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Does restoration success vary with tree size under restoration plantings and regrowth forests?

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Abstract

Several studies evaluate active (i.e., seeding/planting) and passive (i.e., protecting forest regrowth) restoration, but few studies examine successional patterns for different plant sizes. By using biodiversity and structure, we examined whether restoration communities approach old-growth forests over time, and whether restoration success varies for different tree sizes in both active and passive interventions. We examined how initial site conditions affect active restoration. Small (dbh $\geq$ 5 cm), medium ($\geq$15 cm), and large trees ($\geq$30 cm) were measured in 2003–2017 in permanent sample plots in restoration plantings (initially 3–8 years old) and in an old-growth forest in Kibale National Park, Uganda. Trees were also measured in regrowth forests (initially 16 years old) in 2011–2017. We collated information about site conditions from restoration reports. Biodiversity and structure increased over time towards the old-growth forest. Restoration plantings and regrowth forests recovered diversity and structure of small and medium trees except for large trees. Forest recovery increased with proportions of remnant banana plants and shrubs, while isolation from the old-growth forest slowed recovery. Disaggregating vegetation inventory data by tree size may be useful in achieving a holistic measure of restoration. Restorationists could prioritize sites with remnant banana plants and shrubs, and sites closer to old-growth forests in order to achieve better results.

KEYWORDS
active and passive restoration, African tropical forests, competition and facilitation, dispersal limitations, ecological indicators, monitoring and evaluation, priority effects, species diversity and composition, UN decade on ecosystem restoration, vegetation structure

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INTRODUCTION

Ecological restoration is increasingly being applied worldwide to facilitate the recovery of disturbed tropical forests in order to enhance biodiversity and ecosystem services (Gilman et al., 2016; Holl & Aide, 2011). Globally, about 1.8 billion ha of land have been identified as having potential for restoration, and the majority (74%) of these is found in tropical forest landscapes (Bastin et al., 2019). To achieve forest restoration, ambitious initiatives include the implementation of active (i.e., seeding/planting trees) and passive (i.e., protecting forest regrowth) restoration interventions (Fagan et al., 2020). These interventions are mainly funded by climate finance, development banks and agencies, environmental funds, non-governmental organizations, national budgets, and non-traditional funding (FAO & Global Mechanism of UNCCD, 2015). Studies evaluating restoration outcomes help to justify these investments and guide formulation of restoration policies.

Assessing developmental trajectories of restored sites through time is important in determining whether restoration is following its intended trajectory towards a reference ecosystem and when the ecosystem under manipulation may no longer require external assistance to ensure its future health and integrity, in which case restoration can be considered complete (SER, 2004). It is a critical step in the refinement of restoration treatments, enabling the identification of constraints to success and the prediction of restoration outcomes (Matthews & Spyreas, 2010). The most commonly used indicators of restoration success include diversity, composition, and vegetation structure of restored ecosystems, which are evaluated against reference ecosystems (Ruiz-Jaen & Aide, 2005). In this case, restoration success is measured as the similarity in these indicators between restored and reference ecosystems.

Although developmental trajectories during forest restoration are generally characterized by changes in growth forms and plant sizes (Guariguata & Ostertag, 2001), few long-term studies have assessed whether restoration success may vary for different tree sizes and whether these variations are consistent under different restoration interventions. Yet, studying restoration success for different plant size classes enables practitioners to monitor the whole recovery trajectory and make mid-course corrections in management direction (Wortley et al., 2013). Most studies focus on one plant size class which may limit our understanding of the extent to which restoration treatments foster longer term recovery (e.g. Bertacchi et al., 2016; Ssekuubwa et al., 2019). The few studies measuring restoration success for smaller and larger stems focused on species richness, composition, and stem density in only one restoration treatment (Saldarriaga et al., 1988; Wheeler et al., 2016). Saldarriaga et al. (1988) found that species richness recovered much more rapidly (10–20 years) in smaller (>1 cm diameter at breast height, dbh) individuals and at least 40 years were required for species richness of stems ≥10 cm dbh to attain similar values to that of mature forest in slash-and-burn sites in the upper Rio Negro basin of Venezuela and Colombia. The species composition of saplings (dbh 1–5 cm) in regrowth forests tended to be more similar to that of reference forests compared to trees in São Paulo State, southeast Brazil (César et al., 2018). Wheeler et al. (2016) found that active restoration sites had similar density of stems ≥10 cm dbh as the old-growth forest and much lower density of stems ≥30 cm dbh after 18 years in Kibale National Park, Uganda. It is important to note that these results are not general findings across continental scales. Despite some studies showing a variation in recovery of biodiversity and structure for different plant size classes, to our knowledge, this is the first study to discuss its implications on restoration monitoring.

