Colonization of woody seedlings in the understory of actively and passively restored tropical moist forests

Running head: Seedling colonization in afrotropical forests

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ES, VBM, MT conceived the research; ES analyzed the data; ES, VBM, JE, JRST, MT wrote and edited the manuscript.

Abstract

The status of woody seedling colonization gives clues about the self-sustainability of restored forests, a tenet of restoration success. Little is known about woody seedling colonization in restored afrotropical forests. We evaluated effects of restoration methods (active vs. passive), sampling year, restoration age and distance from old-growth forests on seedling colonization in restored afrotropical moist forests. Seedlings were measured in 2011 and 2014 in 71 clusters of 284 permanent sampling plots (12.6 m^2 each) in actively (initially 3–16 years old) and 21 clusters of 63 plots in passively restored forests (initially 16 years old) in Kibale National Park, western Uganda. Seedlings were also measured in nearby old-growth forests in 3 clusters of 5 plots in 2014. We determined species diversity, richness and abundance per plot, and species composition as measures of seedling colonization in restored and old-growth forests. We found that diversity, richness, and abundance of seedlings were significantly higher in passively than actively restored forests. Diversity and richness, but not abundance significantly increased between sampling years and with restoration age. Distance from old-growth forests did not significantly affect diversity, richness and abundance. Species composition of actively and passively restored forests was different from that of old-growth forests after 19 years since restoration started. Our results show that passive restoration should be the preferred method for recovering afrotropical forests, and highlight the effect of continued management on biodiversity of restored forests.

Key words: biodiversity, chronosequence, natural regeneration, restoration plantings, seed sources, self-sustainability of forests

Implications for Practice

- Both active and passive restoration facilitate tropical forest recovery, but passively restored forests may be more self-sustaining from the perspective of woody seedling colonization, when biotic and abiotic conditions are favorable for it.

- Additional interventions such as replanting may be implemented to increase native seedling diversity, richness and abundance in actively restored forests, if restoration budgets can support such interventions.

- Species composition of restored forests may take decades to become similar to reference forests, even when close to seed source from old growth forests.

Introduction

Tropical forests cover about 7% of the world's total land area, possess much of the earth's biodiversity and sequester large amounts of carbon (Pattanayak & Sills 2001). They support livelihoods of millions of forest-dependent people through subsistence use of products such as fuelwood, food, fodder, building materials, and medicinal plants (Rasmussen et al. 2017). However, most forest loss occurs in the tropics and estimates show that tropical forest loss increased by 2,101 km^2/year between 2000 and 2012 (Hansen et al. 2013). Deforestation and forest degradation caused by human activities such as agricultural expansion, settlement, and logging are the main causes of tropical forest loss (Giam 2017). Tropical forest loss has major implications for carbon emissions, biodiversity as well as for human occupants. Restoration provides opportunities to counteract forest loss and recover ecosystem functions, including components of biodiversity (Rey Benayas et al. 2009).

Restoration is an intentional activity to recover degraded or damaged ecosystems (SER 2004). Conservation initiatives call for large-scale forest restoration to offset decades of rapid forest loss (Crouzeilles et al. 2017). For example, the Bonn Challenge is a global initiative to restore 350 million ha of forests worldwide by 2030 (IUCN 2011). It is an implementation platform for international commitments such as the CBD Aichi Target 15 to sustain life on earth, UNFCCC REDD+ goal of reducing greenhouse gas emissions, and Rio+20 land degradation neutrality goal of reversing land degradation. Regional initiatives include the 20x20 effort to restore 20 million ha of forests in Latin America and the Caribbean by 2020 (WRI 2017a), and AFR100 that aims to restore 100 million ha in Africa by 2030 (WRI 2017b). These global and regional initiatives could support restoration of tropical forests either actively or passively.

Active restoration generally involves planting of seedlings or direct sowing, mainly native species (Holl & Aide 2011). Active restoration is prioritized in highly modified landscapes, where human activities such as long history of fire, intensive crop production, livestock grazing and other factors reduced local and landscape resilience (Melo et al. 2013). In such conditions soil seed banks of native species are depleted and seed rain reduced due to dispersal limitations. Passive restoration encompasses, for example, control of livestock grazing and weeds, and protection against fire to facilitate natural regeneration in abandoned sites (Morrison & Lindell 2011). Passive restoration is preferred where disturbance has been light or short lived, natural communities are resilient, and there are no major barriers to forest recovery. Compared to active restoration, passive restoration is considered an inexpensive alternative which requires less technical expertise (Zahawi et al. 2014). Both active and passive restoration methods are used to facilitate tropical forest restoration. According to the Relay Floristics Model of succession, trees and shrubs that initially establish in sites under active and passive restoration facilitate seedling colonization beneath their canopies by ameliorating microclimatic conditions (Mcclain et al. 2011).

