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## Seed harvesting of a threatened African tree dispersed by rodents: Is enrichment planting a solution?

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## ABSTRACT

Non-timber forest products (NTFPs) provide income to local communities with less ecological harm than timber extraction. Yet overharvesting can still influence the regeneration and sustainability of these resources. Developing sustainable harvesting practices for emerging NTFPs depends on the biology of the NTFP species, the ecological context in which management occurs, and its cost in terms of effort and resources. *Allanblackia stuhlmannii* (Clusiaceae) is a canopy tree species whose seeds are a source of vegetable oil and an important food for rodents. In an experiment within the Amani Nature Reserve (Tanzania), we studied how enrichment planting of *A. stuhlmannii* seeds affected germination and establishment rates under varying local levels of seed abundance and rodent activity. Overall, germination and establishment rates were high (4.8% and 2.2%, respectively, after 11 months), while local ecological conditions had a short lived (1–2 weeks) and unexpectedly small influence on the persistence of planted seeds. Given these rates, we estimate a cost of approximately US\$0.14 per seedling. Enrichment planting of seeds, across a range of local ecological conditions, appears to be a viable and cost effective management strategy for increasing *A. stuhlmannii* recruitment in harvested areas.

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## 1. Introduction

Non-timber forest products (NTFPs) such as fruits, seeds, sap, or leaves offer income sources that can be obtained without deforesting parcels of forest. For example, Brazil nuts (*Bertholletia excelsa*), hearts of palm (*Euterpe edulis*), and açai berries (*Euterpe oleracea*) are commonly collected directly from forests. Although NTFP harvest is less damaging than timber extraction or clearing forests for agriculture or pasture, it is not free of environmental consequences (Peters, 1994; Ticktin, 2004; Ticktin and Shackleton, 2011). Harvesting affects regeneration and demography; for example, gathering frankincense resin can reduce seed production (Rijkers et al., 2006) and collection of whole plants can alter the size structure of herb

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populations (Law and Salick, 2005). Sustainable harvest levels vary and depend on species' life history traits (Zuidema et al., 2007). Some tree populations may be able to withstand harvests of up to 92%–93% of a seed crop (Zuidema and Boot, 2002; Emanuel et al., 2005), while such extreme harvest levels may seriously hinder the recruitment of other NTFP species.

Harvesting can also alter interactions between NTFP species and their consumers and mutualists, with unexpected and important consequences. For example, intensive açai berry harvest reduces the diversity of seed-dispersing, frugivorous birds (Moegenburg and Levey, 2002). Many desirable NTFP's are oil-rich seeds and the preferred food sources of scatterhoarding rodents. Well-documented examples include agoutis (*Dasyprocta leporina*) and acouchies (*Myoprocta acouchy*) in Central and South America consuming Brazil nuts (e.g. Jorge and Peres, 2005, Tuck Haugaasen et al., 2011) and *Carapa* spp. (e.g. Jansen et al., 2004). African giant pouched rats (*Cricetomys* spp.) act similarly to agoutis in seed predation and dispersal (Guedje et al., 2003; Nyiramana et al., 2011) but less is known about their effects on NTFP dispersal and regeneration. These conditional mutualists act as seed predators, but also disperse seeds (Theimer, 2004) and increase germination rates by scarifying seeds (Miller, 1995). Their net effect on NTFP demography depends on the abundance of food resources (which can be depleted by harvesting) and the intensity of competition for these resources.

Management strategies for NTFPs focus on maintaining natural recruitment by limiting harvests spatially and/or temporally, or augmenting recruitment by planting additional seeds or seedlings (enrichment planting) (Peters, 1994). Harvest restrictions promote natural dispersal and recruitment processes, but are difficult to enforce in remote or urgently threatened areas (Duchelle et al., 2012). Enrichment planting, the focus of this paper, can also boost recruitment (Makana and Thomas, 2004), but requires time and resources. To date, enrichment planting in tropical forests has primarily been studied in the context of reforestation, rather than sustainable NTFP harvest (Adjers et al., 1995; Schulze, 2008; d'Oliveira and Ribas, 2011; Cole et al., 2011). However, traditional strategies of enrichment planting are known from the Amazon estuary where residents have long planted and managed açai berries (*E. oleracea*) and other desirable NTFP species (Anderson et al., 1995). Experimentally, enrichment planting of Brazil nut (*B. excelsa*) seedlings has been successful, depending on light levels (Kainer et al., 1998; Peña-Claros et al., 2002). In practice, managers interested in enrichment planting must decide between using seeds and seedlings. Seedlings often have higher success, but require additional time, investment, infrastructure, and care. Seeds are more likely to suffer from predation or poor germination under natural conditions, but are easier to transport, store, and plant, and in some cases, may be less expensive (Schulze, 2008; Cole et al., 2011). Ecological context is also important in designing strategies. For example, the ability of scatterhoarding rodents to locate cached (or planted) seeds, and eat or re-cache them (Jansen et al., 2004), could negate the benefits of seed planting, depending on local resource levels. Ultimately, selecting appropriate management approaches requires understanding both the practical and biological factors influencing the survival, germination, and establishment of target species.

