2) hoarded (dispersed), or (3) missing.

To test for the effect of forest disturbance (habitat effects), we followed the experimental procedure *sensu* Aliyu *et al.* (2014). Two 100 m long transects (at least 100 m apart) were placed in each habitat type. A $1 \times 1 \text{ m}^2$ quadrat was placed every 25 m, so five quadrats per transect. Each quadrat was divided into four 0.25 m^2 plots, where five fresh *C. oreophila* seeds were placed; one in the plot centre and one in each corner. Seeds were tagged with a 1 m long white nylon thread following the method of Forget (1990). The experiment was replicated in four periods during the fruiting season: August 18–28 (Period 1), September 5–15 (Period 2), 18–28 (Period 3), and October 2–12 (Period 4). Each period lasted 10 days and fresh seeds were used at the start of each new replicate. Based on our fruiting phenology data (Fig. 1), the abundance of *C. oreophila* producing mature fruit was highest in Period 1 (August), slightly lower in Period 2 and 3 (September), and lowest in Period 4 (October).

In total, we deployed 2400 seeds ($4 \text{ periods} \times 3 \text{ habitats} \times 2 \text{ transects} \times 5 \text{ quadrats} \times 4 \text{ plots} \times 5 \text{ seeds}$). At 10 days, the end of each experiment, the fates of each seed were determined by searching a 10 m radius around each quadrat. Consumed seeds were identified by having been partially consumed or by the presence of a loose thread with no seed attached. Hoarded seeds were classed as those that had either been buried under the soil or cached under leaf litter. Missing seeds were those that could not be accounted for in our searches and may have been consumed, hoarded or simply not detected.

STATISTICAL ANALYSES.—We examined the influence of food abundance (temporal replicates: Period 1, 2, 3, and 4) and forest disturbance (habitat effects: COR, EDG and FRG) on the immediate decisions made by scatter-hoarders when encountering seeds. We specifically wanted to understand how a forest degradation gradient affected the proportion of seeds that succumbed to

different fates. To this end, we tested whether seed consumption was greatest in forest fragments and lowest in core forest, and whether hoarding was greatest in core forest and lowest in fragments. We analyzed our data in a Bayesian framework using a mixed effects multinomial logistic regression model, appropriate for modelling categorical responses (consumed or hoarded) within a hierarchical repeated measures design (Agresti 1986). The seeds within each plot were assumed to have a multinomial distribution with the category-specific probabilities dependent on period (temporal replicate), habitat, transect, quadrat, and plot; for more details refer to Aliyu *et al.* (2014) where a similar approach was implemented. The results of Bayesian analyses are presented in terms of P , posterior probabilities, the probability that a statement is true given the observed data. As P approaches a value of 1.00 there is increasing support for the hypothesis given the data. Rather than being limited to simple pairwise comparisons, a Bayesian approach allows the assignation of a posterior probability to a compound hypothesis, such as $\theta_1 < \theta_2 < \theta_3$. For example, we use the notation $P(\text{COR} < \text{EDG} < \text{FRG})$ to denote the posterior probability of the hypothesis that seed consumption is lowest in core, intermediate in edge, and greatest in forest fragments. We also tested the hypothesis that hoarding would be greatest in the core, intermediate in edge, and lowest in forest fragments, that is: $P(\text{COR} > \text{EDG} > \text{FRG})$.

All the regression model parameters were given non-informative Gaussian priors. The first 5000 iterations were discarded as a burn-in, and the posterior sample statistics and 95% Bayesian credible intervals (CIs) were evaluated from the next 5000 iterations. Convergence and mixing were assessed visually. A Deviance Information Criterion (DIC) was employed for model comparison. The smaller values of DIC correspond to better model fit. We used the statistical software package *WinBUGS* (Spiegelhalter *et al.* 2002) for our analysis. The software *R*, including the *R2WinBUGS* package, was used for additional posterior inference and graphs (Sturtz, S., Ligges, U., Gelman 2005, R Core Team 2014).

RESULTS

Seeds were removed from all plots irrespective of habitat or fruiting period. For any given period in our experiment, by 10 days, most (if not all) seeds had been removed. Of the 2400 *C. oreophila* seeds deployed, 2384 (99.33%) were removed and 1566 (65.69%) were recovered. Of those seeds that were recovered, 890 (56.83%) were consumed, and 676 (43.17%) were hoarded.