Restoration outcomes may be overwhelmed by site-specific factors like the proportion of historical vegetation (Grman et al., 2013) and proximity to old-growth forests. Canopy shade provided by pre-existing trees and shrubs enhances seedling recruitment in accordance with the facilitation model of succession (Elgar et al., 2014). Tree colonization declines with increasing distance from old-growth forests because of lower seed arrival (Holl et al., 2000) and unsuitable microclimates at longer distances compared to shorter distances (Duncan & Duncan, 2000). Understanding the effects of site factors on restoration outcomes can increase the efficacy of restoration interventions (Grman et al., 2013).

Accordingly, we monitored successional patterns of diversity, composition, and structure of small (dbh ≥ 5 cm), medium (dbh ≥ 15 cm), and large trees (dbh ≥ 30 cm) in restoration plantings (3–8-year-old at first sampling) and regrowth forests (16-year-old at first sampling) through a 15-year (2003–2017) and 7-year (2011–2017) monitoring period, respectively. Specifically, we examined whether vegetation communities in restoration plantings and regrowth forests approach those of the surrounding old-growth forest over time, and whether restoration success varies for different tree size classes under different restoration treatments. In addition, we determined the effect of initial site conditions on recovery of diversity, composition, and structure under active restoration. We asked the following questions: (i) do species diversity, composition, and structure increase with increasing time since active and passive restoration? (ii) Does restoration success vary for different tree size classes in the restoration plantings and regrowth forests? (ii) How do initial site conditions influence recovery under active restoration? We discuss implications of our findings for restoration planning, implementation, and monitoring.

METHODS

Study area

Kibale National Park (795 km^2; 00°13′–00°41′ N, 30°19′–30°32′ E) is located in Uganda at an elevation of 900–1500 m (Zanne & Chapman, 2005). The park receives a mean annual rainfall of 1750 mm and mean daily temperature ranges from 15.1 to 23.1°C. The park is a biodiversity hotspot well known for primates (such as *Pan troglodytes*, *Papio anubis*, *Cercopithecus mitis*, *Allochrocebus lhoesti*, and *Lophocebus albi-gena*) (Chapman & Lambert, 2000), elephants, small mammals (e.g. *Praomys jacksoni*, *Dendromus mysticalis* and *Malacomys longipes*) (Isabirye-Basuta & Kasenene, 1987), and several bird species categorized into forest interior specialists, forest generalists, and forest visitors (Dranzoa, 1998). In the southern part of the park where this study was conducted, there is an old-growth forest and forests restored after agricultural abandonment (Figure 1). The old-growth forest is moist semi-deciduous with *Cynometra alexandri*, *Celtis* spp., and *Chrysophyllum* spp. as climax species (Zanne & Chapman, 2005).

Kibale has a long history of human disturbance (Chapman & Lambert, 2000). In 1971, agricultural encroachers growing mainly annual crops (i.e., beans and maize) and perennial crops (i.e., bananas) destroyed about 10,000 ha of forests in the southern part of the park (Chapman & Lambert, 2000). In 1992, the encroachers were resettled outside the park. Subsequently, some of the formerly encroached areas became dominated by elephant grass because frequent fires set by poachers or that spread into the park from neighboring subsistence farms prevented forest succession (Struhsaker, 2003). Some areas with remnant shrubs like *Vernonia* spp., *Flueggea virosa*, and *Hoslundia opposita* and banana plantations were colonized by native tree seedlings due to the facilitative effect of shrubs and banana plants on seedling colonization (Holl et al., 2000; Lins et al., 2020).