The ultimate aim of restoration is to create a self-sustaining ecosystem (SER 2004). For any plant population to become resilient to perturbation, seedlings must colonize and make transition to older life stages (Zambrano et al. 2014). Given the high cost of restoring forests (Brancalion et al. 2016), self-sustainability of restored tropical forests is advocated. Seedling colonization in restored tropical forests contributes to such sustainability (Zambrano et al. 2014). Several factors such as time since restoration started (hereafter restoration age), restoration methods, and distance from seed sources affect seedling colonization in restored forests (Bertacchi et al. 2016). For instance, older restoration sites provide more roosting sites, cover from predators, and fruiting trees to seed-dispersing animals (Catterall et al. 2012), which increases seed rain and seedling colonization compared to younger sites. Actively restored sites displayed greater seedling colonization than passively restored sites in tropical Australia (Florentine & Westbrooke 2004) and Costa Rica (Zahawi et al. 2014). Old-growth forests (i.e., seed sources) in close proximity to restoration sites enhance movement of seed dispersers into restoration sites which results into more seedling colonization than where seed sources are located far away from restoration sites (Chazdon et al. 2009).

As the long-term success of forest restoration rests not just on recovery of tree and shrub layers but on all ecosystem components, including seedlings, the status of seedling colonization is an indicator of restoration success. Thus, evaluating restoration success should include assessing seedling colonization and how it is influenced by restoration age, restoration methods and proximity to seed sources. Knowledge of seedling colonization in restored and old-growth forests is important in ascertaining the potential of restored forests to persist indefinitely under prevailing environmental conditions, their biodiversity conservation role, and can guide choice of restoration methods. However, few studies have directly compared seedling colonization in actively and passively restored sites (e.g., Ruwanza et al. 2013; Carnevale & Montagnini 2002; Florentine & Westbrooke 2004) and none comes from tropical Africa. While some studies have compared seedling colonization among restoration ages in other tropical regions (e.g., Barbosa et al. 2009; Bertacchi et al., 2016), most studies considered short time periods, mostly one sampling date, and cannot detect temporal variations. Thus, our knowledge of seedling colonization in restored forests, and especially restored tropical African forests, is limited.

The aim of this work was to determine whether active or passive restoration methods provide the most suitable habitats for woody seedling colonization in a tropical moist forest in

Kibale National Park, western Uganda. We sought to; (i) compare seedling colonization in actively and passively restored forests, (ii) test effects of restoration age and distance from old-growth forests on seedling colonization, and (iii) test whether actively and passively restored forests have similar seedling species composition as old-growth forests. In addition, we assessed variation in seedling colonization between sampling years (i.e., 2011 and 2014) because we were interested in temporal changes in restoration sites during the sampling period.

We predicted that; (i) woody seedling colonization would be faster in actively than passively restored forests of the same age because of faster recovery under active restoration (Zahawi et al. 2014), (ii) seedling colonization would increase with restoration age due to improvement in microsite conditions as restoration sites mature (Barbosa et al. 2009), (iii) seedling colonization would decrease with increasing distance from old-growth forests because of lower seed arrival at longer distances compared to shorter distances (Souza & Batista 2004), and (iv) there would be more seedling colonization in restored sites in 2014 than 2011 because of temporal development of vegetation between sampling years. To test the predictions, we determined floristic metrics of species diversity, richness, abundance and composition which follow a predictable restoration trajectory over time as indicators of seedling colonization (Suganuma & Durigan 2014).

Methods

Study Area

Kibale National Park (795 km^2) lies in the Albertine Rift in western Uganda (00^{o}13′–00^{o}41′ N, 30^{o}19′–30^{o}32′ E). The park receives an average 1,750 mm of precipitation annually, with average daily temperatures ranging from 15.1–23.1^{o}C. The vegetation varies from ever-green and semideciduous forest in the north to grasslands and woodlands in the southwest, due to a decline in elevation from 1,590 m in the north to 900 m in the southwest (Jacob et al. 2017). The vertebrate community mainly consists of mammals and birds.

This study was conducted south of the park (Fig.1), where old-growth forests are moist semi-deciduous 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). In 1971, agricultural encroachers cleared about 10,000 ha of forests in the south. The forests that survived were mostly fragments along waterways. In 1992, encroachers were resettled outside the park. The formerly encroached areas became dominated by elephant grass (*Cenchrus purpureus* (Schumach.) Morrone) because regular fires spreading from nearby gardens prevented natural regeneration (UWA-FACE 2011).

In 1994, the Government of Uganda, through Uganda Wildlife Authority (UWA), and FACE Foundation started restoring forests as carbon offsets on formerly encroached areas (UWA-FACE 2011). Active and passive restoration methods were implemented. Active restoration involved planting of native tree species every year from 1995 to 2010, except in 2001. The restoration plantings were nursery-grown seedlings and wildings collected from intact forests. The main tree species planted were *Albizia* spp., *Bridelia micrantha* (Hochst.) Baill, *Croton* spp., *Shirakiopsis elliptica* (Hochst.) Esser, *Celtis* spp., and *Warburgia ugandensis* Sprague. Vegetative propagation by cuttings accounted for 5% of trees planted (UWA-FACE 2011). Planting sites were prepared by clearing elephant grass along 2 m wide trails spaced in a 5 x 5 m grid, and planting pits were dug every 5 m along trails at densities of 400 per ha. The planted area was divided into compartments of different sizes and weeding was carried out 2–3 times/year. In addition, fire breaks were cut between compartments, and fires were fought by

UWA. Passive restoration involved protection against fires and livestock grazing in 1995, to facilitate natural regeneration of native woody species. The size of actively and passively restored forests since restoration started was 3,996 and 2,593 ha respectively (Face the Future 2015).