In the present study, we are interested in the management and sustainability of seed harvest of an endemic, threatened tree species in Africa. Nine species of trees from the genus *Allanblackia* (Clusiaceae) are found in moist forests across tropical Africa. They bear large fruits with lipid-rich seeds traditionally pressed for cooking oil. Recently, a coalition of organizations, called the Novella Africa Initiative, has begun working in Tanzania, Nigeria, and Ghana to develop a sustainable supply chain for three species, *A. stuhlmannii*, *A. floribunda*, and *A. parviflora*, as a component of mixed agroforestry (Jamnadass et al., 2010). *Allanblackia* cultivation and harvest, as well as commercial uses for its oil, are active research areas. However, several biological factors currently prevent farms from providing sufficient *Allanblackia* seeds, and wild populations cannot meet the expected demand (Pye-Smith, 2009). Much of the present supply comes from wild populations, including locally managed reserves that permit seed collection. Harvest is also occurring in protected areas where seed collection is prohibited, such as the Amani Nature Reserve in the East Usambara Mountains of Tanzania (NJC & HJN unpub. data).

Given the developing market for *Allanblackia* seeds, and the already extensive harvesting pressure in and outside of protected areas, evaluating strategies for ensuring sustainable *Allanblackia* seed harvests is important and timely. We conducted an 11-month study, tracking the fate of *A. stuhlmannii* seeds experimentally planted in environments spanning a range of seed density and predator activity. By assessing persistence, germination, and establishment rates through time and across environments, we determined the effectiveness and cost of enrichment planting as a management option, as well as the extent to which its success varies with ecological context. Finally, this study extends an NTFP management strategy to an emerging system in Africa, adding to the broader, growing literature on the conservation and management of NTFP species.

## 2. Methods

**Study system.** The Amani Nature Reserve (ANR) (S 5° 6', E 38° 38') protects 8380 ha of lowland and submontane rainforest in the East Usambara Mountains (EUM) in northeastern Tanzania (Tanga region), part of the Eastern Arc Mountains. About 75% of EUM forest has been cleared for tea plantations, non-native timber plantations, and small-scale multicrop farming (Burgess et al., 2007). The EUM receive 1700–2300 mm of rain throughout the year but the heaviest rains are in the short (October–November) and the long (late March–May) rainy seasons (Hamilton and Bensted-Smith, 1989).

*A. stuhlmannii* Engl. (Clusiaceae) is a rainforest canopy tree endemic to the Eastern Arc Mountains of Tanzania. *A. stuhlmannii* is dioecious, with approximately one-third of the mature trees in the forest being reproductive females (Mathew et al., 2009). It is one of the most common canopy tree species in ANR. Each female tree typically produces 3–160 fruits per year, varying considerably among years and individual trees (NJC & HJN unpub. data). Fruits mature over one year into large

(2–5 kg), brown, drupes that fall to the ground when ripe, containing a mean of 36 seeds with mean seed mass of 11.24 g (Mathew et al., 2009). Seeds are 62%–67% fat, and high in stearic and oleic oils, which have the commercially desirable quality of being solid at room temperature and melting at 40–46 °C (Eckey, 1954).

