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RESEARCH ARTICLE

Comparing seed removal rates in actively and passively restored tropical moist forests

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High rates of seed removal can impede forest recovery, but tropical seed removal studies are few and mainly from the neotropics. Little is known about the comparative influences of active restoration (i.e. planting) and passive restoration (i.e. protection of natural regrowth) on seed removal. We conducted an evaluation of seed removal in grasslands, natural forests (tropical moist semideciduous forest), and actively (21-, 17-, 16-, 11-, 8-, and 6-year-old) and passively (21-year-old) restored forests in Kibale National Park, Uganda. We wanted to compare the effect of vegetation type, time since restoration and restoration actions (i.e. active vs. passive) on removal of seeds of five animal-dispersed tree species during wet and dry seasons. Seeds were either fully exposed or placed in closed mesh cages or under a mesh roof. We used differential removal rates between these treatments to attribute seed removal to different animal taxa. Seed removal rate (percentage of seed removed over a 4-day period) was highest in passively restored forests, compared with actively restored forests, grasslands, and natural forests. We detected no significant relationship between time since restoration and seed removal rates within actively restored sites. Seed removal rate from roofed treatments was not significantly different from removal from open treatments but was significantly higher than removal from closed treatments, which we interpret as reflecting the greater effect of small mammals versus insects. Smaller seeds tended to be removed at a greater rate than larger seeds. We discuss the implications of these findings for forest regeneration.

Key words: **active and passive restorations, arrested succession, seed predation, seed removal, time since restoration, tropical forests**

Implications for Practice

- Both active and passive restorations are viable forest restoration approaches worldwide.
- Active restoration had lower seed predation than passive restoration, an indicator that tree recovery may be faster in actively than passively restored forests.
- In cases where it is practically possible, restoration efforts could protect the smaller seeds (e.g. by cages) since they were more vulnerable in all vegetation types.
- Management of tropical forests may need to control predators of small seeds, in order to accelerate restoration. Again, this will depend on the legal status of the seed predator and available methods for control.
- Although active restoration is the most effective approach, further studies should be done to assess the long-term costs and benefits of this practice.

Introduction

Tropical forests have been the epicenter of large-scale forest loss in recent decades (UNEP 2014). Of the world's total tropical forest area, about 46% is fragmented, 30% degraded, and only 24% relatively intact (Minnemeyer et al. 2011). Estimates indicate a dramatic rise (2.5×10^6 ha/year) of net deforestation from 1990 to 2010 (Kim et al. 2015). Forest degradation and deforestation threaten biodiversity (Sala et al. 2000) and affect ecological processes, e.g. pollination and postdispersal seed removal. Restoration enhances the potential of forests for biodiversity conservation by improving habitat quality (Omeja et al. 2011). Restoration initiatives seek to address widespread forest degradation and deforestation. The aim of the Aichi Biodiversity Target 15, within the strategic plan of the Convention on Biological Diversity (2010), is to restore 15% of the degraded ecosystems by 2020.

Restoration can occur either actively or passively. Active restoration generally involves planting but may also include interventions to reduce threats (Rey Benayas et al. 2008). Passive restoration facilitates natural colonization by woody vegetation by reducing threats such as fire and livestock (Morrison & Lindell 2011). Both active and passive restorations are increasingly implemented worldwide (Clewell & Aronson 2007). Active restoration normally results in faster ecosystem

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Author contributions: ES, SRM, DS conceived and designed the research; ES performed the experiments; ES, LEL analyzed the data; all authors wrote and edited the manuscript.

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recovery than does passive restoration (Zahawi et al. 2014). Comparing the effect of the two types of restoration actions on ecological processes is potentially important for understanding the consequences of these alternatives (Matthews & Spyreas 2010). Restored forests often consist of stands differing by age since restoration, forming a restoration age gradient. Information on the status of ecological processes, such as seed removal, along restoration age gradients, compared to natural habitats is relevant when predicting whether forests are recovering to predisturbance conditions.

