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Secondary seed removal in a degraded forest habitat in Madagascar

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Forest restoration is a prime goal within the 2021–2030 UN "Decade of Ecosystem Resoration". As part of these activities, natural regeneration has to be promoted for biological as well as for economic reasons. For this, the processes of seed dispersal, seed predation and germination have to be understood in the original as well as in degraded vegetation formations. We used seed removal experiments to assess post-dispersal processes that influence recruitment along a gradient of forest degradation in Madagascar analyzing seeds of three animal dispersed tree species. The percentage of seeds consumed or dispersed, declined from forest (28.6%) to degraded forest (17.2%) to savanna (10.8%). Only three out of 1080 seeds were cached and remained intact during the 14-day experiment. All three seeds were cached in the forest habitat and none in the degraded forest and savanna. The low percentage of seeds removed may be due to the lack of endemic rodents caching seeds, as only introduced rats were recorded in the area. The species-poor fauna of potential secondary seed dispersers of the region and especially in the degraded areas might represent an obstacle for diverse regeneration in degraded regions of Madagascar.

Restoration of degraded land is a prime goal of the United Nations' "Decade of Ecosystem Restoration" from 2021 to 2030[1]. Within this decade, planting trees is one of the main components of the African Forest Landscape Restoration Initiative (AFR100). Yet, planting trees is expensive and reforestation is all too often based on a few tree species of known properties that will result in species-poor forested landscapes. If areas to be reforested border remnants of natural forests, wind-dispersed seeds are more likely to arrive outside the forest than seeds dispersed by animals[2]. Yet, tree species with animal dispersed seeds dominate in natural tropical forests[3–5]. Thus, natural regeneration could be fostered by attracting seed dispersing animals into the areas to be restored. By depositing seeds of native plants in the reforestation area, animals help to diversify plant species in the regenerating cohort, thus facilitating regeneration towards systems with closer similarity to the original forest composition and reducing costs compared to planting forests of similar diversity[6–10].

Regeneration can be compromised by seed predation or be modified by secondary dispersal in complex interactions[11–14]. While these interactions have been studied intensively within ecosystems, few studies have addressed the question on how natural forest regeneration is affected by secondary seed dispersal or seed predation on fallow land or in degraded forests targeted for forest restoration[15–21].

A better understanding of the processes involved in forest restoration and regeneration and possible ways to achieve the restoration goals efficiently but at low costs is relevant for countries with limited resources. Madagascar is a special case, as most of the islands plants and animals are endemic and community composition of consumers differs from other parts of the world, such as Madagascar having a depauperate community of frugivorous species[22,23]. Therefore it is questionable, whether or not experiences from other parts of the world can be transferred to Malagasy systems without adaptations. At the same time, forest restoration is needed urgently, as this biodiversity hotspots has suffered from excessive habitat destruction, having led to a degree of fragmentation that makes the survival of a large proportion of the endemic biota questionable due to the small size of isolated populations[24–32].

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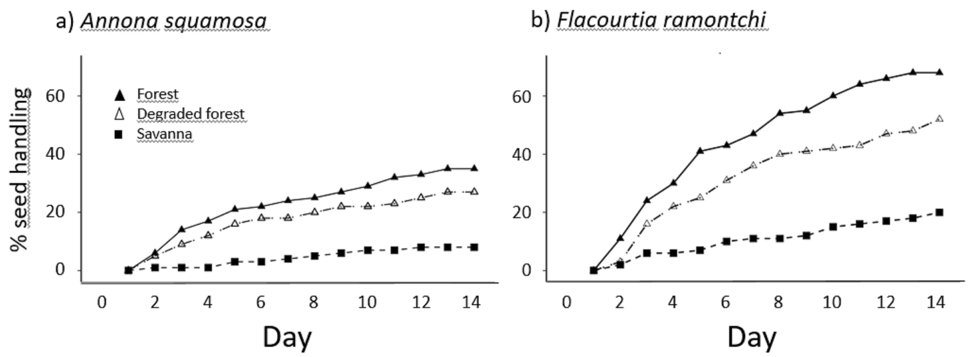

Figure 1. Cumulative percentage of seeds handled (i.e. eaten or removed) over time for (**a**) *Annona squamosa*, (**b**) *Flacourtia ramontchi* in the three different vegetation formations.

