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Recovery of seedling community attributes during passive restoration of a tropical moist forest in Uganda

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Abstract

Aim: There has been a debate about the effectiveness of passive restoration for recovering tropical forests, but few studies quantify the success of passive restoration. The aim of this study was to better understand tropical forest succession under a passive restoration scenario. We compared floristic and functional attributes of seedlings in a passively restored and an old-growth forest, and assessed the effect of restoration age and distance from the old-growth forest on seedling attributes.

Location: Kibale National Park, western Uganda.

Methods: We measured seedlings in a passively restored and an old-growth forest in 2011, 2014 and 2017. We determined species diversity, structure and composition and searched the literature for functional traits. We used generalized linear mixed-effects models to compare seedling attributes between the restored and old-growth forest and determine the influence of restoration age and distance from the old-growth forest.

Results: Seedling species abundance, evenness, basal area and height were similar between the restored and old-growth forest. Wood density and abundance of seedlings of different dispersal modes, habitat types, fruit size categories, and regeneration strategies were also similar between the restored and old-growth forest. However, richness, diversity and composition of seedlings were different. We found a positive effect of restoration age on species abundance and abundance of non-zoochorous, medium-fruited, forest-dependent, non-pioneer light demander and shade-tolerant species, and a negative effect on evenness, wood density, abundance of pioneers and compositional dissimilarity. Basal area of seedlings and the abundance of zoochorous and forest-dependent species declined while compositional dissimilarity increased with distance from the old-growth forest.

Conclusions: Our results provide empirical evidence on the potential of passive restoration to recover the structure and functionality of tropical forests in a relatively short period of time. We demonstrate that the effect of restoration age and distance from the old-growth forest is not straightforward and depends on the attributes measured.

KEYWORDS

disturbance, functional composition, natural regeneration, restoration success, species composition, successional trajectory, tropical forests

1 | INTRODUCTION

Restoration is an essential strategy to reverse tropical forest loss (Chazdon & Uriarte, 2016), and achieve sustainable development goals on climate change, poverty eradication, food security and biodiversity conservation (UNEP, 2019). The UN General Assembly declared 2021–2030 to be the decade on ecosystem restoration. The decade will accelerate global and regional restoration goals (UNEP, 2019). The Bonn Challenge is a global goal to restore 350 million ha of degraded land by 2030 (IUCN, 2011). Regional goals include the African Forest Landscape Restoration Initiative that aims to restore 100 million ha by 2030 (WRI, 2017a), and the Initiative 20 × 20 in Latin America that aims to restore 20 million ha by 2020 (WRI, 2017b). Achieving global and regional restoration goals could mitigate tropical forest loss and generate USD 9 trillion in ecosystem services (UNEP, 2019).

A major impediment to large-scale restoration is financial cost (Parrotta et al., 1997), and so it is critical to identify cost-effective techniques (Uebel et al., 2017). Restoration encompasses active and passive techniques. Active restoration involves using restoration plantings to facilitate recovery (Cruz-Alonso et al., 2019). It is recommended for highly modified landscapes, with a long history of fire, intensive cropping and livestock grazing (Holl & Aide, 2011). On the other hand, passive restoration involves creating suitable conditions for natural regeneration by fencing against livestock grazing or suppressing fires and exotic species (Mansourian & Dudley, 2005). It is suitable where disturbance is light and natural communities are resilient (Holl & Aide, 2011). Stimulating natural regeneration generally entails lower financial cost than active restoration, making passive restoration attractive for large-scale restoration (Holl & Aide, 2011). Prioritizing passive restoration in areas suitable for natural regeneration allows limited resources (e.g. funds, labor and seeds) to be more effectively allocated to areas where active restoration is needed (Chazdon et al., 2017).

Several studies report widespread application of passive restoration (Shoo & Catterall, 2013; Meli et al., 2017), and therefore, it is imperative to assess whether passive restoration can recover degraded forests. A useful way to evaluate restoration success is by comparing attributes of restored forests through time with old-growth forests (Suganuma & Durigan, 2014). Recovery of floristic diversity, structure, composition and functional traits can occur at different rates. For instance, species abundance and richness take shorter time to recover than composition (Crouzeilles et al., 2016; Meli et al., 2017). Early studies show that as succession proceeds, restored forests may converge (i.e., have similar attributes) (White & Walker, 1997) or diverge from old-growth forests (Hobbs et al., 2009). In addition, the distance from seed sources can have a negative effect on attributes of restored forests, thereby influencing recovery (Wijdeven & Kuzee, 2000). Given that passive restoration is gaining momentum across the world, research is needed to understand its implications for future forests.

Few studies quantify the success of passive restoration (Uebel et al., 2017). Moreover, a paucity of restoration studies combine floristic and functional attributes as indicators of success (e.g. Suganuma & Durigan, 2014). Functional trait information such as wood density, dispersal modes, habitat types and successional strategies, when used together with diversity and structural attributes, can provide comprehensive evaluations of restoration success (Derhe et al., 2016). On the other hand, restoration has traditionally targeted recovery of trees and shrubs because they strongly influence forest products and services (Davies & Christie, 2001; Harris et al., 2012). Until recently, little regard has been given to seedlings, though they contribute substantially to biodiversity (Bartels & Chen, 2010) and forest sustainability (Zambrano et al., 2014).

Accordingly, we assessed restoration success using 12 seedling attributes associated with biodiversity, structure, composition and functionality of passively restored forests. We compared attributes between the restored and old-growth forest. In addition, we examined the effect of restoration age and distance from the old-growth forest on seedling attributes in the restored forest (Chazdon et al., 2017). We predicted that: (a) seedling attributes would recover at different rates since biodiversity, structure and ecosystem function do not necessarily follow similar trajectories (Guariguata & Ostertag, 2001); (b) increasing restoration age leads to an increase in species diversity, structural complexity, functional traits and similarity of species composition between the restored and old-growth forest; and (c) seedling attributes would decline with increasing distance from the old-growth forest due to seed and microsite limitations at longer distances (Duncan & Duncan, 2000; Mesquita et al., 2001).