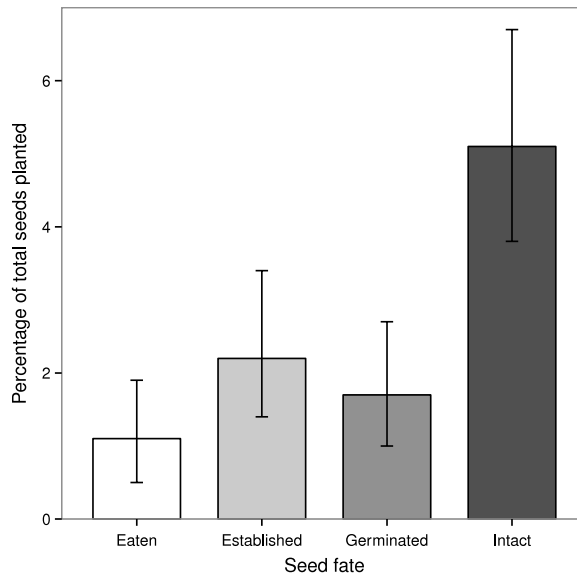
**Plot selection and experimental planting.** To capture natural variation in background fruit abundance in the forest, we established twelve separate 50 × 50 m plots in four different blocks (three plots per block) within the ANR. Each plot was at least 200 m from the forest edge. Plot locations were randomly discovered (Appendix S1) and each plot included canopies of at least four *A. stuhlmannii* trees with fruit. Plots within a block were separated by at least 150 m, and blocks were at least 1200 m apart (Appendix S1). We planted a total of 960 *A. stuhlmannii* seeds sourced from four farmland sites. For all plots in each of two plantings, ten seeds were randomly selected from each seed source and the planting sequence was randomized. Seeds were washed and dried, then weighed immediately before sowing. Within each plot, forty seeds were planted at 2 m spacings in U-shaped transects (to stay within the boundary of the plot); the total number of seeds planted per plot is equivalent to about 2 fruits, plus about 2 fruits worth of tagged seeds in a parallel experiment. Each seed was partially buried 75%–90% under soil or humus and then covered with surrounding leaf litter. The depth was chosen to facilitate censusing the seeds and approximates typical caching behavior of large rodents (CES pers. obs.).

**Censusing plots.** Seeds were experimentally planted twice in 2011, once in late February/early March (referred to as planting 1) and again in late March/early April (planting 2) to increase the sample size. Each block was censused 4, 8, 12, and 28 or 30 days after setup. Planting 1 seeds were also censused at 28, 32, 36, 40, and 58 days (corresponding with planting 2's setup and 4, 8, 12, and 30 day checks). After late April, each block was censused once per month until September 2011; subsequently, blocks were revisited in November 2011 and finally in January 2012 (327 days after beginning the experiment). During each census, the presence and condition of each planted seed was checked by briefly examining the buried seed while wearing a nitrile glove. Seeds were recorded as either present or missing. Present seeds were classified based on their condition as intact, eaten, germinated, established, or rotten (the latter based on visible signs of dessication, fungus, or insect infestation).

**Fruit abundance and rodent activity.** Plots were surveyed for freshly fallen fruits on each census until the end of the fruiting season in 2011. Newly fallen fruits were categorized as available to rodents (either intact or already opened by rodents) or harvested by humans. Fruits harvested by humans are easily distinguished from those attacked by rodents, as humans leave behind the heavy fruit pulp with conspicuous machete marks. To prevent re-counting, fruits were marked with a piece of biodegradable flagging tape (Appendix S1). The mean number of fruits accumulated in a plot between censuses during the fruiting season varied from 0 to 5.25 (mean = 0.76, median = 0.50). The cumulative total number of fruits available to rodents in plots over the course of the experiment ranged from 22 to 175 (mean = 64.75, median = 46.5). Plots varied considerably in proportion of fruit harvested by humans, from 0% to 43%; the proportion across all plots combined was 17%.

Measures of rodent activity were obtained based on images from camera traps, deployed to monitor tagged seeds for a parallel experiment (established and visited on the same schedule, in prep.). One randomly selected station of tagged seeds in each plot had a camera approximately 1.5 m away. Ten Bushnell Trophy Cameras (Bushnell Corporation, Overland, Kansas, USA) recorded animal motion in front of each camera (two plots with extremely low numbers of photographs were excluded from the analyses; Appendix S1). All seed removal was attributed to rodents. Photos of large rodents (giant rats or squirrels) were tallied for each observation interval (the time between subsequent censuses, adjusted for instances when batteries died). Estimates of average daily rodent activity for each plot and census interval were then obtained by dividing the total number of rodent photos by the length of the observation interval. Of photographs with large rodents, giant pouched rats (*Cricetomys gambianus*) were in 80.4% and the remaining 19.6% were squirrels (*Paraxerus* spp.).