	Seed fate					
		Handled				
			Removed			
		Not removed	Not cached	Cached		
	Not handled	Eaten at the seed station	Eaten away from the seed station	Eaten by the end of the study	Not eaten by the end of the study	Total
Forest						
Total count	257	52	44 (41)	4	3	360
% of total	71.4	14.4	10.8	1.1	0.8	
% without *S. birrea*	57.1	21.7	18.3 (17.1)	1.7	1.3	
Deg. forest						
Total count	298	42	20 (19)	0	0	360
% of total	82.8	11.7	5.6 (5.3)	0	0	
% without *S. birrea*	74.2	17.5	8.3 (7.9)	0	0	
Savanna						
Total count	321	16	23 (23)	0	0	360
% of total	89.2	4.4	6.4 (6.4)	0	0	
% without *S. birrea*	83.8	6.7	9.6	0	0	

Table 1. Fates of thread-marked seeds in three vegetation formations of Oronjia, Madagascar. Since none of the seeds of *Sclerocarya birrea* were handled by animals, the results are also presented without this species. Values in brackets are seeds that had disappeared and were not found again and classified as "eaten".

In this study, we describe an experimental study on secondary seed dispersal, seed predation, and fruit dispersal syndromes of tree species regenerating in a natural forest at different states of degradation as well as in the adjacent savanna in northern Madagascar. We use two native and one introduced tree species with fruits consumed by native animals and people alike, thus being of value not just for Madagascar's endemic fauna but also for the local human population that uses not only the fruits but also the wood of these tree species for charcoal making[33–35]. Restoring forests with multi-use species increases the value of these forests for people and thus increases acceptance of reforestation initiatives. Thus, these three tree species fulfill the requirements of being dispersed by primary seed dispersers and their regeneration would contribute to the endeavor of ecosystem restoration to the benefit of people and Madagascar's biota alike. Specific questions were: (1) does tree regeneration differ between habitat types; (2) does post-dispersal seed removal differ between parts of the forest at different states of degradation and the savanna habitat; (3) was seed removal due to secondary dispersal or seed predation.

Results

Seed fates. By the end of the experiment (after 14 days), none of the seeds of *Sclerocarya birrea* had been manipulated or removed by animals at any of the sites. Seeds of the other two species were recovered either at the place where they had been deposited at the beginning of the experiment or in the vicinity. Some seeds could not be recovered despite extensive searching. These seeds were classified as removed and eaten.

Seed removal from the experimental plots continued over the whole 14-day period of seed exposure. Removal was highest in the Forest and lowest in the Savanna. The highest proportion of seeds were removed during the first nights (Fig. 1; Table 1). Without considering *Sclerocarya birrea*, 42.9% of the seeds had been manipulated or removed by animals in the Forest, 25.8% in the Degraded forest and 16.8% in the Savanna. Of the seeds removed

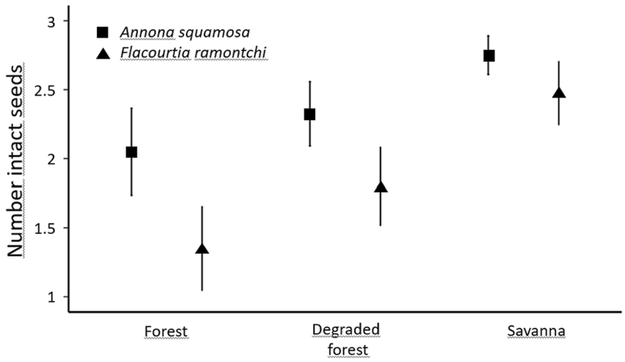

Figure 2. Average number of *Annona squamosa* and *Flacourtia ramontchi* seeds left intact at the experimental plots (N = 40 per vegetation formation) after 14 days. Though the data deviate from normality, values are means and 95% confidence intervals to illustrate differences between groups better than it would be possible with medians and quartiles.