2 | METHODS

2.1 | Study area

This study took place in Kibale National Park (795 km^2), which lies in the Albertine Rift in western Uganda (00°13′–00°41′ N, 30°19′–30°32′ E; Omeja et al., 2011). The park receives a mean annual rainfall of 1,750 mm, with mean daily temperatures ranging from 15.1°C to 23.1°C. Elevation ranges from 1,590 m in the north to 900 m in the southwest which causes a variation in vegetation from evergreen and semi-deciduous forest in the north to grasslands and woodlands in the southwest. The Kibale animal community consists of several species of small, medium and large herbivores (Omeja et al., 2016), birds (Dranzoa, 1998) and arthropods. The study sites are located in the southern part of the park, where the old-growth forest is moist semi-deciduous with *Celtis* spp., *Chrysophyllum* spp. and *Cynometra alexandri* as climax species (Zanne & Chapman, 2005). The old-growth forest is a natural forest and it was selectively logged by pit-sawyers, extracting about 10% of timber trees per ha, but this has had little impact on the forest (Chapman & Lambert, 2000).

2.2 | Restoration interventions

In 1971, agricultural encroachers cleared about 120 km^2 of forests south of the park (Chapman & Lambert, 2000). In 1992, encroachers abandoned the park and the formerly encroached areas became dominated by elephant grass (*Cenchrus purpureus*) because frequent fires set by poachers or spreading into the park from adjacent subsistence farms prevented natural regeneration (Omeja et al., 2011). In 1995, the Government of Uganda, through Uganda Wildlife Authority (UWA), and Face the Future, a Dutch non-governmental organization, started restoring forests as carbon offsets using passive techniques in areas where natural regeneration was feasible (Emmer, 1998). Passive restoration encompassed protecting against fires by controlling poaching, constructing fire lines and monitoring fire incidences by using watch towers (Figure 1a). Fencing (Figure 1b) and trenching which were carried out to control crop raiding by elephants also guarded against livestock grazing in regenerating areas. In areas where natural regeneration was not feasible, active restoration was implemented through planting native species (Omeja et al., 2011). The forest under passive restoration is bordered by the old-growth forest to the east and actively-restored forests to the west. Small streams and remnant forests are scattered within the restored forests. In general, restoration has successfully re-established a forest community in formerly encroached areas (Omeja et al., 2016). Despite the low tree species richness in these successional forests they support a high mammalian diversity (Omeja et al., 2016).

2.3 | Experimental design

A regular sampling grid consisting of clusters of three permanent sampling plots with a spacing of 500 m × 500 m (Figure 2) was applied to three sites of forests undergoing passive restoration using field-map technology (IFER, 1994). The same grid consisting of clusters of four permanent sampling plots was applied to two old-growth forest sites. 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 (Figure 2). The key circle contained a small eccentric subplot (12.6 m^2) located 8 m north from the center of the key circle and a concentric internal circle (201.1 m^2). Seedlings were recorded in the small eccentric subplot.

2.4 | Inventory of seedling assemblages

Seedling inventory was carried out in 2011, 2014 and 2017 during the same period (Feb–May) for each year. Seedlings (diameter < 5 cm and height > 10 cm) were counted, identified to species level following Eggeling (1940), and diameter and height were recorded. For species that could not be identified in the field, we submitted voucher specimens for identification at the Makerere University Herbarium. The same procedure was followed to sample seedlings in the restored forest plots (2011, 2014 and 2017) and old-growth forest plots (2011 and 2017). Sixty-three plots were sampled in the restored forest and five plots in the old-growth forest. The distance from sampling plots in the restored forest to the old-growth forest was estimated using local-area maps and was confirmed by UWA staff.

2.5 | Functional traits

Wood density (g/cm^3) of seedling species was taken from the Tree Functional Attributes and Ecological Database (TFAED) (Harja et al., 2019) and the African Wood Density Database (AWDD) (Carsan et al., 2012), and assigned to stems at species level where possible, otherwise stems were given a family-level mean density (Fauset et al., 2012). TFAED accounted for 30.7% while AWDD for 69.3% of the species. Species- and family-level values were used for 94.9% and 5.1% of stems, respectively. Focusing on sources from Uganda, we searched the literature for dispersal modes, fruit sizes, habitat types and regeneration strategies of seedling species. Dispersal modes were categorized as zoochorous

FIGURE 1 Kibale National Park, western Uganda: (a) a wooden fire watch tower used to detect fire incidences; and (b) a wooden fence in the foreground preventing livestock from accessing naturally-regenerating seedlings and trees in the background

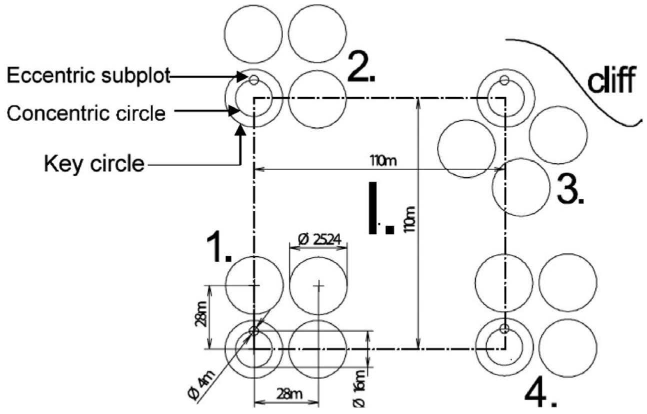


FIGURE 2 The monitoring cluster (I) consisted of three permanent sampling plots (2,000 m^2 each) in the restored forest or four permanent sampling plots in the old-growth forest in Kibale National Park, western Uganda. Each plot comprised four 500-m^2 circles. Each 500-m^2 circle contained a small eccentric subplot for measuring seedlings. Plot 3 was rotated in case an obstacle (e.g., a road, cliff or river) was encountered