Seed removal describes both seed predation and secondary seed dispersal (Vander Wall et al. 2005). Seed predation leads to seed loss which can impede plant recruitment (Holl et al. 2000), whereas secondary seed dispersal can improve recruitment possibilities in certain locations (Bell et al. 2006). For most seeds, in most locations, predation dominates and secondary dispersal is exceptionally rare (about 0.2%) (Wenny 2000; Jansen et al. 2002). Season, seed characteristics, and seed removal agents, like insects, birds, and mammals, may influence seed removal in restored forests and natural habitats (Lima 1985; Ji-Qi & Zhi-Bin 2004; Christianini & Galetti 2007). Canopy sites provide perches for raptors which may reduce seed removal by small ground dwelling herbivores due to predation risk (Walters et al. 2005). Dense herbaceous cover in grasslands protects small ground dwelling herbivores, such as small mammals (Okullo et al. 2013), from predators which increases their seed removal rates.

Seed removal studies (e.g. Holl et al. 2000; Bricker et al. 2010; Hulme & Kollmann 2005; Klinger & Rejmánek 2013) provide insights into effects of seed predation and dispersal on survival and recruitment of species in different habitats. When populations are more seed-limited than microsite-limited seed predation retards forest restoration by reducing seed and seedling densities in restoration sites (Wijdeven & Kuzee 2000). Seed dispersal accelerates forest restoration by moving species to suitable microsites for germination in restoration sites (Bell et al. 2006). Because nearly all taxa from mammals to insects forage on seeds, seed removal experiments could be used to identify seed dispersal taxa in natural and restored habitats. Our knowledge of seed removal in restored forests, and especially restored African forests, is limited. Indeed, no studies have, to our knowledge, directly compared seed removal in active and passive restorations. While there have been some comparisons of seed removal among different vegetation types (Brum et al. 2010; Doust 2011), and among different ages of restoration (Peña-Claros & De Boo 2002; Dominguez-Haydar & Armbrecht 2011), none come from Africa. We conducted our study in Kibale National Park in Uganda to compare seed removal rates of five tropical woody species in a range of sites. We tested whether seed removal varied (1) among natural habitats and restored forests; (2) between actively and passively restored forests; and (3) due to time since active restoration. In addition, we evaluated the effect of seed species, season, and how much of the seed removal is attributed to different taxa (insects, birds, and mammals).

Methods

Study Area

Kibale National Park (795 km^2) lies in western Uganda (00°13′–00°41′N, 30°19′–30°32′E). The park has two rainy seasons, from March to May and September to November. Average annual rainfall is approximately 1,750 mm and mean daily minimum and maximum temperature is 15.1 and 23.1°C, respectively. Over the last 30 years, forest restoration has decreased grassland and increased native forest cover inside the park: today, land cover is 74% unlogged and regenerating forest, 15% bare ground and short grasses, 6% tall grasses, 4% wetland, and 1% shrubs (Jacob et al. 2017). Elevation in the park declines from 1,590 m in the northwest to 900 m in the southwest, which corresponds to an increase in temperature, and a decrease in rainfall, reflected in the change from evergreen and semideciduous forest in the north and center, to grasslands and woodlands in the southwest (Jacob et al. 2017).

The study was located south of the park where the natural vegetation is moist semideciduous with *Cynometra alexandri* C. H. Wright as a climax species on poor soils, and *Celtis* spp. and *Chrysophyllum* spp. on rich soils (Zanne & Chapman 2005). The grasslands are a result of past human clearing and are dominated by *Hyparrhenia* spp., *Cymbopogon nardus* (L.) Rendle, and elephant grass (*Cenchrus purpureus* [Schumach.] Morrone) (Chapman & Lambert 2000). Because the grasslands are protected from fires and livestock grazing, they are being colonized by trees species like *Combretum* spp., *Acacia seyal* Delile, *Entada abyssinica* Steud. ex A. Rich., *Erythrina abyssinica* Lam. ex DC., *Phoenix reclinata* Jacq., and *Millettia dura* Dunn, and shrubs of *Acanthus* spp., *Vernonia* spp., *Flueggea virosa* (Roxb. ex Willd.) Royle, and *Hoslundia opposita* Vahl (Fig. 1). A recent study (i.e. Jacob et al. 2017) in west-central Kibale confirms that grasslands are a stage of succession rather than degraded habitats with arrested succession. We chose Kanyanchu, Isunga, Ngeza, and Mpokya grasslands for this study because they had not burned the previous year. The grasslands are bounded by natural forests and forest-dependent animals which frequently forage in these grasslands are accelerating forest regrowth (J. Soyita 2016, personal communication).