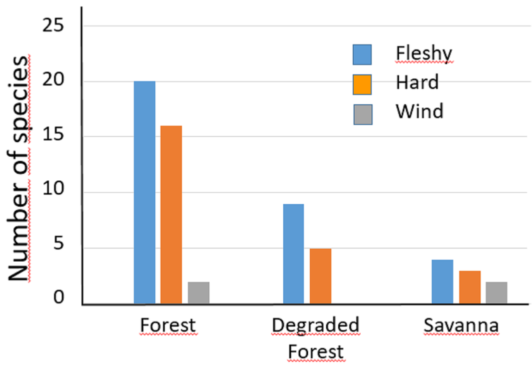

Figure 3. Representation of plant species with different types of fruit and seed dispersal in different vegetation formations.

from the experimental plots, only three seeds survived until the end of the 14-day period buried in the Forest habitat. None of the seeds classified as handled in the Degraded forest and in the Savanna survived undamaged.

When using the individual plots as the units for analyses, the number of seeds left intact at the seed plots differed between vegetation formations for *Annona squamosa* (Kruskal Wallis analysis of variance: $H = 13.53$, $p < 0.001$, $df = 2$) as well as for *Flacourtia ramontchi* ($H = 27.67$, $p < 0.001$, $df = 2$). The number of seeds left intact differed between the two species in the Forest and in the Degraded forest (Mann–Whitney U-test: $z = 3.08$ and $z = 2.69$, respectively; both $p < 0.05$ Bonferroni corrected; N = 40 plots per vegetation formation; Fig. 2). There was no difference between the two species in the Savanna ($U = 1.70$; $p > 0.05$; Fig. 2). *Sclerocarya birrea* is not considered as no seeds of this species had been manipulated by animals in the plots.

Regeneration. We identified 58 different woody plant species with a diameter below 5 cm in the 36 2 × 2 m^2 plots, 48 species in the Forest, 16 in the Degraded forest, and 9 in the Savanna. The number of regenerating species per plot was highest in the Forest with a median of 6 species per plot. The medians for the Degraded forest and the Savanna were 3 plant species per plot for both vegetation formations. The number of regenerating species per plot was significantly higher in the Forest than in the other two vegetation formations (Mann–Whitney-U: $z > 3.35$, $p < 0.01$ for both comparisons; Bonferroni corrected; N = 12 plots per vegetation formation). The numbers did not differ between Degraded forest and Savanna ($z = 0.66$, $p = 0.5$).

Regeneration varied with 1–19 plants with a stem diameter below 5 cm per 2 × 2 m^2 plot. There were three outliers with 27 and 174 plants per 2 × 2 m^2 plot in the Forest and one plot with 40 plants in the Savanna. The median numbers of woody plant individuals per 2 × 2 m^2 plot for the Forest, Degraded forest and Savanna were 12.0, 5.5 and 11.0 individuals, respectively. Only the Forest plots differed significantly from the plots in the Degraded forest (Mann–Whitney-U: $z = 3.71$, $p < 0.01$). None of the other pairwise comparisons was significant.

In the regeneration plots, the Forest had about 20 woody species with fruits dispersed by frugivores and 2 woody species that are wind-dispersed. In the Savanna, the representation of woody species dispersed by animals or wind was four and two species, respectively (Fig. 3). The representation of plants with different dispersal syndromes (fleshy or arillate fruits or seeds for dispersal by vertebrates, hard fruits, winged for wind dispersal) in the regeneration plots did not differ between vegetation formations (chi-square = 4.08, $df = 4$, $p = 0.42$).