(animal-dispersed) or non-zoochorous (wind or other abiotic vector) following Eggeling (1940). Fruit size was based on maximum length or diameter, whichever is bigger, and categorized as small (<1 cm), medium (1–3 cm) and large (3.1–>5.0 cm; Babweteera & Ssekuubwa, 2017). Regeneration strategies were defined as pioneers (unable to establish in closed-forest shade), non-pioneer light demanders (seedlings are present in the understorey but require higher light environments to reach adult size) or shade-tolerants (able to establish in closed-forest shade) following Eggeling (1940) and Synnott (1985); classification was possible for 99.1% of stems. Habitat type was classified as open habitat (occurring in woodland, grassland, rocky places, bush/thickets and swamp), forest-dependent (occurring in forest interior, edge, and/or riverine forest), or forest non-dependent (occurring in at least one of the open habitats and at least one of the forested habitats; Lwanga, 1996). Only eight individuals belonged to open habitat (woodland), so this habitat type was not considered for further analysis.

2.6 | Statistical analysis

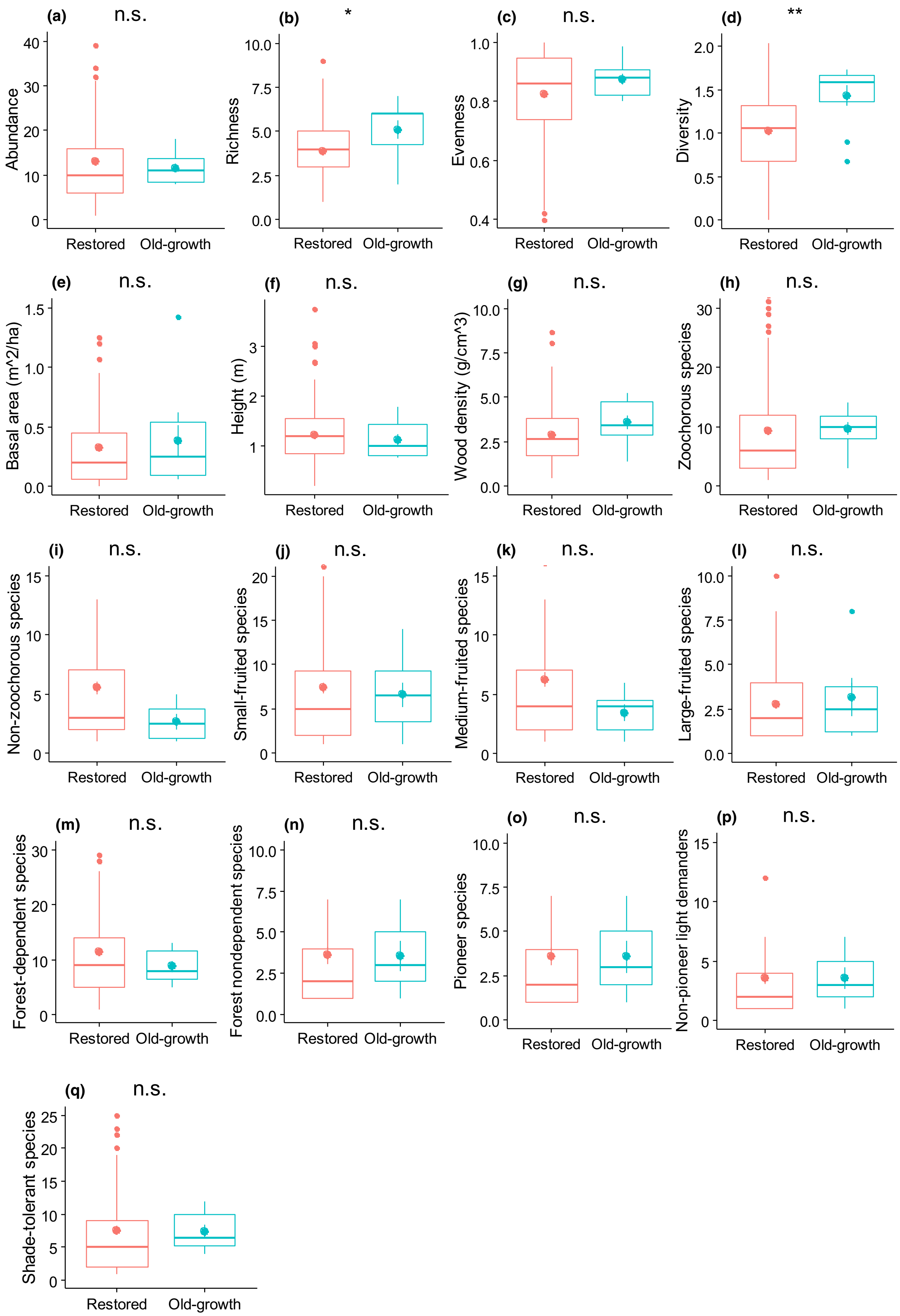
Statistical analysis was done in R version 3.4.4 for Windows (R Core Team, 2018). We calculated restoration age as the difference between sampling year (2011, 2014 and 2017) and the year restoration activities started, i.e., 1995. To assess the completeness of our seedling survey in the restored and old-growth forest, we generated sample-based species accumulation curves using the *iNEXT* package (Appendix S1; Chao et al., 2014). We computed species abundance, richness, evenness (Pielou's Index), and diversity (Shannon–Wiener Index) per plot of the restored and old-growth forest using the *vegan* package (Oksanen et al., 2016). We calculated basal area (m^2/ha), assuming a circular shape of the cross-section of seedling stems (Torres & Lovett, 2013), average height and total wood density (g/cm^3) per plot. We also calculated the sum of abundance per plot of seedlings of different dispersal modes, fruit size categories, habitat types and regeneration strategies. We explored differences among plots based on the seedling attributes using Principal Components Analysis (Zuur et al., 2007).