The actively restored forests of different ages are geographically close to each other, with a 24-km maximum distance between the two most distant areas (Fig. 1). The passively restored forests are also close to each other with a distance of 19 km between the most distant areas. The forests restored actively and passively in 1995 are bordered by the old-growth forest. Small streams and highly diverse native forest fragments are scattered throughout the actively and passively restored forests.

Experimental Design

A regular sampling grid consisting of clusters of four permanent sampling plots with a spacing of 500 x 500 m (Fig. 2) was applied to compartments of actively restored forests and two old-growth forest compartments using Field Map technology (IFER 1994). The same grid consisting of clusters of three permanent sampling plots was applied to compartments of passively restored forests. Each sampling plot (2,000 m^2) consisted of four 500 m^2 circles, i.e., one key circle at the bottom left of each plot, and three other circles. The key circle contained a small eccentric subplot (12.6 m^2) located 8 m north from the key circle center, and a concentric internal circle (201.1 m^2). Woody seedlings (diameter < 5 cm and height > 10 cm) were measured in eccentric subplots and trees were recorded in all plots. Woody seedlings were counted, identified to species level, and diameter, height and origin (i.e., whether planted or from natural regeneration) were recorded. Species identification followed guides by Katende et al. (1995) and Eggeling

(1940). The same procedure was followed to sample vegetation in 2011 for actively and passively restored forests, and 2014 for actively and passively restored and old-growth forests. Data for each year was collected during the same period (February–May). We acquired the data from Face Foundation through a data sharing agreement. Table 1 shows the plots surveyed in study sites. Distance from old-growth forests or remnant forests to sampling plots in restored forests was estimated using local area maps and was confirmed by UWA staff.

Statistical Analysis

We calculated floristic metrics of species diversity (using Shannon–Wiener index), richness and abundance of woody seedlings per plot in actively and passively restored forests using R package *BiodiversityR* (Kindt & Coe 2015). We excluded planted seedlings from the analysis because we were interested in seedlings recruited after restoration started. To compare values of the floristic metrics among our sites, we fitted generalized linear mixed-effects models for each floristic metric as a response, with restoration methods, sampling year, restoration age, and distance from old-growth forests as fixed effects using *lme4* package in R version 3.4.4 for Windows (R Core Team 2017, Pinheiro & Bates 2000). For diversity, we fitted models with a Gaussian error structure and identity link function. For richness, we fitted models with a Poisson distribution of errors and log link function (Pinheiro & Bates 2000). For abundance, we fitted models with a negative binomial distribution of errors and log link function because of over dispersion (Zuur et al. 2013). We used a nested random effect structure following our hierarchical spatial design (plot nested within cluster nested within compartment). We used backward elimination, where we fitted initial models containing all candidate fixed effects and used likelihood ratio tests (LRT) to judge if their influence on the response was statistically significant ($p < 0.05$) (Pinheiro

& Bates 2000). Models with only one candidate predictor variable were tested against an intercept-only model. We checked model adequacy using validation techniques in Zuur et al. (2013), including residuals versus fitted values to verify homogeneity, QQ-plots and histograms of residuals to assess normality, and residuals versus each explanatory variable to check independence (Fig. S1–S6). Subset of data and candidate fixed effects differed between two sets of analyses as specified below.

Effect of restoration methods and sampling year on species diversity, richness and abundance of woody seedlings

The data in this set of analysis consisted of actively and passively restored forests that were 16 years old in 2011 and 19 years old in 2014. We controlled for effects of restoration age and distance from old-growth forests by comparing similarly aged actively and passively restored forests that were bordered by old-growth forests. To determine the relationship of diversity, richness and abundance of seedlings with restoration methods and sampling year, we fitted each covariate as a two–level factor variable, i.e., restoration methods (active vs. passive) and sampling year (2014 vs. 2011), and used LRT against an intercept-only model.

Effect of restoration age and distance from old-growth forests on species diversity, richness and abundance of woody seedlings

In this set of analysis, we used data on actively restored forests that were 3–16 years old in 2011 (and 6–19 years old in 2014). Passively restored forests were excluded from this analysis because they were all restored in 1995 yet we were interested in the effect of restoration age. There was no interaction between restoration age and distance from old-growth forests (Fig. S7).

To determine the relationship of diversity, richness and abundance of seedlings with restoration age and distance from old-growth forests, we fitted age and distance as continuous covariates, and sampling year as two–level factor variable, then used LRT against an intercept-only model.

Woody seedling species composition in restored and old-growth forests

We used data collected in 2014 to compare seedling species composition of old-growth forests and 19-year old actively and passively restored forests. We excluded the 2011 data from this analysis because they did not include old-growth forests. Species composition was analyzed using nonmetric multidimensional scaling (NMDS) ordination in R package *BiodiversityR* (Kindt & Coe 2015; R Core Team 2017). The NMDS was generated from a Bray-Curtis dissimilarity matrix based on whether species were shared among restored forests and old-growth forests. We used Bray-Curtis distances, calculated from differences in abundance of each species because our data consisted of species abundances (Kindt & Coe 2015). Abundance values were $\log_{10}$ (n+1) transformed to reduce the influence of highly abundant species. Sites that are close together in the NMDS graph are interpreted as being similar in species composition, while sites that are far apart are interpreted as containing different species. We calculated Similarity percentages (SIMPER) using R package *BiodiversityR* to determine the contribution of seedling species to dissimilarity among restored and old-growth forests.