	Forest	Degraded forest	Savanna
Feces: Cattle	20/27	57/25	12/27
Feces: Goats	0/1	0/1	15/22
Feces: Total	20/28	57/26	27/49
Median number of regenerating trees < 5 cm in diameter	12.5/11.5	5/7	12/7.5

Table 2. Livestock feces recorded along two transects and median number of regenerating trees < 5 cm in diameter per 2 × 2 m^2 vegetation plot in three different vegetation formations in Oronjia, Madagascar. The values for the two transects are separated by "/".

Small mammal survey. We compiled a total of 400 trap-nights, 160 trap-nights in the Forest and Degraded forest and 80 trap-nights in the Savanna. In the Savanna we could trap only along one of the transects because traps disappeared quickly at the second transect. We did not catch any native rodent species but only one introduced *Rattus rattus* as possible seed predators in the Degraded forest and eight rats in the Savanna. *Setifer setosus* is primarily insectivorous and cannot damage or swallow seeds of the size used in our study. The Sherman traps as well as the cameras recorded *Setifer setosus* in the Forest and the Degraded forest habitat. The cameras did not provide any additional information relevant for the biodiversity inventory or the regeneration study.

Grazing. Grazing pressure by cattle was highest on one transect in the Degraded forest and lowest on one transect in the Savanna. Goat fecal pellets were mostly restricted to the savanna that is closer to the village than the other vegetation formations (Table 2). The number of regenerating plants per 2 × 2 m^2 plot decreases with increasing number of feces along the transect, though this relationship is not significant due to small sample size (Pearson correlation $r = -0.79$, $p = 0.06$, $n = 6$).

Discussion

In the forest habitat of northern Madagascar, the number of woody species in the regenerating cohort decreased with increasing forest degradation. In contrast, the number of woody plant individuals was similar in the forest habitat and in the savanna but lower in the degraded forest. Judging from the presence of livestock fecal samples, the degraded forest seemed to suffer most from livestock grazing, possibly resulting in the low number of plants in the regenerating cohorts in the degraded forest. Removal of seeds from the experimental plots also declined with degradation of the habitat. Seed removal resulted in seed predation but to a low percentage (< 1%) also in caching seeds intact and thus contributing to forest regeneration. The latter occurred only in the least degraded habitat type. The higher proportion of seeds removed in forest than non-forest habitat matches the results in other parts of the tropics, such as in Madagascar[16,36], Asia[20], South America[37], and Africa[13], but are inconsistent with data from Australia[38] or other parts of the Americas[18,39].

Compared to other sites, the proportion of seeds removed in Oronjia is very low, even in the least disturbed habitat. This may be due to the rarity of native rodents that would cache seeds. Our own small mammal survey was not extensive enough to document the whole small mammal community of the site. But more extensive surveys to the east at the Montagne des Français[40] and the west at the Montagne d'Ambre[41,42] revealed very low capture rates of *Eliurus* spp., probably the only native rodent species of the region that acts as secondary disperser and caches seeds[43]. In addition to obviously low abundance of this genus in the region, *Eliurus* spp. seem very sensitive to forest degradation[32,44,45], thus limiting its role as seed disperser in degraded habitats.

Analyzing general patterns of forest regeneration in native forests as well as anthropogenic landscapes[46] ought to consider a multitude of possible factors, such as the community composition of frugivores, primary and secondary seed dispersers and seed predators[12,36], seed size and seed chemistry[38,47], soil conditions and other ambient characteristics[13,37]. The lack of secondary dispersal and predation of *Sclerocarya birrea* seeds was unexpected. There are other examples that rodents do not consume seeds that are too large to be carried away and consumed away from the site where the seeds had been deposited, though size is not the only factor that determines seed dispersal[36,39,47–49]. Once germinated, seedlings face other constraints, such as competition, drought, fire or grazing[50–54] to name but a few. In our case, the prevailing factor may be livestock grazing (Table 2) as it had also been identified in other parts of Madagascar while fire was recorded only once between 2006 and 2016 in Oronjia[55].