**Statistical analyses.** We were interested in understanding how environmental variables influenced the proportion of seeds transitioning between states or categories of seed fate and recruitment (present/intact, eaten, germinated, or established) over a fixed interval of time. This includes considering persistence rates (i.e. the proportion of seeds that remained where planted between successive observations) as well as germination or establishment rates. To address these questions, we used generalized linear mixed models (GLMMs). These allowed us to model proportional data according to a binomial distribution and include covariates using a logit link function, while controlling for experimental design by incorporating random effects. In particular, all GLMM results include random effects for distinct plots which were nested within blocks. We selected the GLMM approach as an alternative to another commonly used method, Cox proportional hazards models for survival analysis, to enable the inclusion of nested random effects. We adopted model comparison methods (based on Akaike information criteria, or AIC) to assess different models and their covariates based on likelihood and parsimony (Burnham and Anderson, 2002; Bolker, 2008). Additionally, we calculated a conditional (variance explained by fixed and random effects) and marginal (variance explained by fixed effects) coefficient of determination ( $R^2$ ) with the R package MuMIn in the best fitting model selected via model comparison (Bartoń, 2014). Where noted in specific analyses, some covariates were mean/variance standardized to facilitate effect size comparisons. Finally, we used a  $\chi^2$  test to compare the proportions of seeds germinating and persisting from different collection sources (confidence intervals were obtained from the exact method, R package binom Dorai-Raj, 2014). All analyses were performed in R 2.15.1 (R Core Team, 2013) using packages bbmle (Bolker and Team, 2014) and lme4 (Bates et al., submitted for publication).



**Fig. 1.** Fate of *Allanblackia stuhlmannii* seeds in January 2012 at the last census, 10–11 months after enrichment planting. Removed seeds account for the remaining 90% of all planted seeds (not shown). Bars indicate 95% confidence intervals calculated for binomial parameters (proportions) using the R package binom (Dorai-Raj, 2014).

### 3. Results

**Germination and establishment.** We observed germination in 4.8% of all seeds planted in the forest (46 out of 952, 3.6%–6.4% 95%CI) throughout the experiment. Of these, 0.9% (9 out of 952, 0.4%–1.8% 95%CI) were absent in the last census, meaning they were removed by rodents sometime after germinating. Seeds that germinated during the observation period (even if they later disappeared) were significantly heavier ( $t = 2.321$ ,  $df = 950$ ,  $p = 0.010$ ) than seeds that had not yet germinated or had disappeared (mean 13.00 g and 11.78 g, respectively). Germination occurred slowly, and was primarily observed 5–9 months after planting (Fig. 2(d)), varying from 30 to 327 days. The average time until observed germination differed between the two plantings ( $t = 4.1829$ ,  $df = 44$ ,  $p < 0.001$ ), with seeds in planting 1 germinating more slowly (mean = 247 days after planting, or ~8.2 months) than in planting 2 (mean = 176 days after planting, or ~5.8 months). About 50% more seeds germinated in planting 2 ( $n = 28$ ) as compared to planting 1 ( $n = 18$ ), although more seeds persisted to the final census from planting 1 ( $n = 47$ ) than planting 2 ( $n = 39$ ). Finally, seed source did not have a significant effect on either proportion of seeds persisting until the last observation ( $\chi^2 = 4.3256$ ,  $df = 3$ ,  $p = 0.2284$ ) or germinating ( $\chi^2 = 1.1304$ ,  $df = 3$ ,  $p = 0.7697$ ).

As of the last observation 10–11 months after initial planting, a total of 2.2% of planted seeds (21, 1.4%–3.4% 95%CI) had established, producing a shoot visible above ground (Fig. 1). However, establishment rates could reach as high as 9%, as in the last census 49 viable seeds remained (with no signs of rot or desiccation) and 16 still had only a radicle (germinated but not established). Germination and establishment occurred long after the *Allanblackia* fruiting season, and for sufficiently few seeds that these germination rates could not be related with any confidence to average rodent activity or cumulative fruit abundance, both measured during the fruiting season.