Results

Effect of restoration methods and sampling year on species diversity, richness and abundance of woody seedlings

Passively restored forests had higher diversity (LRT: χ^2 = 5.23, *df* = 1, *p* = 0.02), richness (LRT: χ^2 = 7.52, *df* = 1, *p* = 0.01) and abundance of seedlings (LRT: χ^2 = 6.91, *df* = 1, *p* = 0.009) than similarly aged actively restored forests (Table S1). Diversity (LRT: χ^2 = 8.72, *df* = 1, *p* = 0.003) and richness of seedlings (LRT: χ^2 = 5.80, *df* = 1, *p* = 0.02) significantly increased between sampling years (Fig. 3, Table S1). There was no significant effect of sampling year on abundance of seedlings (LRT: χ^2 = 3.42, *df* = 1, *p* = 0.06, Table S1).

Effect of restoration age and distance from old-growth forests on species diversity, richness and abundance of woody seedlings

There was a significant positive effect of restoration age on diversity (LRT: χ^2 = 14.145, *df* = 1, *p* = <0.001, Fig. 3) and richness of seedlings (LRT: χ^2 = 11.295, *df* = 1, *p* = 0.001, Fig. 3). The abundance of seedlings was not significantly affected by restoration age (LRT: χ^2 = 3.125, *df* = 1, *p* = 0.077, Table S2). There was no significant effect of distance from old-growth forests on diversity (LRT: χ^2 = 1.296, *df* = 1, *p* = 0.255), richness (LRT: χ^2 = 2.516, *df* = 1, *p* = 0.113) and abundance of seedlings (LRT: χ^2 = 0.258, *df* = 1, *p* = 0.611, Table S2).

Effect of restoration methods on woody seedling species composition

The best ordination of species composition yielded a two-dimensional solution found after 200 iterations (final stress = 0.24). The NMDS ordination showed that the species composition of 19-year old actively and passively restored forests was markedly different from that of old-growth forests (Fig. 4). More plots in passively than actively restored forests had similar species composition to old-growth forests (Fig. 4). SIMPER analysis confirmed the result of NMDS, with a high degree of average dissimilarity from old-growth forests for actively (95.3%) and passively restored forests (87.7%). SIMPER analysis also confirmed that passively restored forests were slightly more similar to old-growth forests than actively restored forests. Seedling species which were more abundant in old-growth forests contributed most to dissimilarity between actively restored and old-growth forests, i.e., *Uvariopsis congensis* Robyns & Ghesq. (10%), *Blighia unijugata* Baker (9%), and *Tabernaemontana johnstonii* Pichon (5%) (Table S3). *U. congensis* (10%), *Funtumia africana* (Benth.) Stapf (9%) and *B. unijugata* (7%) contributed most to dissimilarity between passively restored and old-growth forests (Table S4).

Discussion

Effect of restoration methods on species diversity, richness and abundance of woody seedlings

Our results showed that diversity, richness and abundance of seedlings were significantly higher in passively than similarly aged actively restored forests. This implies that seedling colonization occurs faster in passively than actively restored forests, contrary to our prediction of faster colonization in active than passive restoration. Previous studies present mixed results, for example, passive restoration can have higher (Morrison & Lindell 2011), lower (Ruwanza et al. 2013) or similar seedling colonization to active restoration (Gilman et al. 2016).

Our observation of faster seedling colonization in passively than actively restored forests could be linked to seed removal, a process that describes both seed predation and dispersal (Vander Wall et al. 2005). Seed predation impedes seedling colonization (Holl et al. 2000) while dispersal improves colonization of seedlings (García et al. 2005). More recently, Ssekuubwa et al. (2017) showed that the rate of removal of seeds of woody species in our sites was higher for passively than actively restored forests. If the seed removal guild in our sites is composed of more seed dispersers than predators, then possibly more seeds reach suitable microhabitats for germination, and seedling predation is reduced which increases colonization in passively restored forests. Previous studies reported successful seedling colonization following seed removal in tropical forests (Hollander & Vander Wall 2004; Jansen & Forget 2001).

Our result of faster seedling colonization in passively than actively restored forests may be confounded by densities of legacy trees at the onset of restoration, and how restoration was implemented. Although actively and passively restored sites had similar land use history, it is possible that they differed in densities of legacy trees. Legacy trees facilitate forest recovery in Kibale (Jacob et al. 2017) but their densities at the onset of restoration were not known. Further, passive restoration in Kibale was initiated through colonization of opportunistic and locally adapted species, which leads to high diversity of native species (Chazdon & Guariguata 2016). Conversely, active restoration encompassed 21 species, yet such a low species number often lacks the full range of functional traits found in passive restoration (Chazdon & Guariguata 2016). The high diversity in passive restoration creates more resources for seed dispersers which facilitates seed arrival into suitable microhabitats for germination, thereby increasing seedling colonization (Crouzeilles et al. 2017). Besides, restoration often starts with experimenting seed/seedling sources, species mixtures, planting densities and tending regimes to inform subsequent activities (Murcia & Aronson 2014). Thus, actively restored sites may lag behind nearby passively restored sites because such factors hinder a predictable, unidirectional ecosystem response to restoration (Brancalion et al. 2016).