When averaging across all temporal replicates, we found little evidence for habitat effects on seed fates (Fig. 2A). The hypothesis that seed consumption would be highest in forest fragments and lowest in the core forest was weakly supported by habitat averages: $P(\text{COR} < \text{EDG} < \text{FRG}) = 0.1983$. There was only slightly more support for our hypothesis that average hoarding was greatest in the core forest and lowest in forest fragments: $P(\text{COR} > \text{EDG} > \text{FRG}) = 0.2535$. We also present

the average across habitats in each temporal replicate (Fig. 2B). We did not however specifically test any hypotheses regarding differences among periods on habitat-averaged fates because of the interaction between habitats and period (Fig. 3; Table 1). Indeed, it was only when considering each temporal replicate separately that habitat effects became apparent. The hypothesis that seed consumption would increase with forest disturbance ($COR < EDG < FRG$) was very poorly supported at the start of the fruiting season (Period 1, $P = 0.0326$), and strongly supported in the middle of fruiting season (Period 2 and Period 3, $P > 0.9966$ and 0.9089 , respectively). By the end of our experiment, consumption rates among habitats was equivalent (Period 4, $P = 0.1066$). In contrast, support for the hypothesis that the proportion of hoarded seeds was greater in less disturbed forest ($COR > EDG > FRG$) was very well supported in all periods, though there was less support for this at the end of the fruiting season (Period 1, 2, and 3, $P \geq 0.9886$, 0.9840 , and 0.9800 , respectively; Period 4, $P = 0.7034$).

DISCUSSION

The ability for scatter-hoarding mammals to move large seeds and provide seed dispersal for large-seeded tree species may be increasingly necessary due to the decline of many historical primary dispersers (Jansen *et al.* 2012, Babweteera *et al.* 2007, Ripple *et al.* 2016). However, the role scatter-hoarders play—as antagonistic predators or mutualistic dispersers—is contingent on ecological context. We provide evidence that forest disturbance influences a conditional seed dispersal mutualism between scatter-hoarding mammals and *Carapa oreophila* in an Afromontane forest system. By comparing the proportion of different seed fates across temporal replicates, our data also suggests that these habitat effects might themselves be reliant on the amount of food available to scatter-hoarding rodents. Together, habitat and fruiting phenology might drive recruitment dynamics of *C. oreophila* at our study site, Ngel Nyaki Forest Reserve (Nigeria).

The proportion of removed *C. oreophila* seed in our study was large, 84.5–100% across all seasons and plots. Direct comparisons of seed removal rates among secondary seed dispersal studies can be difficult due to differences in length of experimental duration. With respect to removal rates and number of exposure days for seeds, some examples from large-seeded Neotropical trees are: 65% in *Astrocaryum aculeatum*, 30 days (Jorge & Howe 2009); 83% in *Astrocaryum standleyanum*, 8 days (Jansen *et al.* 2012); 80% on average in *Oenocarpus mapora*, 6 days (Beckman & Muller-Landau 2007); and 100% in *Bertholletia excelsa*, 2 days (Augaasen *et al.* 2010). Our observed removal rates for the Afrotropical *C. oreophila* is certainly comparable to these; however, our study sits at the higher-end removal rates, with some experimental plots experiencing complete seed depletion, at the end of—or even before—our 10 day trials. High removal rates by scatter-hoarders are important if they are to contribute appreciably to seed dispersal (Theimer 2005, Schupp 1993),

but the nutrient rich seeds of *C. oreophila* also make it an attractive food source. Given our observed removal rates were more-or-less similar across habitats (core, edge, and forest fragments), habitat-specific differences in scatter-hoarder behavior will determine whether these mammals act as dispersers or predators.

Forest fragmentation and disturbance are often associated with higher rates of seed predation (Jorge & Howe 2009, Forget *et al.* 1999, Aliyu *et al.* 2014). Indeed, the likelihood that scatter-hoarders choose to immediately consume a seed (versus hoard and disperse it) is expected to be greater when food is scarce (Vander Wall & Beck 2012, Augaasen *et al.* 2010, Jansen *et al.* 2004). Phenology records at Ngel Nyaki indicate very few moderate- and large-seeded species other than *C. oreophila* were fruiting during our study and that the onset of *C. oreophila* fruiting began after a period of potentially low food abundance (Fig. 1). The posterior probability means for hoarded seed proportions showed a negative trend from core, to edge, to forest fragments, across all four temporal replicates (Fig 3). It therefore appears that the decision of scatter-hoarding rodents to hoard seed might be more likely in less disturbed forest, regardless of the amount of food available.