**Seed persistence.** For a seed to be observed to germinate and establish in this study, it had to remain where it was initially planted, so it must not have been consumed or removed and reached by rodents. Consequently, factors affecting the probability of seed persistence could have an indirect effect on germination and establishment rates (both observed and actual). As of the last census in January 2012, 10–11 months after planting and across all plots and both plantings, 9.0% of seeds had persisted where they were planted as either intact, germinated, or established (86 out of 952, 7.3%–11.0% 95%CI). Most removal occurred within the first 30 days (Fig. 2(b)), as rodents located newly planted seeds. We found that over the first 12 days post-planting, and across both experimental plantings, seed persistence decreased with increasing rodent activity and it was lower in plots with more fruits (Tables 1 and 2). Additionally, an important positive interaction moderated the negative effects of both high rodent activity and fruit abundance (Table 2). Seeds in the first planting were slightly less likely to persist for the first 12 days compared to the second planting. Overall, however, the marginal  $R^2$  for the best model was 0.07, meaning that only 7% of the variation was explained by fixed effects; including random effects increased conditional  $R^2$  to 0.35.

Over longer intervals, neither these biotic variables nor planting time explain variation in seed persistence between plots (GLMMs including average daily rodent activity over the first 40 days and cumulative fruit abundance failed to outperform null models, Table 3 and Table S2). Likewise, neither germination or establishment rates are predictable given these factors. Census data reveal that, unexpectedly, a second precipitous drop in the number of seeds persisting (Fig. 2(a)) occurred 5–6 months after planting (between days 148 and 183), after camera trapping had ceased and after the end of the *Allanblackia*

**Table 1**

GLMM<sup>a</sup> model comparison results for seed persistence of *Allanblackia stuhlmannii* from enrichment planting through the third census (day 12 of each planting).

Model covariates (fixed effects)	dAIC <sup>b</sup>	df
Planting + fruit.abund <sup>c</sup> * rodent.activity <sup>d</sup>	0	7
Planting + rodent.activity	2.7	5
Planting + fruit.abund + rodent.activity	3	6
Planting + rodent.activity + seed.mass <sup>e</sup>	3.7	6
Planting + seed.mass + fruit.abund + rodent.activity	4.2	7
Planting + rodent.activity * seed.mass	4.3	7
Null (intercept only)	6.9	3
Planting	8.3	4
Planting + seed.mass	8.9	5
Planting + fruit.abund	9.7	5
Planting + seed.mass + fruit.abund	10.4	6
Planting + seed.mass * fruit.abund	12.3	7

<sup>a</sup> All models included random effects of plot nested within block, controlling for experimental design, and used binomial distribution and logit link function.

<sup>b</sup> dAIC refers to the difference in Akaike Information Criteria (AIC) values between a given model and the model with the lowest AIC in the comparison set (Burnham and Anderson, 2002).

<sup>c</sup> fruit.abund is the average fruit abundance in a plot over the first 12 days of a planting (fruits/day).

<sup>d</sup> rodent.activity is the average large rodent activity in a plot over the first 12 days of a planting (photos/day).

<sup>e</sup> seed.mass is the mean-standardized mass of seeds (gm).

**Table 2**

Coefficient estimates for the best model of seed persistence of *Allanblackia stuhlmannii* over the first 12 days identified by model comparison (Table 1) along with marginal and conditional R<sup>2</sup>.

Best model (Planting + fruit.abund * rodent.activity)	
Fixed effects	Estimate (SE)
Intercept	2.18 (0.71)
Planting	−0.60 (0.21)
fruit.abund	−1.47 (0.58)
rodent.activity	−0.48 (0.14)
fruit.abund:rodent.activity	0.42 (0.18)
Random effects	Variance (SD)
Block	< 1 × 10 <sup>−11</sup> (< 1 × 10 <sup>−5</sup> )
Plot:Block	1.44 (1.20)
Model fit	
log Likelihood	−458.5
df	7
Marginal R <sup>2</sup>	0.07
Conditional R <sup>2</sup>	0.35