The faster seedling colonization in passively than actively restored forests probably shows that passive restoration should be the preferred method when conditions are favorable for it (Holl & Aide 2011). When there is no condition for natural regeneration, the unique method available is active restoration (Holl & Aide 2011). Besides, passive restoration has been shown to be a more cost effective method for recovering forests and biodiversity under favorable conditions (Chazdon & Guariguata 2016).

Effect of sampling year, restoration age and distance from old-growth forests on species diversity, richness and abundance of woody seedlings

There was a significant positive effect of sampling year and restoration age on diversity and richness implying that seedling colonization increases as restoration sites mature, consistent with our second and fourth predictions. However, the abundance of seedlings was not affected by sampling year and restoration age. Our results of a positive effect of sampling year and restoration age confirm the prediction of the successional theory that ecosystem attributes increase progressively with age, and support observations from previous studies (e.g., Bertacchi et al. 2016; Marques et al. 2014). For instance, Capers et al. (2005) found that diversity of seedlings increased with age in tropical forests in Costa Rica over a 5-year period for sites initially 5–26 years old. Similarly, diversity of seedlings increased overtime in a Costa Rican wet forest (Gilman et al. 2016). The positive effect of sampling year and restoration age on diversity and richness may be linked to modulation of microsite limitations to seedling colonization due to temporal development of restoration sites (Wijdeven & Kuzee 2000).

Plant populations may be seed-limited or microsite-limited which potentially reduces seedling colonization in restoration sites (Wijdeven & Kuzee 2000). Ssekuubwa et al. (2017)

showed that seed removal in our study sites was not influenced by restoration age. If we interpret seed removal as secondary seed dispersal (Vander Wall et al. 2005), then the seed removal rates reported by Ssekuubwa et al. (2017) could indicate a uniform availability of seeds for germination among restoration sites of different ages. Thus, seedling colonization in our sites may be more microsite-limited than seed-limited. As restoration sites mature, microsite limitations may be modulated which facilitates more seedling colonization in older than younger sites (Bertacchi et al. 2016), implying that microsites are a stronger limiting factor to seedling colonization in younger than older sites. The progressive increase of diversity and richness with age shown by this study, and other ecosystem components such as trees (Garcia et al. 2016), arthropods (Nyafwono et al. 2014) reported in previous studies highlight the biodiversity benefits of continued management of restored forests.

We found no significant effect of distance from old-growth forests on diversity, richness and abundance of seedlings, contrary to our third prediction. Our results are consistent with results from plantations in northern Australia (Keenan et al. 1997) and a tropical rainforest in Madagascar (Klanderud et al. 2009). The non-significant effect of distance from old-growth forests may be due to actively restored forests in this study being geographically close to each other, with a 24-km maximum distance between the two most distant areas which could facilitate a uniform movement of seed dispersing species among the sites.

Woody seedling species composition in restored and old-growth forests

NMDS ordination showed that species composition of actively and passively restored forests was markedly different from that of old-growth forests after 19 years since restoration started. This observation highlights the long recovery time for species composition of tropical forests. This view is supported by previous studies which showed long recovery time for species composition under passive restoration, for example, > 30 years in Costa Rica (Letcher & Chazdon 2009), and active restoration, for example, 40–70 years in Brazil (Suganuma & Durigan 2014). However, there were more plots in passively than actively restored forests that were similar to old-growth forests which possibly shows that restoration success is higher under passive relative to active restoration. Previous studies (e.g., Morrison & Lindell 2011; Crouzeilles et al. 2017) also found higher success in passively than actively restored tropical forests.

We conclude that active and passive restoration methods provide suitable habitats for colonization of woody seedlings which facilitates tropical forest recovery. Passive restoration seems to be better than active restoration, but it is possible under limited conditions. For sites which experienced severe or long-lived disturbance and there are dispersal limitations, passive restoration may fail so active restoration would be a more suitable method for restoring forests. Seedling colonization increased with restoration age which is consistent with successional trajectories of vegetation change patterns, and highlights the importance of continued management of restored forests for biodiversity conservation. Although this study was conducted in a single protected area, we believe that the results are representative of other protected areas abandoned by agricultural encroachers in the tropics, especially tropical Africa.

Further studies are necessary to examine how seedling colonization is linked to seed removal and microsite conditions under active and passive restoration, to further guide choice of restoration methods. Such studies should involve paired experimental comparisons of active and passive sites in the same location, with similar land use history and replicated across landscapes, in order to avoid a mismatch between sites that causes a positive site selection bias (Reid et al.

2018). We also recommend testing the effect of seedling colonization on tree establishment in restoration sites to understand its long term effects.

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Tables

Table 1. Study sites, restoration years, number of compartments, clusters and sampling plots at each site in Kibale National Park in western Uganda. Old-growth forests are of unknown size (N/A). The restored forests were sampled in 2011 and 2014 while old-growth forests were sampled in 2014.