There are 13 species of primates in Kibale (Chapman & Lambert 2000). Seeds constitute a portion of the diet of chimpanzees (*Pan troglodytes*), olive baboons (*Papio anubis*), blue monkeys (*Cercopithecus mitis*), l'hoesti monkeys (*Allochrocebus lhoesti*), vervet monkeys (*Chlorocebus aethiops*), and gray-cheeked mangabeys (*Lophocebus albigena*). The park has 14 species of small mammals associated with forest or grassland habitats (Isabirye-Basuta & Kasenene 1987) of which *Hylomyscus stella*, *Praomys jacksoni*, *Thamnomys venustus*, *Lemniscomys striatus*, *Dendromus mysticalis*, and *Malacomys longipes* exhibit granivorous feeding behavior. The Kibale bird species can be categorized into forest interior specialists, forest generalists, and forest visitors (Dranzoa 1998). The seed eating species include; Red-headed Bluebill (*Spermophaga ruficapilla*),

Figure 1. Study sites in Kibale National Park in western Uganda. (A) Grasslands (*Hyparrhenia* grass) are bounded by natural forest and are being colonized by woody vegetation, (B) 6-year-old restoration plantings with a tree uprooted by elephants, (C) trampling of trees by elephants in 6-year-old restoration plantings, (D) passively restored forest with low shrubby undergrowth, and (E) natural forest with less undergrowth.

Tambourine Dove (*Turtur tympanistria*), Black-and-white Mannikin (*Lonchura bicolor*), and Red-faced Crimsonwing (*Cryptospiza reichenovii*). The ant community of Kibale consists of species such as *Aenictogiton sulcatus*, *Cyphoidris werneri*, *Tetramorium aculeatum*, *Cerapachys* spp., and *Crematogaster* spp.

Kibale has a long history of human disturbance (Chapman & Lambert 2000). In 1971, agricultural encroachment led to forest degradation and deforestation in the southern part of the park (Chapman & Lambert 2000). In 1992, encroachers were resettled outside the park. Subsequently, the formerly encroached areas became dominated by elephant grass because fires prevented natural regeneration. In 1994, the Government of Uganda, through UWA, and in collaboration with Forests Absorbing Carbon dioxide Emissions (FACE) Foundation started a restoration program to establish carbon offsets on the formerly encroached land (UWA-FACE 2009). Active and passive actions were used to restore forests. Passive restoration involved protection against fires and livestock grazing to facilitate natural regeneration in 1995. Active restoration involved planting of native tree species from 1995 to 2010, every year except 2001 (Face the Future 2015). Initial plantings were raised from seeds or collected as wildings from forest areas that were not encroached (UWA-FACE 2009). The main tree species planted were *Albizia* spp., *Bridelia micrantha* (Hochst.) Baill, *Croton macrostachyus* Hochst. ex Delile, *Shirakiopsis elliptica* (Hochst.) Esser, *Celtis gomphophylla* Baker, and *Warburgia ugandensis* Sprague. Vegetative propagation by cuttings accounted for 5% of the trees planted (UWA-FACE 2009).

Planting sites were prepared by clearing grass along a series of 2-m-wide trails spaced in a 5 × 5 m grid, and digging planting pits every 5 m along the trails. The planting density was 400 per ha. The planted area was divided into a series of compartments of different sizes and weeding was carried out two to three times a year. In addition, fire breaks were cut between compartments, and fires were fought by UWA-FACE staff. The size of actively and passively restored forests since the start of restoration activities was 3,996 and 2,593 ha, respectively (Face the Future 2015). The planted compartments, except one compartment, and the passively restored forests are bounded by natural forests. Kibale is experiencing an exponential increase in elephant numbers (Omeja et al. 2016), and the elephants favor restored forests (Omeja et al. 2016) because the recovering forests have better food quality than natural forests (Gogarten et al. 2012). Pit trapping (hunting for ivory) in passively restored forests has driven elephants to seek refuge in actively restored forests where they graze and trample vegetation (Fig. 1). Consequently, the passively restored forests have more low shrubby vegetation than actively restored forests. In the 21-year-old planted compartments, the mean number of species and diameter at breast height ([DBH], 1.3 cm) are 2.9 and 19.8 cm, respectively (Omeja et al. 2016). The most common tree species are *B. micrantha*, *S. elliptica*, and *Funtumia latifolia* (Stapf) Stapf. In comparison, the mean number of species and DBH in the natural forest are 85.0 and 24.7 cm, respectively (Omeja et al. 2016).