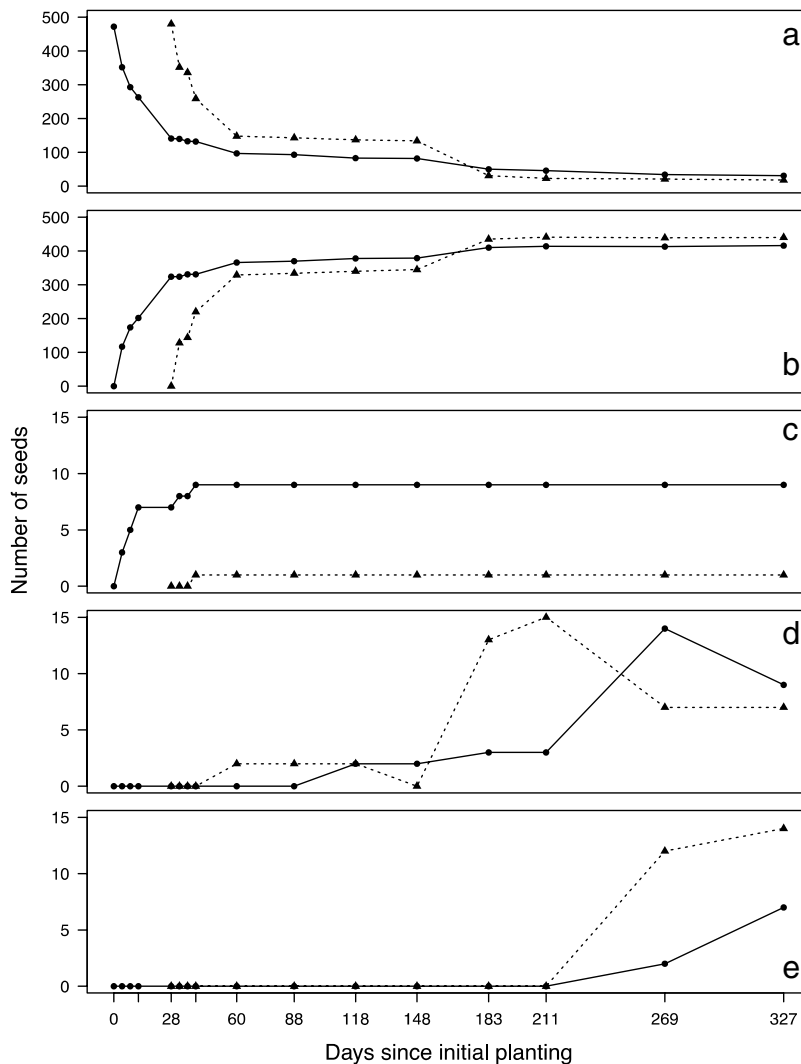
fruiting season. This major seed removal event greatly reduced both the mean number of seeds remaining in each plot and across plantings ( $t = 3.0041$ ,  $df = 46$ ,  $p = 0.0043$ ) as well as the variance in persistence rates ( $F = 2.5259$ ,  $df = 23$ ,  $p = 0.03071$ ). This suggests that a previously unknown aspect of the ecology of *Allanblackia* and its relationship with seed predators may be responsible for variation in germination and establishment rates between plots.

#### 4. Discussion

Enrichment planting can be an effective way to enhance seedling establishment of *Allanblackia*, an emerging NTFP resource. Our experiment shows that close to 1 in 10 planted seeds may escape detection by rodents over the course of nearly a year. We document establishment rates of 2.2% for planted seeds; in comparison, tagged seeds left on top of forest litter had only 0.3% establishment over the same time period (CES et al. in prep.). This estimate is conservative, because in this enrichment planting experiment we could not observe the fate of removed seeds. It is possible that the seeds were moved to areas of lower conspecific tree (and hence seed) density, as demonstrated by agoutis in Panama (Hirsch et al., 2012). In a parallel seed-tagging experiment, two-thirds of removed seeds were scatterhoarded rather than being immediately consumed (CES et al. in prep.). Rodents may have cached a similar proportion of planted seeds, some of which will germinate and establish unobserved. Finally, given that a related species, *A. parviflora*, can take up to three years to germinate (Ofori et al., 2011), a significant fraction of seeds that had yet to establish by the last observation, 11 months after planting, likely remained viable.