To compare seedling attributes between forest types and determine the effect of restoration age and distance from the old-growth forest, we fitted generalized linear mixed-effects models (glmm) with each attribute as a response, and forest type, restoration age, and distance as fixed effects using the *lme4* package (Pinheiro & Bates, 2000). To account for among- and within-sites differences in environmental conditions, we included a nested random effect following the hierarchical spatial design of this study, i.e., plot nested within cluster nested within site. Random effects were selected by comparing nested models with and without a random effect using Akaike's Information Criterion (AIC). Models with the full random effect structure were selected because they had the lowest AIC values (Appendix S2). For evenness, diversity, basal area, height and wood density models, we used a Gaussian error structure and identity link function (Pinheiro & Bates, 2000). For species abundance, richness, and abundance of seedlings belonging to different dispersal modes, fruit size categories, habitat types and regeneration strategies, we used a Poisson distribution of errors (Pinheiro & Bates, 2000). Text depictions of statistical models can be found in Appendix S2. We checked model adequacy using validation techniques in Zuur et al. (2013), including residuals vs fitted values to verify homogeneity, quantile–quantile (Q–Q) plots to assess normality, and residuals vs each explanatory variable to check independence (Appendices S3, S4). Subset of data and candidate fixed effects differed between two sets of analyses as specified below.

2.6.1 | Comparing species diversity, structure and functional traits between the restored and old-growth forest

To compare attributes between the restored and old-growth forest, we fitted glmm with each attribute as a response and forest type (i.e., restored vs old-growth) as the only fixed effect (Pinheiro & Bates, 2000). The nested random effect structure comprised plot ($n = 68$) nested within cluster ($n = 24$) nested within site ($n = 6$). The statistical significance ($p < 0.05$) of forest type in each glmm was tested using the likelihood ratio test (*LRT*; Crawley, 2013).

FIGURE 3 Boxplots for observed values of seedling attributes in Kibale National Park, western Uganda: (a) species abundance; (b) richness; (c) evenness; (d) diversity; (e) basal area; (f) height; (g) wood density, and abundance of: (h) zoochorous; (i) non-zoochorous; (j) small-fruited; (k) medium-fruited; (l) large-fruited; (m) forest-dependent; (n) forest non-dependent; (o) pioneer; (p) non-pioneer light demander; and (q) shade-tolerant species, each measured per plot in the restored and old-growth forest. Asterisks indicate significance levels (**, $p < 0.001$; *, $p < 0.05$), n.s., no significant difference


(a) n.s.
Abundance
0 10 20 30 40
(b) *
Richness
0.0 2.5 5.0 7.5 10.0
(c) n.s.
Evenness
0.4 0.6 0.8 1.0
(d) **
Diversity
0.0 0.5 1.0 1.5 2.0
(e) n.s.
Basal area (m^2/ha)
0.0 0.5 1.0 1.5
(f) n.s.
Height (m)
1 2 3
(g) n.s.
Wood density (g/cm^3)
0.0 2.5 5.0 7.5 10.0
(h) n.s.
Zoochorous species
0 10 20 30
(i) n.s.
Non-zoochorous species
0 5 10 15
(j) n.s.
Small-fruited species
0 5 10 15 20
(k) n.s.
Medium-fruited species
0 5 10 15
(l) n.s.
Large-fruited species
0.0 2.5 5.0 7.5 10.0
(m) n.s.
Forest-dependent species
0 10 20 30
(n) n.s.
Forest nondependent species
0.0 2.5 5.0 7.5 10.0
(o) n.s.
Pioneer species
0.0 2.5 5.0 7.5 10.0
(p) n.s.
Non-pioneer light demanders
0 5 10 15
(q) n.s.
Shade-tolerant species
0 5 10 15 20 25
Restored
Old-growth

2.6.2 | Effect of restoration age and distance from the old-growth forest on species diversity, structure and functional traits

To determine the effect of restoration age and distance from the old-growth forest, we fitted glmm with each attribute as a response, while age and distance as continuous fixed effects (Pinheiro & Bates, 2000). We excluded the old-growth forest from this analysis. The random effect structure comprised plot ($n = 63$) nested within cluster ($n = 24$) nested within site ($n = 4$). The statistical significance of age and distance in each glmm was tested using *LRT* (Crawley, 2013).

2.6.3 | Species composition of seedlings in the restored and old-growth forest

To compare species composition of seedlings between the restored and old-growth forest, we computed the Bray–Curtis dissimilarity index and visualized it using non-metric multidimensional scaling ordination via the metaMDS function in the *vegan* package (Oksanen et al., 2016). We used permutational multivariate analysis of variance (PERMANOVA) to test for compositional differences between the forest types via the adonis function. We used similarity percentages (SIMPER) to determine the contribution of seedling species to compositional dissimilarity between the forest types. To assess the effect of restoration age and distance from the old-growth forest on compositional dissimilarity of seedlings between the restored and old-growth forest, we fitted glmm with the Bray–Curtis index (first axis of the NMDS) as a response, and restoration age and distance as continuous fixed effects (Pinheiro & Bates, 2000). The random-effect structure comprised plot ($n = 63$) nested within cluster ($n = 24$) nested within site ($n = 4$). The statistical significance of age and distance in the glmm was tested using *LRT* (Crawley, 2013).