Table 1. Vegetation types, study sites, and number of sample plots at each site in Kibale National Park in western Uganda. Some of the study sites are of unknown size (N/A).

Vegetation Type	*Study Site ID (Area in ha)*	*No. of Plots*
Natural forest	1 (N/A)	2
	2 (N/A)	2
	3 (N/A)	2
	4 (N/A)	2
21-year-old restoration plantings	101 (61.7)	2
	102 (185.3)	2
	103 (64.3)	1
	108 (83.3)	2
17-year-old restoration plantings	205 (184.7)	3
	206 (368.7)	3
16-year-old restoration plantings	001 (23.4)	1
	301 (315.8)	3
11-year-old restoration plantings	403 (65.5)	2
	404 (14.6)	2
8-year-old restoration plantings	701 (15.4)	2
	702 (100.1)	2
6-year-old restoration plantings	901 (84.3)	2
	902 (15.6)	2
Passively restored forests	1 (N/A)	3
	2 (N/A)	2
	3 (N/A)	6
Grasslands	Ngeza (110)	4
	Isunga (25.5)	4
	Mpokya (500)	4
	Kanyanchu (80)	4

Study Design

The study sites were compartments located within: (1) actively restored forests (21-, 17-, 16-, 11-, 8-, and 6-year-old restoration plantings); (2) 21-year-old passively restored forests; (3) natural forests near the UWA-FACE station in Mainaro; and (4) grasslands (Kanyanchu, Isunga, Ngeza, and Mpokya) (Table 1). Each vegetation type was comprised of compartments of varying sizes. At each site, two plots were established randomly (except for one site planted in 1995 and 2000 where one plot was already established), spaced at a minimum of 30 m apart and no less than 30 m from the boundary. Each plot consisted of two seed stations placed 5 m apart (Fig. 2). Each seed station included three treatments: open (seeds placed on the forest floor could be accessed by all seed removal agents), roofed (a sheet of wire mesh 10 × 20 cm supported by four metal rods of height 5 cm excluded primates and birds but could be accessed by small mammals), and closed (a wire-mesh cage of width 10 cm, length 20 cm, and height 10 cm, mesh size = 0.5 cm to prevent entrance of seed removal agents except invertebrates) placed within 30 cm of each other. The roofed and closed treatments were stabilized using iron rods. Although the roofed treatments were designed to exclude birds and primates by obscuring visibility from above, they could not prevent primates moving on ground from removing seeds because the roofs were small, and this may influence the outcome of the comparison of the different taxa.

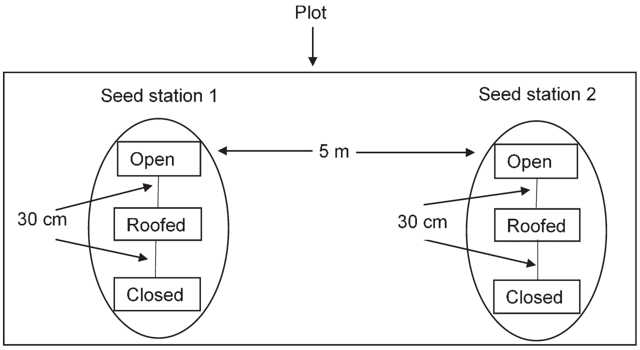

Figure 2. Study design, each plot consisted of treatments open, roofed, and closed at each seed station in Kibale National Park in western Uganda.

Table 2. Mean seed weights of the study species placed in treatments in Kibale National Park in western Uganda.

Species	*Mean Seed Weight (g* ± SD, n = *50 of Each Species)*
Croton macrostachyus	0.06 ± 0.01
Bridelia micrantha	0.07 ± 0.02
Phoenix reclinata	0.20 ± 0.03
Groundnuts	0.37 ± 0.01
Maesopsis eminii	1.26 ± 0.19
Cordia millenii	2.16 ± 0.33