Variation in these germination and establishment rates was unrelated to measured biotic variables, including the activity of rodents (conditional mutualists) and local abundance of *Allanblackia* fruits, despite the potentially important role of rodents as seed predators. Limited evidence suggests these variables have a significant, but weak, effect on the persistence of planted seeds over the short term. Seeds were less likely to persist when rodent activity was high, consistent with heightened foraging activity leading to higher rates of predation and caching. Persistence probabilities also declined in plots with





**Fig. 2.** The number of *Allanblackia stuhlmannii* seeds in different fate categories changes through time, as rodents remove and consume seeds, and germination and establishment occur. Values for the first and second plantings are shown separately in solid and dashed lines, respectively. Categories consist of (a) intact where planted (undisturbed), (b) missing/removed, (c) eaten, (d) germinated, and (e) established seeds. Categories (b) and (c) are cumulative measures. Note different y-axis scales for (a)–(b) and (c)–(e).

increased fruit abundance. This relationship may be driven by an indirect effect of fruit abundance on the actual abundance of rodents, although activity and fruit abundance were not correlated. Another possible seed predator, the bushpig (*Potamochoerus larvatus*), was not captured in any camera-trap photographs. Smaller rodents, such as mice, were infrequently recorded interacting with seeds. In future studies, estimates of rodent abundance in addition to foraging activity could produce better estimates of seed predation and removal risk, clarifying these patterns. Additional work could also focus on the spatial scale at which these rodents perceive resource abundance and make foraging decisions, which would inform the area over which fruit abundance should be measured.

Ultimately, the factors affecting short term persistence patterns may have had little influence on long term germination and establishment rates due to the overwhelming effects of an unexpected, second major removal event which significantly reduced the number of seeds remaining and reduced variance among plots. This occurred 5–6 months after planting and it may correspond to a period of low food abundance for rodents in the forest. August is the middle of the cool dry season (Hamilton and Bensted-Smith, 1989). Giant rats are known to eat a wide variety of food items and are by no means *Allanblackia* specialists since they are found in many places in Africa where *Allanblackia* does not occur. However, *Allanblackia* seeds are highly palatable to rodents in Amani; rodent trapping censuses found it to be as preferable as coconut (Cordeiro et al., 2009). Perhaps after depleting their own stores during a lean time, rodents were more likely to go cache-thieving and discover planted seeds, which can dramatically increase dispersal distance upon re-caching (Jansen et al., 2012). Local studies of rodent food preferences and phenology could be used in combination to test this hypothesis, but presently the dietary details of rodents are poorly known in the Eastern Arc Forests. Disentangling the effects of biotic interactions and seasonal variation in resource abundance on the demography and management of *Allanblackia* remains a significant challenge.

**Table 3**GLMM<sup>a</sup> model comparison results for seed persistence from planting of *Allanblackia stuhlmannii* until the last observation period.

Model ID	Model covariates (fixed effects)	dAIC <sup>b</sup>	df
1 <sup>c</sup>	Planting + cml.fruit <sup>d</sup>	0	5
2 <sup>c</sup>	Null (intercept only)	0.9	3
3 <sup>c</sup>	Planting	1.3	4
4 <sup>c</sup>	Planting + cml.fruit + std.rod.act <sup>e</sup>	1.3	6
5 <sup>c</sup>	Planting + std.rod.act	1.5	5
6 <sup>c</sup>	Planting + seed.mass <sup>f</sup> + cml.fruit	1.9	6
7	Planting + seed.mass	3.1	5
8	Planting + seed.mass * cml.fruit	3.2	7
9	Planting + seed.mass + cml.fruit + std.rod.act	3.2	7
10	Planting + cml.fruit * std.rod.act	3.2	7
11	Planting + std.rod.act + seed.mass	3.3	6
12	Planting + std.rod.act * seed.mass	5.3	7

<sup>a</sup> All models included random effects of plot nested within block, controlling for experimental design, and used binomial distribution and logit link function.

<sup>b</sup> dAIC refers to the difference in Akaike Information Criteria (AIC) values between a given model and the model with the lowest AIC in the comparison set (Burnham and Anderson, 2002).

<sup>c</sup> The coefficients associated with the best models (dAIC ≤ 2) can be found in (Table S2).

<sup>d</sup> cml.fruit corresponds to the cumulative total number of ripe *Allanblackia* fruits available to rodents in a plot over the course of the 2011 fruiting season.

<sup>e</sup> std.rod.act is the standardized average large rodent activity (photos) per day in a plot over the first 40 days of the experiment.

<sup>f</sup> seed.mass is the mean-standardized mass of seeds (gm).