Though the establishment of any given plant is influenced by many stochastic events, one of the first requirements for many plant species seems to be that their seeds are protected from desiccation, hoarded in a suitable place for germination, and hopefully forgotten by the hoarding animal[18]. Despite high seed predation levels, there are always some seeds cached intact or are still able to germinate despite having been partially eaten[56,57]. In the present study, only three out of 204 seeds handled by secondary seed dispersers and predators remained intact after the 14-day study period. Seed caching was only recorded in the forest environment. The proportion of surviving seeds may be low in this as well as in other studies[20,58], but given the large number of seeds produced over the lifetime of a tree, even the low "escape rate" from seed predation is sufficient to guarantee survival of the lineage in most cases. Thus, high seed predation as measured by the removal of seeds from experimental plots, does not necessarily have to result in low regeneration. Rather, renaturation might be more successful with a species-rich community of seed eaters, including possible seed predators. Yet, degraded forest habitats and fallow

Species	Length	Diameter
Annona squamosa	14.5 ± 1.4	7.9 ± 0.7
Flacourtia ramontchi	6.4 ± 0.8	5.2 ± 0.4
Sclerocarya birrea	28.3 ± 0.9	20.0 ± 1.2

Table 3. Mean seed sizes (with standard deviation) in mm; N = 10 for each species.

land have a reduced community not only of primary seed dispersers, but also of secondary seed dispersers and seed predators that would hoard seeds and forget at least some of them that can then germinate[45,59–61].

The present results may be relevant for the current efforts to restore forest habitats during the UN "Decade of Ecosystem Restoration"[1]. Within this endeavor, tree species diversity could be increased by facilitated restoration by luring primary seed dispersers into the area to be regenerated by planting fruit trees[7,34,35]. While this is certainly the first step necessary to bring seeds into the degraded landscape with different seed banks than the original forest[62,63], it might be equally important to make sure that the habitat is also suitable for native secondary seed dispersers and seed predators, though, at first sight, this seems as counter-intuitive as promoting cattle and weedy shrubs for forest regeneration[57,64]. In a country like Madagascar that is famous for its unique flora and fauna, it is debatable whether non-native trees should be used for forest restoration[65]. Since people need forest resources, forest restoration has to take human needs into account in order to increase the value of a forest to the local people. For the time being, this is being done by using mostly exotic tree species as their growth properties and requirements are well known. But this can also be done by integrating many native and endemic tree species of value for animals and humans alike[34]. In either case it is important to know more about the processes involved in tree regeneration of native and exotic tree species to arrive at multi-use forests without promoting invasive species[66,67].

Methods

Study area. The study was carried out in the Oronjia Protected Area (IUCN category V) in northern Madagascar, located between 12° 14′ 00.8″ S–12° 18′ 48.1″ S and 49° 22′ 44.8″ E–49° 23′ 34.0″ E between January and April 2019 by the end of the wet season. Average annual rainfall was around 1122 mm between 1981 and 2017, with 90% falling between November and April. Different anthropogenic pressures and military use have led to a degradation of Oronjia's forest. Since 2007, conservation interventions were carried out in Oronjia, which culminated in the designation as a New Protected Area ("Nouvelle aire protégée") in 2015. Today, the forest is in the process of regeneration, but the collection of yams and livestock breeding of cattle and goats remain[55,68]. Three habitat types were assessed within Oronjia: Forest, Degraded forest and Savanna. The three habitats were contiguous.