Study sites	**Restoration year (area in ha)**	**Compartments**	**Clusters**	**Plots**
Actively restored forests	1995 (688.8)	8	15	60
	1996 (591.8)	7	11	44
	1997 (168.6)	1	3	12
	1998 (359.7)	2	4	16
	1999 (565.2)	2	12	48
	2000 (339.2)	2	6	24
	2002 (15.6)	1	1	4
	2003 (30.0)	1	1	4
	2004 (98.3)	2	3	12
	2005 (282.1)	5	6	24
	2006 (79.8)	2	3	12
	2007 (89.9)	1	3	12
	2008 (115.5)	2	3	12
Passively restored forests	1995 (2593)	4	21	63
Old-growth forests	N/A	2	3	5
Total		**42**	**95**	**352**

Figure captions

Figure 1. Monitoring clusters in actively and passively restored forests and old-growth forest in Kibale National Park, western Uganda. The actively restored forests are of different planting years (i.e., 1995–2010). Passively restored forests are of a single restoration year (i.e., 1995). The open space below the 1999 restoration plantings is a protected grassland within the park being colonized by trees and shrubs. The open spaces among the restored forests are remnant forests.

Figure 2. The monitoring cluster (I) consisted of four permanent sampling plots in compartments of actively restored forests (or three permanent sampling plots in compartments of passively restored forests) in Kibale National Park, western Uganda. Each sampling plot was composed of four 500 m^2 circles. Plot 3 was rotated because of an obstacle (e.g., a road, cliff or river). Woody seedlings (diameter < 5 cm and height > 10 cm) were measured in eccentric subplots and trees were recorded in all plots.

Figure 3. Predicted values of species diversity, richness and abundance of woody seedlings in actively and passively restored forests sampled in 2011 (red bars) and 2014 (blue bars) in Kibale National Park, western Uganda. Error bars show 95% confidence intervals for the mean (see Table S1). Differences were considered significant when $p < 0.05$.

Figure 4. Predicted species diversity and richness of woody seedlings plotted versus age of restored forests in Kibale National Park, western Uganda. Dotted lines show 95% confidence intervals for the mean (see Table S2). Note the exponential relationship between richness and restoration age, a consequence of the log link function.

Figure 5. Axes 1 (Dim1) and 2 (Dim2) of the two-dimensional NMDS ordination of woody seedling species composition for actively and passively restored forests and old-growth forests in Kibale National Park, western Uganda (Note that five plots were measured in the old-growth forest).

Figures

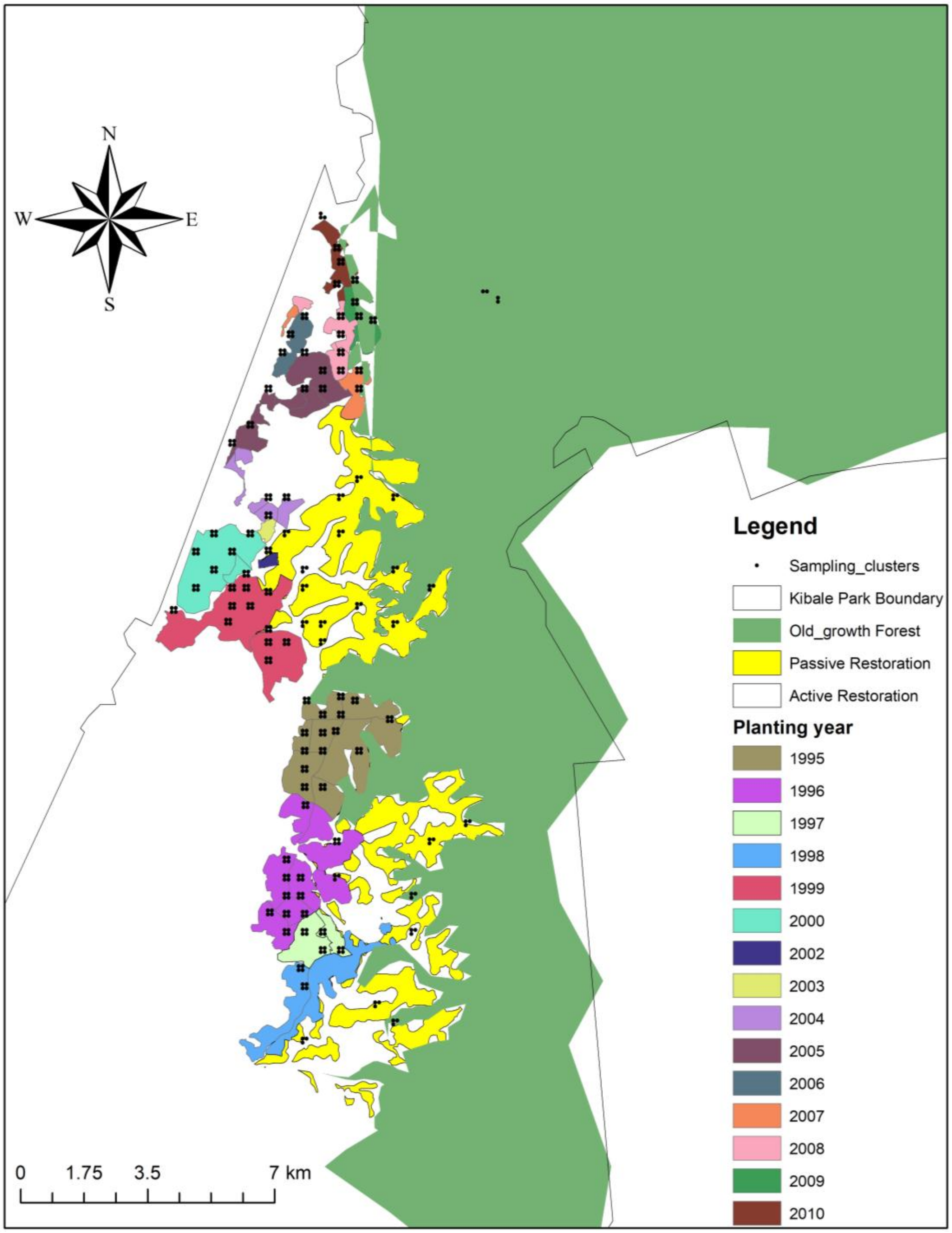
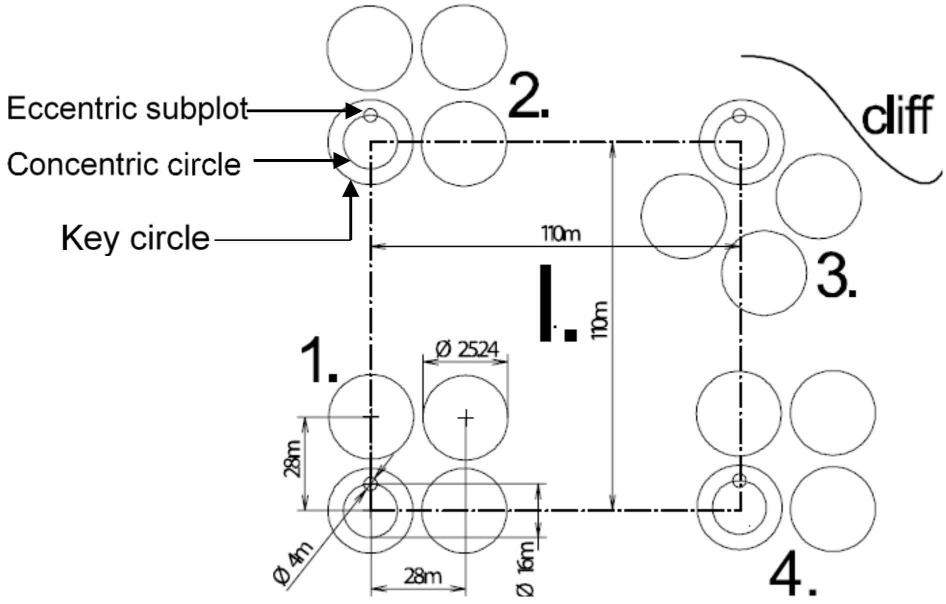