Forest restoration encompassed active and passive interventions by Uganda Wildlife Authority (UWA) and Face the Future, a non governmental organisation (NGO) from the Netherlands, with the aim of establishing carbon offsets (Ssekuubwa et al., 2018). Active restoration involved planting of native species every year from 1995 to 2010 (except in 2001) in areas (3996 ha) with limited potential for natural recovery due to presence of fewer spontaneously regenerating seedlings as a result of elephant grass competition and fires (Ssekuubwa et al., 2018). 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 (Omeja et al., 2011). The planting density was 400 seedlings per ha. The main species planted were *Albizia* spp., *Bridelia micrantha*, *Croton macrostachyus*, *Shirakiopsis elliptica*, *Celtis gomphophylla*, and *Warburgia ugandensis*. The planted area was divided into a series of compartments (i.e., sites) of different sizes and weeding was carried out two to three times a year (Omeja et al., 2011). The areas with a high potential for natural recovery (2593 ha) due to the presence of many spontaneously regenerating seedlings were left to undergo natural forest regrowth (Ssekuubwa et al., 2018). The restoration plantings and regrowth sites were protected against fires by controlling poaching, constructing fire lines, and monitoring fire incidences by using watch towers (Ssekuubwa et al., 2018; Ssekuubwa, van Goor, Snoep, Riemer, Wanyama, & Tweheyo, 2021). Fencing and trenching which were carried out to control crop raiding by elephants also guarded against livestock grazing. The regrowth forests are bordered by the old-growth forest to the east and restoration plantings to the west.

Experimental design and vegetation inventory

Field-Map technology was used in laying out study plots and vegetation inventory (IFER, 2014). It is a software and hardware technology for effective computer-aided field data collection and data processing. It combines a flexible real-time GIS software Field-Map with electronic equipment for mapping trees and dendrometric measurements (IFER, 2014). The electronic measurement devices include a combination of laser range-finder + electronic inclinometer + electronic compass (RIC) for tree height measurement, upper tree diameter measurement, tree crown projection, and profile delineation, a global positioning system (GPS) used by Field-Map both for navigation and mapping, and an electronic caliper for measuring tree diameter (IFER, 2014).

A regular sampling grid consisting of clusters of four permanent sample plots with a spacing of 500 × 500 m (Figure S1) was applied to 15 sites (i.e., compartments) of restoration plantings and two sites of the old-growth forest using Field Map technology (IFER, 2014). The same grid consisting of clusters of three permanent sample plots was applied to four sites of regrowth forests. Each sample plot (2000 m^2) consisted of four 500 m^2 circles, that is, one key circle at the bottom left of each plot, and three other circles (Figure S1). The key circle contained a