We placed one intact seed of *Croton macrostachyus* (Euphorbiaceae), *Bridelia micrantha* (Euphorbiaceae), *Phoenix reclinata* (Palmae), *Maesopsis eminii* Engl. (Rhamnaceae), *Cordia millenii* Baker. (Boraginaceae), and groundnut (*Arachis hypogaea L.*, Fabaceae) within each treatment. The seeds of all species were placed approximately at an equal distance from the perimeter of each treatment, that is, in the center of each treatment. All five tree species are dispersed by animals and are commercially important (Katende et al. 1995). We included groundnuts, an agricultural crop, because we believed that groundnuts would be attractive to many potential removal agents and would thus measure removal potential if the tree seeds were found to be unattractive. Mean seed weights of the study species vary from 0.06 ± 0.01 to 2.16 ± 0.33 g (Table 2). Seed status (i.e. untouched, damaged, and removed) was assessed every 4 days over 36 days in each season (nine intervals). Damaged and removed seeds were replaced. The study was performed in the rainy season (3 November 2015–8 December 2015) and dry season (7 January 2016 to 11 February 2016). The total sample size (number of seeds subjected to removal over a 4-day period) was 34,560.

Statistical Analysis

Generalized linear mixed-effects models with binomial error structure and logit link were fitted with the function *glmer* from the R package *lme4* in R version 3.3.2 for Windows (R Core Team 2016). We used a nested random effect structure following our hierarchical spatial design (seed station nested within plot nested within compartment). The response variable was removed (1) or not (0). We used backward elimination, where we fitted initial models containing all candidate fixed effects and interactions and used likelihood ratio tests (LRT) to judge if variables provided a significant model improvement (Pinheiro & Bates 2000). Models with only one candidate predictor variable were tested against an intercept-only model. Subset of data and candidate fixed effects differed among analyses as specified in the following sections.

Seed Removal as a Function of Vegetation Type, Restoration Action, and Time Since Restoration. Initially, we used only the open treatments accessible to all seed removal agents. To determine the relationship of seed removal rates with vegetation type, we fitted vegetation type as a four-level factor variable (active restoration, passive restoration, grassland, and natural forest) and used the LRT against an intercept-only model. Second, to determine the relationship with restoration age, we fitted number of years since restoration action both as a continuous and as a factor variable (two different models) and used the LRT against intercept-only models. To determine the relationship with restoration actions, we compared the predicted seed removal rates of active restoration (with year fitted as factor variable) with the predicted seed removal in passive restoration.

Estimating the Contribution of Different Seed Removal Agents. The aim of the second set of analyses was to clarify the principle seed removal agents using data from all treatments. Candidate fixed effects included treatment (open, roofed, or closed), seed species, season (wet and dry), vegetation type (same as above), and if the contribution of each seed removal taxon depended on vegetation type (the second-order interaction treatment × vegetation type).

Results

Seed removal rates (percentage of seed removed over a 4-day period) from open treatments differed among vegetation types (LRT: $\chi^2 = 13.6$, $df = 3$, $p = 0.003$), with the highest rates in passive restoration sites (Table S1, Supporting Information, and Fig. 3). Seed removal rates from grasslands, natural forests, and actively restored forests were not significantly different (Fig. 3 and Table S1).

Overall, seed removal rates did not change with time since restoration (Fig. 4). We detected no support for including either planting year as a linear effect (LRT: $\chi^2 = 0.51$, $df = 1$, $p = 0.47$) or as a factor ($\chi^2 = 4.1$, $df = 5$, $p = 0.54$). Among the actively restored forests, 11- and 16-year-old restoration plantings had the highest (38.8 ± 1.4%) and lowest rates (35.5 ± 1.4%) of seed removal, respectively. The probability of seed removal in 21-year-old passively restored forest was higher than in the actively restored forest of the same age (Fig. 4).

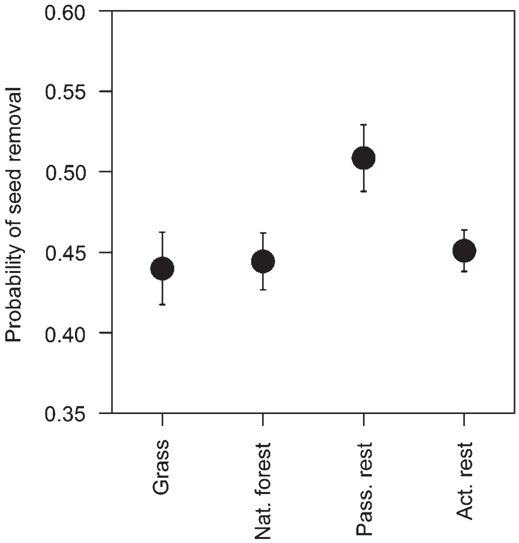

Figure 3. Probability of seed removal (per 4-day periods) as a function of vegetation type, consisting of two types of natural habitat; grassland (Grass) and natural forest (Nat. forest), and two types of restoration habitat, passive (Pass. rest) and active (Act. rest), in Kibale National Park in western Uganda. Point estimates are predicted values from a generalized linear mixed model (see Table S1). Error bars are ±1 SE.