3 | RESULTS

We recorded 2,431 seedlings (diameter < 5 cm and height > 10 cm) across 70 species in 63 plots in the restored forest and 113 seedlings across 26 species in five plots in the old-growth forest (Appendix S5). *Uvariopsis congensis* was the most abundant species with 616 and 22 stems in the restored and old-growth forest, respectively. We recorded 44 and seven species restricted to the restored and old-growth forest, respectively. Sample-based species accumulation curves showed that the sampling effort was adequate to characterize the seedling community in the restored forest but the old-growth forest may harbor more species than actually sampled (Appendix S1). Data exploration using Principal Components Analysis showed no unique differences in seedling attributes among plots within the restored and old-growth forest (Appendix S1).

3.1 | Comparing seedling attributes in the restored and old-growth forest

Species abundance per plot (*LRT*: $\chi^2 = 0.004$, $df = 1$, $p = 0.952$; Figure 3a) and evenness (Pielou's Index) per plot ($\chi^2 = 0.869$, $df = 1$, $p = 0.351$; Figure 3c) were similar between the restored and old-growth forest (Appendix S6). Species richness per plot ($\chi^2 = 4.969$, $df = 1$, $p = 0.026$; Figure 3b) and diversity (Shannon–Wiener Index) per plot ($\chi^2 = 8.370$, $df = 1$, $p = 0.004$; Figure 3d) were lower in the restored than in the old-growth forest (Appendix S6). The basal area per plot ($\chi^2 = 0.179$, $df = 1$, $p = 0.672$; Figure 3e) and average height per plot ($\chi^2 = 0.360$, $df = 1$, $p = 0.549$; Figure 3f) did not differ between the restored and old-growth forest (Appendix S6).

There was no significant variation in functional traits between the restored and old-growth forest. Wood density per plot ($\chi^2 = 3.784$, $df = 1$, $p = 0.052$; Figure 3g) was not different between the restored and old-growth forest (Appendix S6). The restored forest had similar abundance per plot of zoochorous ($\chi^2 = 0.108$, $df = 1$, 0.743; Figure 3h) and non-zoochorous species as the old-growth forest ($\chi^2 = 0.687$, $df = 1$, $p = 0.407$; Figure 3i). The abundance per plot of seedlings of small-fruited ($\chi^2 = 0.001$, $df = 1$, $p = 0.973$; Figure 3j), medium-fruited ($\chi^2 = 0.646$, $df = 1$, $p = 0.422$; Figure 3k) and large-fruited species ($\chi^2 = 0.199$, $df = 1$, $p = 0.656$; Figure 3l) was not different between the restored and old-growth forest (Appendix S6). The abundance per plot of forest-dependent ($\chi^2 = 0.553$, $df = 1$, $p = 0.457$; Figure 3m) and forest non-dependent species ($\chi^2 = 0.249$, $df = 1$, $p = 0.648$; Figure 3n) was similar between the restored and old-growth forest (Appendix S6). There was no significant difference in the abundance per plot of pioneers ($\chi^2 = 2.130$, $df = 1$, $p = 0.144$; Figure 3o), non-pioneer light demanders ($\chi^2 = 0.174$, $df = 1$, $p = 0.677$; Figure 3p) and shade-tolerants ($\chi^2 = 0.067$, $df = 1$, $p = 0.797$; Figure 3q) between the restored and old-growth forest (Appendix S6).

Species composition of seedlings (Bray–Curtis pairwise distances) varied similarly within the restored and old-growth forest ($F = 1.480$, $df = 1$, $p = 0.228$) but differed significantly between the forest types (adonis: $r^2 = 0.029$, $df = 1$, $p = 0.028$; Figure 6a). SIMPER showed that *Uvariopsis congensis* (16%) and *Funtumia africana* (11%), which were more abundant in the restored forestm and *Blighia unijugata* (9%) and *Teclea nobilis* (5%), which were more abundant in the old-growth forest, contributed most to percentage dissimilarity between the forest types (Appendix S7).

3.2 | Effect of restoration age and distance from the old-growth forest

Species abundance (Table 1; Figure 4a) and the abundance of non-zoochorous (Table 1; Figure 4d), medium-fruited (Table 1; Figure 4e), forest-dependent (Table 1; Figure 4f), non-pioneer light demander (Table 1; Figure 4h) and shade-tolerant species (Table 1; Figure 4i) all showed a significant positive relationship with restoration age (Appendix S8). There was a significant negative relationship between

TABLE 1 Effect of restoration age and distance from the old-growth forest on seedling attributes in the restored forest in Kibale National Park, western Uganda

	Restoration age		**Distance from old-growth forest**	
Seedling attributes	**LRT, *df* = 1**	***p***	**LRT, *df* = 1**	***p***
Abundance	12.897	<0.001	1.946	0.163
Richness	0.103	0.749	2.107	0.147
Evenness	3.868	0.049	1.329	0.249
Diversity	1.867	0.172	1.042	0.307
Basal area	0.072	0.788	4.378	0.036
Height	0.007	0.932	1.728	0.189
Wood density	8.790	0.003	3.047	0.081
Zoochorous species abundance	0.628	0.428	3.824	0.048
Non-zoochorous species abundance	27.783	<0.001	1.873	0.171
Small-fruited species abundance	1.544	0.214	2.711	0.100
Medium-fruited species abundance	53.669	<0.001	1.944	0.163
Large-fruited species abundance	0.005	0.943	0.429	5.513
Forest-dependent species abundance	12.589	<0.001	3.487	0.026
Forest non-dependent species abundance	0.689	0.407	1.037	0.309
Pioneer species abundance	14.915	<0.001	0.382	0.537
Non-pioneer light demander species abundance	23.601	<0.001	1.879	0.171
Shade-tolerant species abundance	17.206	<0.001	0.748	0.387
Compositional similarity	8.457	0.004	4.865	0.027