While we predicted that the proportion of consumed seeds would increase from core, to edge, to forest fragments, this was strongly supported during Periods 2 and 3 only (Table 1). Such temporal shifts in the influence of habitat on rodents' decisions to immediately consume seeds appear to covary with shifts in seed availability. Habitat disturbance did not affect consumption rates immediately after an apparent seed shortage (Period 1) or when *C. oreophila* seeds were becoming scarce (Period 4), but did when *C. oreophila* seeds were relatively abundant over several weeks (Periods 2 and 3). This implies that seeds produced in the middle of high fruiting periods, and in less disturbed forest, are less prone to immediate consumption and might have a greater chance of being hoarded. We know from over 10 years of field observations at Ngel Nyaki that accumulation of *C. oreophila* seeds under parental trees has never been observed (H. Chapman, pers. comm.). This corroborates with the high removal rates measured in this study, further highlighting *C. oreophila* seed as an especially attractive food source that is unlikely to saturate granivores to a level where seeds go largely undetected. Consequently, in *C. oreophila*, all seeds are expected to encounter scatter-hoarding rodents, so ecological context will thus be exceedingly important in determining the overall benefit these mammals provide.

Our results are particularly relevant in understanding the importance and effectiveness of scatter-hoarding mammals as dispersal agents for large-seeded trees in anthropogenically disturbed landscapes. Most of our understanding about secondary dispersal in tropical forests comes from Neotropical studies, where evidence suggests scatter-hoarders may currently be the only dispersal agents for trees that have lost their primary dispersers (Forget 1996, Jansen *et al.* 2004, 2012). In the Afrotropics, it is apparent that defaunation of large-bodied frugivores correlates with stunted

recruitment in dependent trees (Babweteera 2009, Babweteera *et al.* 2007, Babweteera & Brown 2010, Thia *et al.* 2016). However, few empirical studies have investigated the role of scatter-hoarders as dispersers of large-seeded trees, yet alone explicitly tested the conditionality of this mutualism (Aliyu *et al.* 2014, Nyiramana *et al.* 2011, Moupela *et al.* 2014, Rosin & Poulsen 2017). Previous work we conducted at Ngel Nyaki illustrated how species-specific seed traits can be important in modulating habitat effects on seed fate (Aliyu *et al.* 2014). Rosin and Poulsen (2016) have also shown that seed size can be a strong predictor of which members of the granivore community will interact with particular tree taxa in a lowland Gabon forest. Certainly, while growing empirical works in the Afrotropics indicate that scatter-hoarders contribute highly to the secondary movement of seeds, long-term studies are required to determine the ultimate fates of these seeds (with respect to their dispersal distance, survival, and establishment into seedlings).

A caveat of this study is that despite recovering ~66% of all seeds there were still a sizeable number of seeds whose fates remain unknown. We did not directly test hypotheses on the missing data, but our results evidenced that differences among habitats in missing data varied across temporal replicates (Fig. 3). Additionally, the actual amount of missing data also varied across temporal replicates (Fig. 2B). These habitat differences and temporal effects imply the ecological processes contributing to missing data might not be consistent across our study—though experimental error in recovering seed within the bounds of the study is also a contributing factor. Consequently, while we can provide assessment of how habitat effects (testing whether seed fates differ along a forest disturbance gradient) change across the fruiting season, we cannot assess the overall proportions of each seed fate. Indeed, missing data is a general problem in seed fate studies that requires the use of tracking technologies to truly remove all ambiguity in inferences (Hirsch *et al.* 2012).

One additional caveat is that we counted recovered loose threads as consumed instead of missing, which has the potential to inflate consumption rates. While it is possible that rodents may have bitten through the string and taken the seed elsewhere, or that the thread may have broken off the seed, neither scenario seems likely because: (1) preliminary data and prior work at Ngel Nyaki (Aliyu *et al.* 2014) suggests that scatter-hoarders are unfazed by threaded seeds; and (2) the thread was highly durable and pierced through the seed, so unless scatter-hoarders had selectively removed it, the seed would have to be gnawed through in order for the thread to become detached.