Figure 1.



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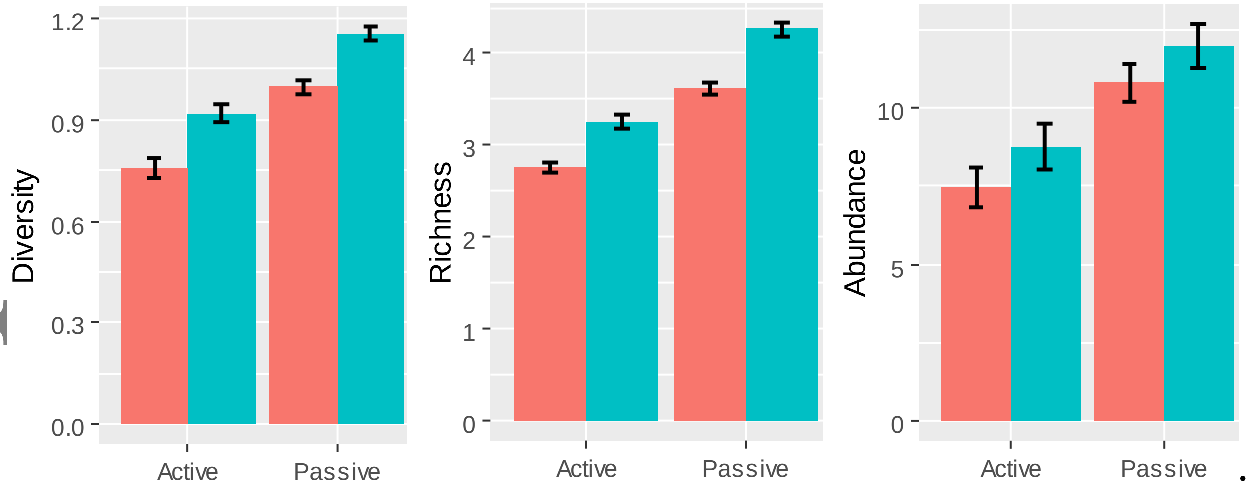
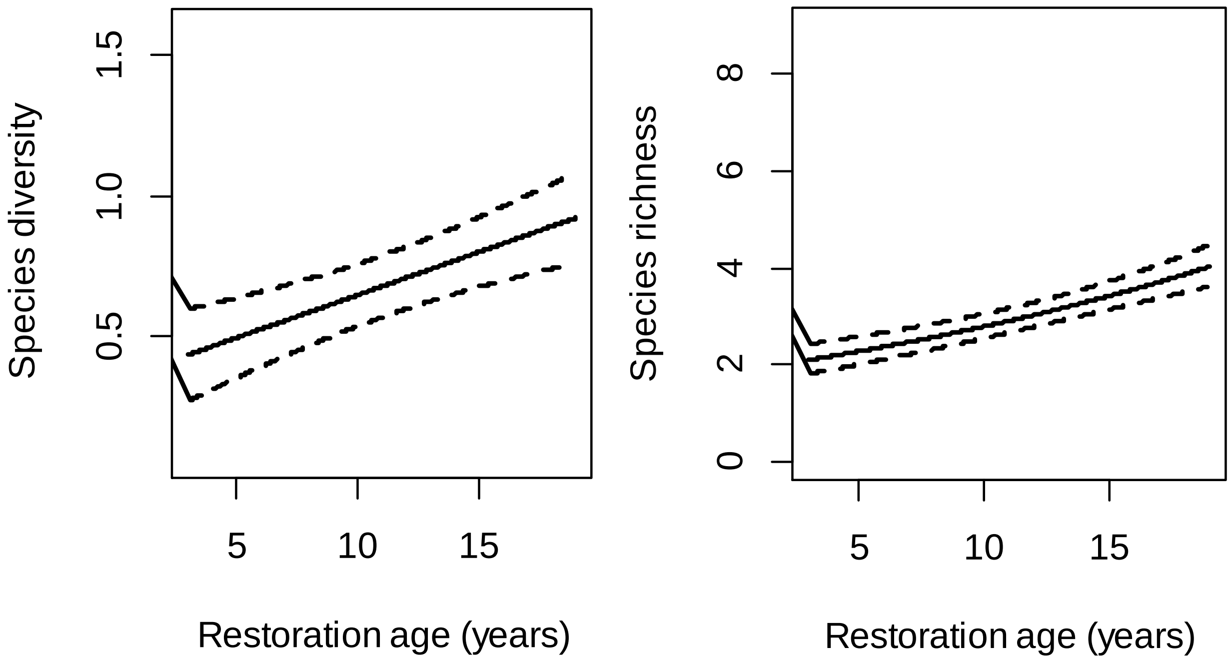