Note: Abbreviations: LRT, likelihood ratio test (χ^2); *df*, degrees of freedom.

restoration age and evenness (Table 1; Figure 3b), wood density (Table 1; Figure 3c), abundance of pioneers (Table 1; Figure 3g) and compositional dissimilarity (Table 1; Figure 6b; Appendix S8). Species richness, diversity, basal area, height and the abundance of zoochorous, small-fruited, large-fruited and forest non-dependent species all did not vary significantly with restoration age (Appendix S8).

The minimum and maximum distances from the old-growth forest to plots in the restored forest were 0.5 and 5.7 km, respectively. There was no significant relationship between distance from the old-growth forest and species abundance, richness, evenness, diversity and height of seedlings (Table 1; Appendix S8). Basal area (Table 1; Figure 5a) and the abundance of zoochorous (Table 1; Figure 5b) and forest-dependent species (Table 1; Figure 5c) showed a significant negative relationship with distance from the old-growth forest (Appendix S8). Compositional dissimilarity increased significantly with distance from the old-growth forest (Table 1; Figure 6c; Appendix S8). Wood density and the abundance of non-zoochorous, small-fruited, medium-fruited, large-fruited, forest non-dependent, pioneer, non-pioneer light demander and shade-tolerant species all did not show a significant variation with distance from the old-growth forest (Table 1, Appendix S8).

4 | DISCUSSION

Recent debate has centered on the effectiveness of passive restoration in mitigating biodiversity loss and reinstating functionality (Prach & del Moral, 2015). Our results suggest that passive restoration facilitates rapid recovery of seedling community structure and functional traits (Letcher and Chazdon, 2009), but is slower to recover species diversity and composition. The results should be interpreted cautiously because sample-based species accumulation curves revealed that the old-growth forest may harbor more species than actually sampled. Besides, our statistical analysis might be affected by the unbalanced study design arising from unequal sampling in terms of plots (63 in the restored vs five in the old-growth forest) and sampling years (2011, 2014, 2017 for the restored vs 2011 and 2017 for the old-growth forest).

4.1 | Comparing seedling attributes between the restored and old-growth forest

We found a variation in recovery rates of floristic and functional traits which supports our prediction of different rates of recovery of seedling attributes, and confirms the view that attributes can vary in recovery rate (Norden et al., 2015). The restored forest exhibited similar seedling species abundance and evenness as the old-growth forest but lower richness and diversity. This implies that although the restored forest attained similar species dominance as the old-growth forest within 22 years, more time is needed to recover the number of seedling species. However, the restored forest recovered basal area and height of seedlings which suggests recovery of productivity (Torres & Lovett, 2013) and structural complexity, important for carbon storage and conservation of some animals inhabiting the forest understorey (Yirdaw et al., 2019).

Seedling assemblages in the restored and old-growth forest exhibited similar functional traits. First, wood density was similar which suggests that the restored forest supports similar abundance of faster-growing species (i.e., pioneers with lower wood density) and slower-growing species (i.e., shade-tolerants with higher wood density) as the old-growth forest (Tabarelli et al., 2008; Santos et al., 2008). Consistent with this, there was no difference in the abundance of pioneers, non-pioneer light demanders and shade-tolerant species between the restored and old-growth forest. Second, the abundance of zoochorous (animal-dispersed) and non-zoochorous (abiotically