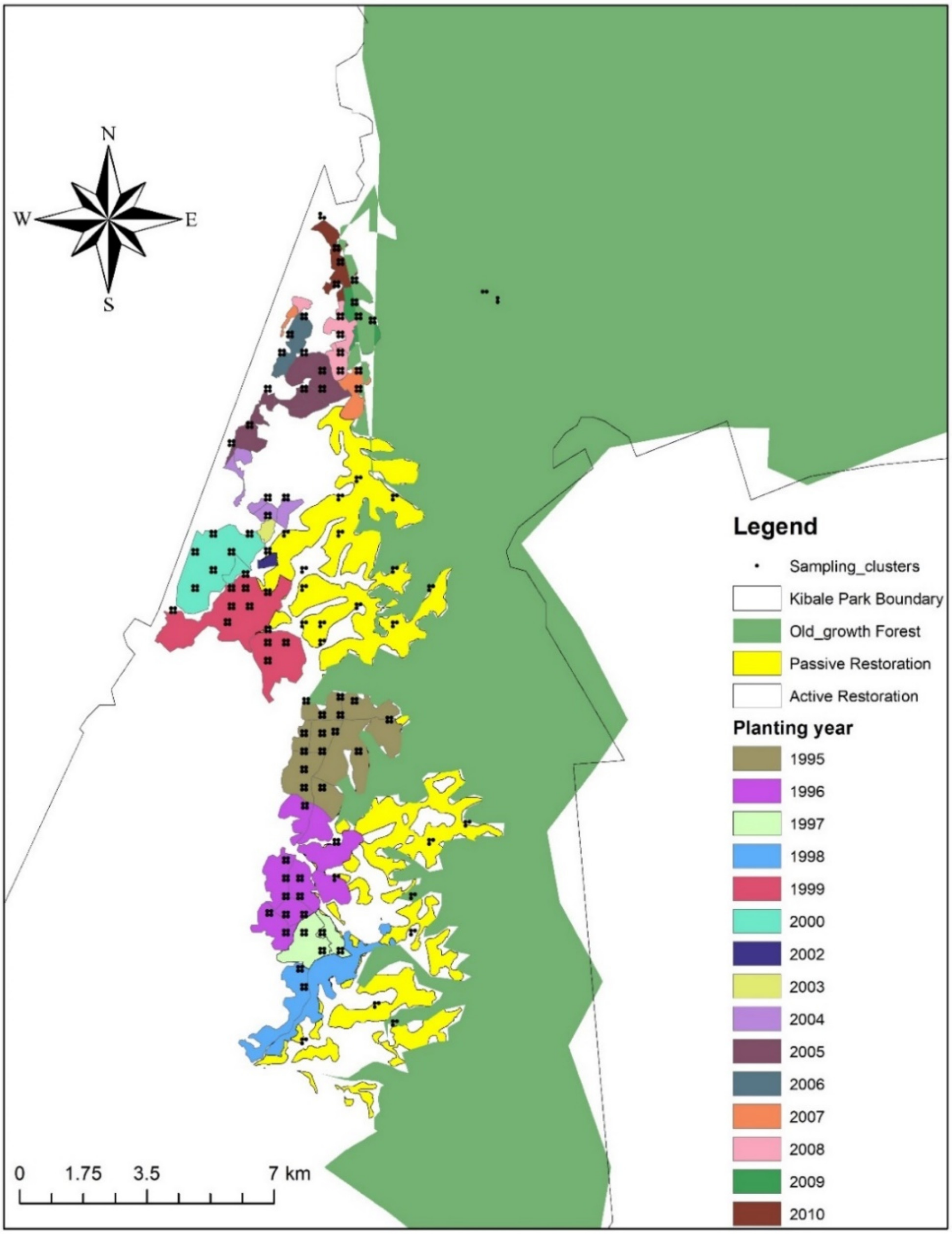

FIGURE 1 Clusters of sample plots in restoration plantings (active restoration), regrowth forests (passive restoration), and old-growth (reference) forest in Kibale National Park, Uganda. The restoration plantings are of different planting years (i.e., 1995–2010). The regrowth forests are of a single 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

small subplot (12.6 m^2) located 8 m north from the centre of the key circle and a concentric internal circle (201.1 m^2) (Figure S1). Overall, there were five plots in the old-growth forest, 63 in the regrowth forests, and 320 in restoration plantings (Table S1). The restoration plantings were sampled in 2003, 2008, 2011, 2014, and 2017, the old-growth forest in 2003, 2011, and 2017, and the regrowth forests in 2011, 2014, and 2017 (Table S1).

Small trees (dbh ≥ 5 cm) were measured in the concentric internal subplot, medium trees (dbh ≥ 15 cm) in the entire key circle, and large trees (dbh ≥ 30 cm) in the remaining three circles. The plot sizes and tree size classes in this study are specified for carbon monitoring projects in Uganda (IFER, 2011). All qualifying trees were mapped using Field-Map and identified to species level following Katende et al. (1995) and Eggeling (1940). Stem diameter was measured using an electronic caliper at breast height (1.3 m), unless there were irregularities at this height or trees were shorter. For individuals with buttresses or other stem irregularities at breast height, dbh was measured above the buttresses or stem irregularities. Tree height and crown width were remotely measured using the RIC of Field-Map.