Figure 3



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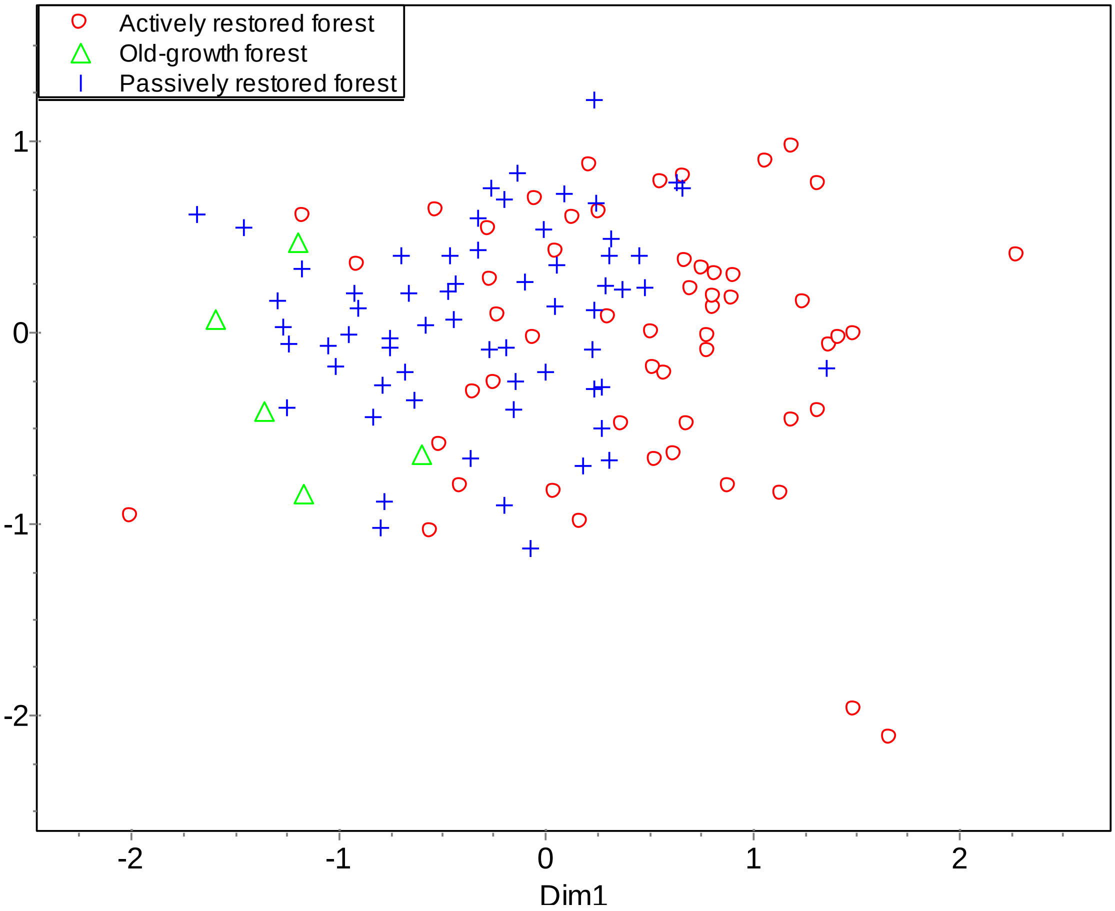

Figure 5.