Rosin and Poulsen (2016) have made headway in the Afrotropics by combining telemetric tagging and camera traps to determine the dispersal distance, initial fates, and disperser species of *Gambeya lacourtiana* and *Chrysophyllum lacourtiannum* in a lowland Gabon forest. While it has been previously speculated that rats of the genus *Cricetomys* are likely one of the most important secondary dispersers of many large-seeded Afrotropical trees (Aliyu *et al.* 2014, Nyiramana *et al.*

2011, Dutton *et al.* 2014, Moupela *et al.* 2014), Rosin and Poulsen infer the contrary. Their work suggests a greater predatory role of *Cricetomys* rats, while the African brush-tailed porcupine, *Atherurus africanus*, might be responsible for longer dispersal distances. Both these mammal species occur at our study site and camera traps have demonstrated their utilization of *C. oreophila* seed as food. Certainly, if Rosin and Poulsen's observations are translatable across African forests, some of our missing data may be attributed to larder-hoarded seed by *Cricetomys* rats and a small proportion to seed moved by *A. africanus* to distances beyond our searching limit. Future work at Ngel Nyaki is underway to understand the relative roles and dispersal services provided by these different rodent taxa.

In summary, this study indicates that scatter-hoarders may hoard more seeds in less disturbed forest, but difference among habitats might only be marginal if food availability alters the immediate decision of scatter-hoarders to consume (instead of hoard) seeds. Anthropogenic disturbance disrupts tropical forests in a multitude of ways through the manipulation of the physical environment, which ultimately has consequences for the abundance, diversity, and behavior of resident plants and animals. The declines in recruitment of large-seeded tree populations may lag behind the loss of their frugivore mutualists due to their long generation times. In developing models to predict tree species recruitment in the face of change, seed traits and food abundance are two key factors likely to influence a scatter-hoarder's strategy with regards to immediate consumption of seeds versus storing them for later consumption. Understanding the most likely scenarios that shift the relationship of scatter-hoarders from mutualists to predators will be necessary in predicting and managing recruitment of large-seeded trees in degraded landscapes.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c377tq8> (Aliyu *et al.* 2018).

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FIGURES AND TABLES

FIGURE 1. Fruiting phenology of 15 moderate- and large-seeded tree species expected to be potential food sources of large granivorous rodents at Ngel Nyaki Forest Reserve. Trees occur along monthly-monitored transects and the number of trees with mature fruits are illustrated for each month. Fruiting of *Carapa oreophila* is represented by the thick black line and black dots. The occurrence of temporal replicate periods used in this study are indicated: Period 1 = 18–28 August (P1); Period 2 = 5–15 September (P2); Period 3 = 18–28 September (P3); Period 4 = 2–12 October (P4).

FIGURE 2. Posterior mean probabilities (P) of a *Carapa oreophila* seed being consumed, hoarded, or missing, with corresponding 95% Bayesian credible intervals (CIs): (a) averages for habitats across temporal replicates (COR = core forest; EDG = edge forest; FRG = forest fragments); and (b) averages for temporal replicates across habitats (Period 1 = 18–28 August; Period 2 = 5–15 September; Period 3 = 18–28 September; Period 4 = 2–12 October).

FIGURE 3. Posterior mean probabilities (P) and 95% Bayesian credible intervals (CIs) for each *Carapa oreophila* seed fate (consumed = top panel; hoarded = middle panel; missing = bottom panel) by temporally replicated periods (Period 1 = 18–28 August; Period 2 = 5–15 September; Period 3 = 18–28 September; Period 4 = 2–12 October).

Period 3 = 18–28 September; Period 4 = 2–12 October) and habitat (COR = core forest; EDG = edge forest; FRG = fragment forest).

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TABLE 1. Posterior probability support for hypotheses regarding the seed fates (consumed or hoarded) of *Carapa oreophila* in different forest habitats (COR = core forest; EDG = edge forest; FRG = fragment forest). Inequality statements describe the direction of our hypotheses, which were tested in four temporal replicates (Periods 1–4) during the peak fruiting season to determine temporal variability in habitat effects.

Temporal replicate	Consumed	Hoarded
	COR < EDG < FRG	COR > EDG > FRG
Period 1: 18–28 Aug	0.0326	0.9886
Period 2: 5–15 Sep	0.9966	0.9840
Period 3: 18–28 Sep	0.9098	0.9800
Period 4: 2–12 Oct	0.1066	0.7034

- Anthocleista vogelii*
- Anthonotha noldeae*
- Beilschmiedia mannii*
- Carapa oreophylla*
- Chionanthus africanus*
- Entandrophragma angolense*
- Garcinia smeathmannii*
- Isolona deightonii*
- Khaya grandifoliola*
- Millettia barteri*
- Parkia filicoidea*
- Pouteria altissima*
- Santiria trimera*
- Symphonia globulifera*
- Syzygium guineense*

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