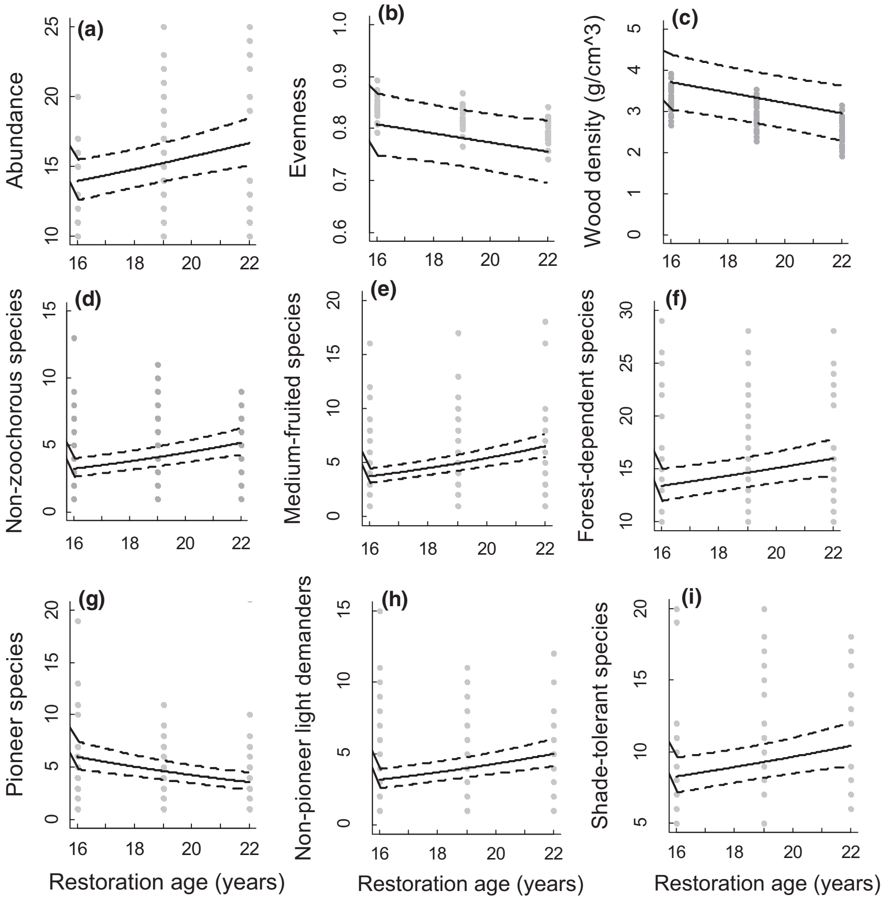


FIGURE 4 Predicted values of seedling attributes in Kibale National Park, western Uganda: (a) species abundance; (b) evenness; (c) wood density; and abundance of: (d) non-zoochorous; (e) medium-fruited; (f) forest-dependent; (g) pioneer; (h) non-pioneer light demander; and (i) shade-tolerant species, each measured per plot in the restored forest against restoration age

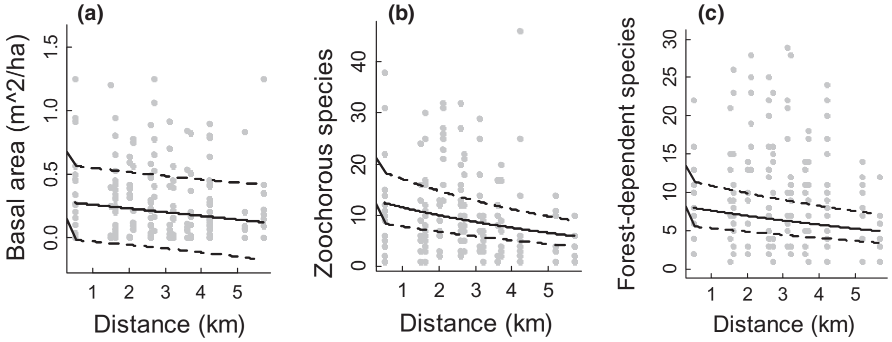


FIGURE 5 Predicted values of seedling attributes in Kibale National Park, western Uganda: (a) basal area; and abundance of: (b) zoochorous; and (c) forest-dependent species, each measured per plot in the restored forest against distance from the old-growth forest

dispersed) species was not different between the restored and old-growth forest suggesting recovery of these dispersal modes. Since seed mass varies between zoochorous and non-zoochorous species and seed size is related to fruit size (Howe, 2016), our results imply that seeds of different sizes arrive at suitable microsites for germination in the restored forest. In line with this, our results showed similar abundance of small-fruited, medium-fruited and large-fruited species between the restored and old-growth forest. In a way, the recovery of zoochorous dispersal and different fruit sizes suggests recovery of populations of animals dispersing small, medium and large fruits. Indeed, animal densities have increased due to forest restoration in our sites (Omeja et al., 2016). Third, we found similar abundance of forest-dependent and forest non-dependent species between the restored and old-growth forest. As forest-dependent and forest non-dependent species survive in at least one of the forested habitats, e.g. forest interior, edge, and riverine (Lwanga, 1996), our results suggest a shift by the restored forest from early successional habitats predominated by species adapted to open environments to a more old-growth forest-like community.

In contrast to the rapid recovery of seedling community structure and functional traits, the restored forest did not recover species composition (Bray–Curtis pairwise distances) which implies that restored forests can attain similar structural complexity and functionality as old-growth forests even with different species composition (Suganuma & Durigan, 2014). Therefore, if the restoration goal is rehabilitation, i.e., reparation of ecosystem functioning, without the re-establishment of the full species composition (SER, 2004), passive restoration is a suitable technique. The different species

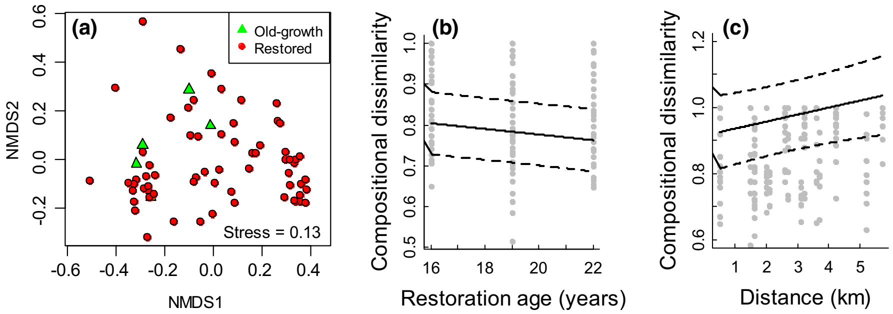


FIGURE 6 Seedling species composition in Kibale National Park, western Uganda: (a) non-metric multidimensional scaling ordination (NMDS) based on Bray–Curtis dissimilarity between the restored and old-growth forest at the plot scale using relative abundance data; (b) predicted values of Bray–Curtis dissimilarity at the plot scale in the restored forest against restoration age; and (c) distance from the old-growth forest

composition of seedlings between the restored and old-growth forest can be partly linked to the restored forest being younger (i.e. 22 years old) as evidence from tropical forests elsewhere shows that species composition takes more than 50 years to recover (Aide et al., 2000; Manuel et al., 2018). In addition, there was considerable variation in seedling species composition among plots within the sites which may be attributed to variation in microsites (Mendoza et al., 2009), which were not assessed in this study. In this regard, the potential effect of microsites on species composition of seedlings needs to be investigated.