Effect of Treatment and Seed Species

Although the effects of treatment, seed species, season, vegetation type on seed removal rates, and the interaction between treatment and vegetation type were statistically significant (LRT: $\chi^2 = 18.1$, $df = 1$, $p < 0.001$; Table S1) two factors explained most of the variation in seed removal rates. First, seed removal in open and roofed treatments was similar, but much higher than closed treatments (Fig. 5 and Table S1). Second, seeds of different species differed widely in removal rates (Table S1). From open treatments, *Croton macrostachyus* suffered the highest mean level of seed removal across all sites, 97.4 ± 0.3%, followed by *Bridelia micrantha*, 86.1 ± 0.8%. The remaining three species had substantially lower mean seed removal across all sites with *Phoenix reclinata* suffering only 27.6 ± 1.0%, *Maesopsis eminii* 13.4 ± 0.8% and *Cordia millenii* 4.5 ± 0.4% (Table S1). In comparison, removal of groundnuts was 79.4 ± 0.6%. Seed mass was negatively correlated with rate of seed removal for the five tree species (Pearson correlation of Removal and Mass, $r = -0.74$, $p < 0.001$). Other significant effects were smaller, e.g. removal rates were marginally greater in the dry season (38.5 ± 0.5%) than in the wet season (37.2 ± 0.5%) ($p < 0.001$, Table S1). There was also a significant interaction between treatment and vegetation type ($p < 0.001$, Table S1) mainly reflecting the greater relative increase in seed removal from open treatments in passively restored areas compared to others (Fig. 5).

Variation Between and Within Sites

Seed removal varied among sites, particularly in restoration plantings (Figs. S1 & S2). There was a significant positive correlation among seed removal rates across all species regardless of seed size (Fig. S3 and Table S2). There was a substantial between-site variation in seed removal for many of the species and vegetation types (large boxes in the box plots; Figs. S4 & S5). However, the variance pattern was remarkably consistent when comparing vegetation types and time since restoration (comparing panels in Figs. S4 & S5).

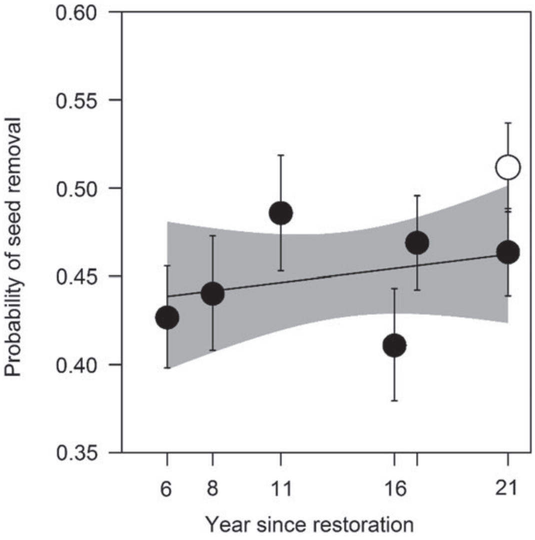

Figure 4. The effect of time since active restoration for probability of seed removal in treatments exposed to all seed removal agents in Kibale National Park in western Uganda. The line is the predicted linear effect of time since active restoration and gray polygon is the ±95% confidence intervals (see Table S1). Time since active restoration falls into six age classes with unequal time interval and was therefore in addition analyzed as a factor variable (black filled point estimates with ±1 SE). All passive restorations are 21 years of age and for which predicted seed removal is plotted as a white point estimate with ±1 SE.