Phenology data collected in Amani over several years revealed that inter-annual fruit production is highly variable, as with many rodent-dispersed woody plants (Herrera et al., 1998). Most female trees have at least a few fruits every year, but some years most trees have an abundance of fruit, resulting in (NJC and HJN, unpub. data). We did not find a clear effect of background fruit abundance on long-term seed persistence. This suggests that, within the ranges we observed, it is equally worthwhile to plant seeds in low- and high-density areas. It is also worth noting that the year of the experiment (2011) was a relatively low year for *Allanblackia* fruit production in Amani (CES, pers. obs.). As a result, the levels of fruit abundance observed in plots were probably at the low end of the possible range. Repeating the same experiment in other years in the same plots is likely to encompass a much different distribution of fruit abundance. However, it is notable that even in a year with low seed availability, some planted seeds escaped detection by rodents, which is promising for the potential for successful enrichment planting.

On the practical side, there are two main ways to implement enrichment planting: (1) land managers (e.g. landholders or village leaders) could coordinate the active planting of seeds, perhaps targeting specific, overharvested locations; (2) seed collectors could informally be encouraged to follow guidelines such as planting one seed for each fruit harvested. The latter approach is consistent with recommendations for preventing the degradation of wild stocks through selective harvesting (Peters, 1994). Economic considerations are important to either method. *Allanblackia* seeds provide an important supplemental source of income to households, as local wages are typically only \$1.50/day (Bullock et al., 2011). It is crucial to consider the social and economic effects of an informal enrichment planting scheme, including the cost to collectors. Planting one seed per fruit collected (1 seed out of 36 on average) results in a missed opportunity cost of about 2.8% of their potential harvest, which is a loss of US\$1.15 per year for an average household. Although the price of *Allanblackia* seeds will change over time, the 2.8% reduction in harvest would remain roughly the same if harvesters planted one seed per fruit. Given the 2012 value of *Allanblackia* seeds and our estimates of establishment rates, the cost per seedling produced is approximately US\$0.145 (Appendix S1).

Improvements to enrichment planting methods are possible and merit further studies. For example, we planted seeds at depths achievable with just a stick for digging (such as a seed harvester instructed to plant seeds). Increasing planting depth reduces residual odors at the surface and it has been shown to decrease seed removal (Vander Wall, 1993). In Panama, experimentally cached palm seeds (*Astrocaryum standleyanum*) persisted in greater numbers if they were first de-fleshed (Jansen et al., 2010). This is consistent with research showing that more odoriferous seeds are easier for naïve rodents to find (Stapanian and Smith, 1984). Fresh *Allanblackia* seeds have a distinctive odor, suggesting that *C. gambianus*, with a keen sense of smell, may find planted (or cached) seeds by scent (Poling et al., 2011; Mgone et al., 2012). In our experiment, seeds were washed manually with water to remove all fruit pulp. As informal planting schemes may not allow for this level of processing, unwashed seeds should be tested. Finally, several studies suggest seed size can regulate detectability (Jansen et al., 2004; Wang and Chen, 2009), although in our experiment it had no detectable effect on removal, germination, or establishment.

## 5. Conclusion

We tested seed enrichment planting as a management strategy and calculated the approximate cost in terms of the value of weight in seeds needed to produce one seedling. While species interactions and ecological dynamics could alter the

contexts in which seed enrichment planting is effective, the variables we examined yielded no strong evidence of these effects over the long term. These variables did affect seed persistence over the short term; we suspect long-term effects are weakened or negated by unobserved and intriguing biotic interactions long after the initial planting. Improved measures of rodent abundance or activity, along with knowledge of the scale at which these under-studied rodents make foraging decisions, would be useful for future studies. Estimates of germination and establishment rates from this study, along with additional demographic data for later life stages, can and should be used to make demographic projections critical for understanding the sustainability of the NTFP harvest of *Allanblackia*. Enrichment planting using seeds may also be an affordable and viable option for other wild-harvested seed crops such as Brazil nuts and *Carapa* spp. It is important to implement an experimental approach before widespread adoption of enrichment planting since local conditions can affect predation, especially in more degraded forest fragments that may not have adult trees as a natural seed source. For example, Brazil nut seeds are more predated and dispersed shorter distances in fragments compared to continuous forest (Jorge and Howe, 2009). Furthermore, future investigations should examine the potential consequences of seed harvesting for shifting rodent diets to other non-target plant species. Even for NTFPs, it is important to understand the ways in which harvest can alter biotic interactions and use that information to inform management decisions.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2015.02.011>.

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