4.2 | Effect of restoration age and distance from the old-growth forest on seedling attributes

We found a positive relationship between restoration age and seedling species abundance which is consistent with our prediction of species diversity increasing with restoration age. This observation may be attributed to species capable of surviving under forest shade (Liebsch et al., 2008). Indeed, this study showed that the abundance of shade-tolerant species increased with restoration age. Nevertheless, species evenness declined with restoration age which demonstrates a shift from low to high species dominance within the seedling community (Zhang et al., 2012). Early in succession, light is not a limiting resource and several species with rapid growth rate and short life span invade restoration sites which potentially reduces species dominance and increases evenness. As succession proceeds, the forest canopy closes and light becomes a limiting factor leading to dominance of shade-tolerant species, which likely lowers species evenness over time (Zhang et al., 2012). On the other hand, seedling species richness, diversity, basal area and height did not vary significantly with restoration age, although Marques et al., (2014) and Bertacchi et al. (2016) showed that they increase with restoration age in tropical sites. The longer recovery periods, i.e., 21–59 years and 10–55 years in Marques et al., (2014) and Bertacchi et al. (2016), respectively, may explain this discrepancy in the effect of restoration age.

Surprisingly, wood density of seedling species declined with restoration age, despite other studies showing that wood density is positively related to shade tolerance which is reported to increase with forest age (Valladares & Niinemets, 2008; Chave et al., 2008). Since certain pioneers had the highest wood density (*Diospyros mespiliformis*; wood density = 0.98, *Diospyros abyssinica*; wood density = 0.78), the decline in wood density may be due to a decline in the abundance of pioneers with restoration age as revealed by this study. The abundance of zoochorous seedling species was not affected by restoration age which contradicts Liebsch et al. (2008) who reported a positive effect of restoration age on the proportion of animal-dispersed species. Conversely, the abundance of non-zoochorous and forest-dependent seedling species increased with restoration age which may be linked to microsite conditions (Wijdeven & Kuzee, 2000). Since microsites are modulated during restoration (Bertacchi et al., 2016), it is likely that the abundance of non-zoochorous and forest-dependent species increases with restoration age due to modulation of microsites.

In addition, our results showed that restoration age did not affect the abundance of seedlings of small- and large-fruited species but positively influenced the abundance of seedlings of medium-fruited species. Since most tropical species are animal-dispersed (Howe, 2016) and we showed that restoration age did not affect the abundance of seedlings of animal-dispersed species, it is likely that microsites other than dispersal influence establishment of species of different fruit sizes in our sites. We speculate on a variation in effects of microsites on establishment of species of different fruit sizes but this needs further investigation. Also, we showed that the abundance of seedlings of pioneers declined while the abundance of seedlings of non-pioneer light demanders and shade-tolerant species increased with restoration age. As light is the limiting resource in the understorey of tropical forests (Montgomery & Chazdon, 2001) and light levels decline during succession (Denslow & Guzman, 2000), shade-intolerant species could become less common while shade bearers become more common over time (Dent et al., 2013). Furthermore, we found a decline in compositional dissimilarity, which implies that the seedling species composition of the restored forest is shifting towards that of the old-growth forest (Liebsch et al., 2008).

Consistent with our prediction of seedling attributes declining with increasing distance from the old-growth forest, the results showed that basal area of seedlings and the abundance of seedlings of zoochorous and forest-dependent species declined with distance from the old-growth forest. Increasing distance from seed sources induces dispersal limitations by exposing seed dispersers to predators in edge-affected habitats (Holl et al., 2000). This may reduce seed arrival which in turn reduces zoochorous species abundance at longer distances (Holl et al., 2000). Besides, edge effects increase seedling mortality because microsite conditions (e.g. lower humidity and higher temperatures) further away from the old-growth forest are less favorable for seedling growth (Tabarelli et al., 2008), which may reduce basal area and abundance of seedlings of forest-dependent species (Duncan & Duncan, 2000). The increase in compositional dissimilarity of seedlings with distance from the old-growth forest may be attributed to the decline in the abundance of seedlings of zoochorous and forest-dependent species in the restored forest.

In conclusion, passive restoration is effective for rapid recovery of structure and functional traits of seedling communities of tropical forests. Recovering the species diversity and composition of the seedling community may necessitate complementing passive with active interventions like enrichment planting of species only recorded in the old-growth forest (e.g. *Cola gigantea*, *Strombosia scheffleri*, and *Lovoa swynnertonii*). Continued development of restoration sites enhances ecosystem diversity and functionality of the seedling community. Passive restoration is effective for sites which are on average 3 km from the old-growth forests.

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AUTHOR CONTRIBUTIONS

ES and MT conceived the research idea; WVG, MS, KR, and FW collected data; ES and MT performed statistical analyses and wrote the paper. All authors contributed to revision of the manuscript.

DATA AVAILABILITY STATEMENT

Data necessary to reproduce all results and figures have been uploaded as Supplementary Information. The raw data are available in Zenodo.org at https://doi.org/10.5281/zenodo.4362142.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Sample-based species accumulation curves for the restored and old-growth forest and PCA biplots for seedling attributes.

Appendix S2. Description of statistical models.

Appendix S3. Validation graphs for models comparing seedling attributes between the restored and old-growth forest.

Appendix S4. Validation graphs for models on the effect of restoration age and distance from the old-growth forest.

Appendix S5. Functional traits of seedling species in the restored and old-growth forest.

Appendix S6. Fixed and random effects for models comparing seedling attributes between the restored and old-growth forest.

Appendix S7. Percentage contribution of seedling species to compositional dissimilarity between the restored and old-growth forest.

Appendix S8. Fixed and random effects for models on the effect of restoration age and distance from the old-growth forest on seedling attributes in the restored forest.

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