Discussion

Effect of Restoration Method, Time, and Vegetation Type

Seed removal in passively restored forests was significantly higher than in grasslands, natural, and actively restored forests, and there was no significant effect of time since onset of the active restoration on seed removal. Although seed removal rates in passively restored forests have increased relative to both grasslands and natural forests, those in actively restored forests were comparable to natural forests already after 6 years (i.e. the youngest measured actively restored sites). Small mammals tend to be relatively abundant in degraded habitats (Jeffrey 1977; Caro 2001; Conde & Rocha 2006). Since seed removal did not differ between the open and roofed treatments (that would matter for arboreal seed predators), but were considerably higher than the closed treatment (available to insects only), we suspect that the main seed removal agents are small mammals, and that the species that occur in our study area are mainly seed predators and not seed dispersers (Isabirye-Basuta & Kasenene 1987). Past human activities could have benefited the small

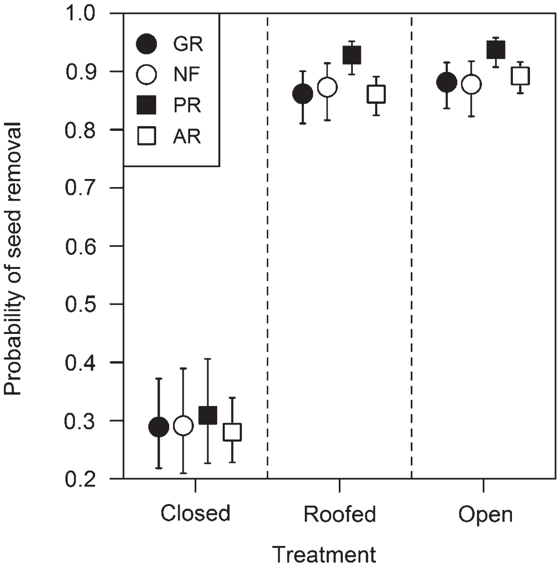

Figure 5. The probability of seed removal as a function of the interaction between vegetation type and treatment in Kibale National Park in western Uganda. The predicted effect is for wet season and the species *Bridelia micrantha*. AR. active restoration; GR, grassland; NF, natural forest; PR, passive restoration. Error bars are ±1 SE.

mammals by reducing densities of small- and medium-sized predators (such as mongoose, snakes, and birds of prey) (Caro 2001). The biomass, density, and diversity of small herbivores have been reported to decrease as a consequence of restoration actions (Briani et al. 2004; Stone 2007). Before people moved out and restoration began, forests were degraded and it is plausible that there were few medium-sized predators feeding on small herbivores. The small- and medium-sized predators may have returned/increased more rapidly in actively restored sites than in passively restored sites. Consequently, small herbivores may have been reduced because of predation in actively restored sites. Although not tested in this study, if these causal relationships are correct we would expect that actively restored sites should have a higher natural seedling density than passively restored sites because of reduced seed predation in actively restored sites (Wijdeven & Kuzee 2000; Klinger & Rejmánek 2013).

In addition, as a result of forest restoration, Kibale is experiencing an exponential increase in elephants (Omeja et al. 2016) which preferentially forage in actively restored forests. Grazing and trampling of vegetation by elephants in actively restored forests potentially reduces the abundance and diversity of small herbivores by exposing them to predators (Keesing 1998). This reduces seed removal rates in actively compared to passively restored forests with more safe areas for small mammals to move among allowing more complete searching of the area.

Seed removal in grasslands and natural forests was surprisingly not different. Furthermore our data indicate that small mammals play a similar role in both vegetation types. The grasslands in Kibale are bordered by the natural forest. Removal agents may forage in the grasslands even if they originate elsewhere (since there is no barrier between the vegetation types). Various elements of forest fauna will readily forage in adjacent habitats (Jacob et al. 2017). It is also possible that seed removal agents typical of grasslands utilize the natural forests as supplementary foraging resources thereby causing similar rates of removal in both the vegetation types.

We found lower seed removal rates (11–13% per day) than reported in most comparable neotropical studies involving seeds of varying sizes (e.g. Pinto et al. 2009—50%; Brum et al. 2010—81%; Dominguez-Haydar & Armbrecht 2011—90% per day). The lower rates of seed removal in our study may be linked to the generally lower diversity of zoochorus fruiting trees in Afrotropics compared to Neotropics, which could limit the density and diversity of both resident and nomadic (i.e. migrating birds) frugivores (Hockey 2005). This assumption is supported by our cage experiment which suggests that birds were not the main seed removal agents in the study area. Although other seed removal studies did generally have higher removal rates than our findings, some rates were comparable (i.e. Willson 1988—12%; Linzey & Washok 2000—13%, per day; Doust 2011—13%).