Seed removal experiments. The experimental setup followed[20] to facilitate further comparative analyses. In each habitat type, two transects of 475 m each were installed. Each transect was subdivided in 25 m intervals. Seed stations were established at each of the 25 m intervals along each of the transects, adding up to 20 seed stations (study points) per transect and 120 stations in total. At each seed station three seeds of each of the three plant species described below were deposited in a 1 m square located 1 m off the transect with 50 cm distance between seeds. Seeds of *Annona squamosa*, *Flacourtia ramontchi* and *Sclerocarya birrea* were used for the experiments. Seeds were extracted from ripe fruits collected directly from trees in case of *Annona squamosa* and *Flacourtia ramontchi* and from fallen fruits or bought from local people for *Sclerocarya birrea*. Fruit pulp was removed from the seeds. Mean seed sizes ranged from 6.4 × 5.2 mm in *Flacourtia ramontchi* to 28.3 × 20.0 mm in *Sclerocarya birrea* (Table 3). These tree species were chosen because of their economic value, because seeds of all three species are dispersed by native primary seed consumers, because seed size covered a wide range of sizes, and because seeds were available in sufficient quantities to complete the experiments in a standardized way. A 50 cm cotton thread was attached to each seed with non-toxic glue to facilitate the search for seeds removed from the experimental plots. Seed stations were checked daily for signs of feeding or insect infestation over a period of 14 days. Seeds that disappeared were searched for in the vicinity within a radius of about 5 m. Seeds were classified as eaten if seed fragments were found and cached if seeds were found below the soil surface or below leaf litter. Cached seeds were also monitored for the 14-day period. Seeds damaged by insects or rodents were classified as "eaten".

Regeneration. At the study points 1, 4, 8, 12, 16 and 20 of each transect woody plants were identified and their size were recorded in a plot of 2 × 2 m^2 (= 6 plots per transect). Identification was not possible for some of the seedlings. They were identified to the highest taxonomic unit or recorded as "unknown". The circumference of each plant was measured before the first branching or at breast height. For plants with multiple stems, only the largest stem was measured. Circumferences were transformed into diameters. For the regeneration study only trees with a diameter < 5 cm were included.

Fruits were classified as "fleshy" (attracting fruigivores), "hard" (no external flesh but attractive for seed predators), "wind dispersed". Fruit types were taken from the Generic Tree Flora of Madagascar[33].

Small mammal survey. Small mammals were trapped with Large Sherman Live Traps set in duplicates at each study point along the transects. Traps measured 7.6 × 8.9 × 22.9 cm and have been used in many standardized small mammal surveys in Madagascar and in the region (e.g.,[40,42]). At each study point, one Sherman trap was set on the ground and one was set up in trees or shrubs, resulting in 40 traps per transect. Traps were baited daily with peanut butter and banana before sunset and set for four consecutive nights in March and April 2019. Animals were identified, marked by hair clipping to be able to identify recaptures and released at the site of capture. In addition to the Sherman traps, five camera traps (Dörr Snapshot Wildlife Camera) were placed at the seed stations haphazardly. Cameras were only set in the Forest and Degraded forest because of the risk of theft in the open Savanna habitat.

Grazing. Grazing pressure by goats and cattle was estimated by counting feces along the transects. Fecal remains estimated to be older than 48 h were not considered.

Data analysis. For data deviating from normality, non-parametric tests were used as indicated in the Result section. For multiple pairwise comparisons, *p* values were Bonferroni corrected. Statistical analyses were run with SPSS (25.0). For the graphical illustration of differences between groups in analyses that were based on the individual plots, means and 95% confidence intervals were used instead of boxplots with medians, quartiles and ranges as they would be the appropriate graphical match for non-parametic statistical tests. This option was chosen because the number of intact seeds can vary between 0 and 3 per tree species and seed station. If we would plot standard box-whisker-plots, all six groups would cover the full range of values between 0 and 3, making visual comparisons difficult. In this case, confidence intervals allow easier visual comparisons of differences between groups than box-whisker-plots.

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Author contributions

P.M.A.F., A.D.L., J.R., J.S. and K.J.E.S. performed the experiments. P.M.A.F., A.D.L., K.J.E.S. and J.U.G. developed the concept and wrote the manuscript. All authors reviewed the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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