Effect of Treatment and Seed Species

Seed removal in open and roofed treatments was relatively similar but higher than closed treatments, suggesting that majority of the seed removal is due to small mammals rather than insects, birds, and primates. Although our experiment was designed to disentangle predation effect of invertebrates, small-sized mammals, medium-sized mammals, and birds, it is possible that primates and small ground birds could remove seeds from roofed treatments because the cages we used were relatively small. For birds this is unlikely because we did not encounter any ground birds during the study and informal discussions with park employees revealed that large ground dwelling birds like Nahan's Francolin (*Francolinus nahani*) and Crested Guineafowl (*Guttera pucherani*) only occur at low densities. Also, the removal of the aril (fruit) from the seeds, prior to our experiment, seems to have reduced the possibility of seed removal by birds because arils are visual cues which attract birds to fruits (Francisco et al. 2007). If primates removed seeds, we would expect open treatments in natural forests to have correspondingly higher seed removal than open treatments in grasslands and young restoration sites because primates are more associated with forested sites. However, there was no variation in seed removal in open treatments between grasslands, active restoration sites, and natural forests.

Previous studies have documented that small mammals may act as seed dispersers by moving and caching seeds that may not be recovered and thus germinate (Forget & Vander Wall 2001) and such mechanisms may be beneficial to forest restoration. However, small mammals are also among the most pervasive seed predators limiting plant recruitment (Bricker et al. 2010), which retards forest restoration. Studies elsewhere indicate that low proportions of seeds removed by small mammals finally establish, e.g. 2 seedlings out of 923 seeds in a cloud forest in Costa Rica (Wenny 2000), and 1 seedling out of 489 seeds in a rainforest in French Guiana (Jansen et al. 2002). Although even infrequently dispersed seeds may contribute to restoring tree diversity over large spatial scales, they contribute little to tree densities during forest regrowth. Small mammals are also highly efficient at finding caches, and there is experimental evidence for high seed pilferage by conspecifics (Jansen & Forget 2001) which limits seed survival. Also Russo (2005) and Iob and Vieira (2008) showed that scatter hoarding among small mammals is infrequent and it occurs at short distances from parent plants. Thus, small mammals as a functional group seem to be more important as seed predators than as seed dispersers.

Seed predators retard forest restoration by reducing seed densities which limits tree recruitment (Wijdeven & Kuzee 2000) in restoration sites. Thus, seed predators may affect the ability of restored forests to sustain themselves, a tenet of successful restoration (SER 2004). Studies show that seed predation reduces recruitment in grasslands (Bricker et al. 2010), temperate (Holl et al. 2000; Hulme & Kollmann 2005), and neotropical forests (Klinger & Rejmánek 2013). In comparison, we still know little about the effects of seed predation on tree recruitment and restoration of afrotropical forests. Our study suggests that if seed supply is the limiting factor for regeneration, seed predation is a stronger limiting factor in passive restorations than in active restorations.

There was a negative correlation between seed mass and seed removal. The smaller seeded (*Croton macrostachyus* and *Bridelia micrantha*) species were removed more frequently than larger seeded species (*Phoenix reclinata, Maesopsis eminii*, and *Cordia millenii*) across all treatments. The high rate of removal of smaller seeds may further support our hypotheses that small mammals are the dominant seed removal guild, since small mammals preferentially forage on smaller seeds within the size range considered in our study (Vieira et al. 2003). Such seed size-dependent effects may act as a filter on the species recruited during forest restoration.

In conclusion, in terms of seed predation, active restoration seems to be more efficient than passive restoration in recovering forests. In active restoration, the level of seed predation was similar to levels as natural forest within a few years, whereas predation levels were high after more than 20 years of passive restoration. The higher seed predation in passively restored areas is possibly due to the relatively high densities of granivorous small mammals in degraded habitats. Although actively restored sites have lower seed predation, actively planting seed and seedlings is generally costlier than passive restoration. It is therefore also important to evaluate the costs of active restoration against the associated benefit for the full restoration trajectory.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Effects of treatment, season, and vegetation type on seed removal.
Table S2. Pairwise correlations of seed removal among species.
Figure S1. Conditional boxplot of seed removal from closed cages/treatments versus individual sites.
Figure S2. Conditional boxplot of seed removal from open treatments versus individual sites.
Figure S3. Multiple pairwise scatterplots showing the relationship between seed removal of various species.
Figure S4. Conditional boxplot of seed removal from closed treatments versus species.
Figure S5. Conditional boxplot of seed removal from open treatments versus species.

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