The initial site conditions studied were proximity (i.e., distance) to the closest boundary of the old-growth forest and proportions of elephant grass, short grass, banana plants, and remnant shrubs before restoration plantings were implemented. The proximity of each plot in restoration plantings to the closest boundary of the old-growth forest was estimated using local area maps with assistance from UWA staff. We obtained information about the initial vegetation conditions for the planted area from restoration records except for sites planted in 2008–2010 and the regrowth areas for which such information was not available. The initial vegetation conditions were visually estimated by one person in the restoration team at the commencement of restoration activities (W. Chemutai 2014, Warden Forest Restoration–UWA, personal communication).

Statistical analyses

Statistical analyses were done in R version 3.4.4 (R Core Team, 2020). To assess the completeness of the vegetation inventory in the restoration plantings, regrowth forests, and old-growth forest, we used the iNEXT package to generate species accumulation curves (Chao et al., 2014). We computed species richness (number of species), evenness (Pielou's Index), and diversity (Shannon–Wiener Index) of small, medium, and large trees per plot of the restoration plantings, regrowth, and old-growth forests using the Vegan package (Oksanen et al., 2013). To determine species composition for different tree sizes, we computed Bray–Curtis similarity index between the old-growth forest (with plots merged into a single community) versus each plot in restoration plantings and regrowth forests using the Vegan package (Oksanen et al., 2013). We calculated total stem density (stems/ha), basal area (m^2/ha), height (m), and crown width (m) for different tree sizes per plot of the restoration plantings, regrowth forests, and old-growth forest.

Variation of diversity, composition, and structure over time

To assess the variation of diversity, composition, and structure over time and evaluate restoration success for the restoration plantings, we fitted separate mixed-effects models for small, medium, and large trees with richness, evenness, Shannon–Wiener diversity, compositional similarity, stem density, basal area, height, and crown width as response variables (Pinheiro et al., 2014). For each response, the model included sampling year as an eight-level factor variable (2003, 2008, 2011, 2014, 2017, R2003, R2011, and R2017) as the explanatory variable. We kept data from different sampling years in restoration plantings (2003–2017) and old-growth reference forests (R2003–R2017) separate to control for temporal pseudoreplication. To account for among and within-site differences in environmental conditions, plot nested within cluster and site were included as random effects. For richness we fitted a model with log-link function, assuming a Poisson distribution of errors. For stem density we fitted a model with log-link function, assuming a negative binomial distribution of errors as the initial Poisson model was overdispersed (Crawley, 2013). For evenness, diversity, basal area, height, and crown width, we fitted respective models with identity link function, assuming a normal distribution of errors.

For compositional similarity (Bray–Curtis index), we fitted beta regression models with a logit link function since similarity values by their nature are continuous and bound at 0 and 1.

We used diagnostic tools in the DHARMa package (Hartig, 2021) to evaluate model fits (i.e., using normality and dispersion tests). The statistical significance of sampling year was determined using the likelihood ratio test. Similar models were fitted to assess the variation of diversity, composition, and structure over time and evaluate restoration success for the regrowth forests with sampling year as a five-level factor variable (2011, 2014, 2017, R2011, and R2017). We considered restoration success as the absence of significant differences in biodiversity and structure between the old-growth forest versus restoration plantings and regrowth forests for the different sampling years.

Influence of initial site conditions on active restoration

Relationships among site conditions were visualized using a correlation matrix. Highly correlated pairs of variables (≥±0.5) were visually compared using the *pairs* function in Lattice package (Crawley, 2013). The proportion of elephant grass was highly correlated with the proportion of shrubs ($r = -0.7$, Figure S2) and moderately correlated with the proportion of short grass ($r = -0.5$, Figure S3), so elephant grass was not included in further analyses (Crawley, 2013). To assess the influence of initial site conditions on recovery under active restoration,

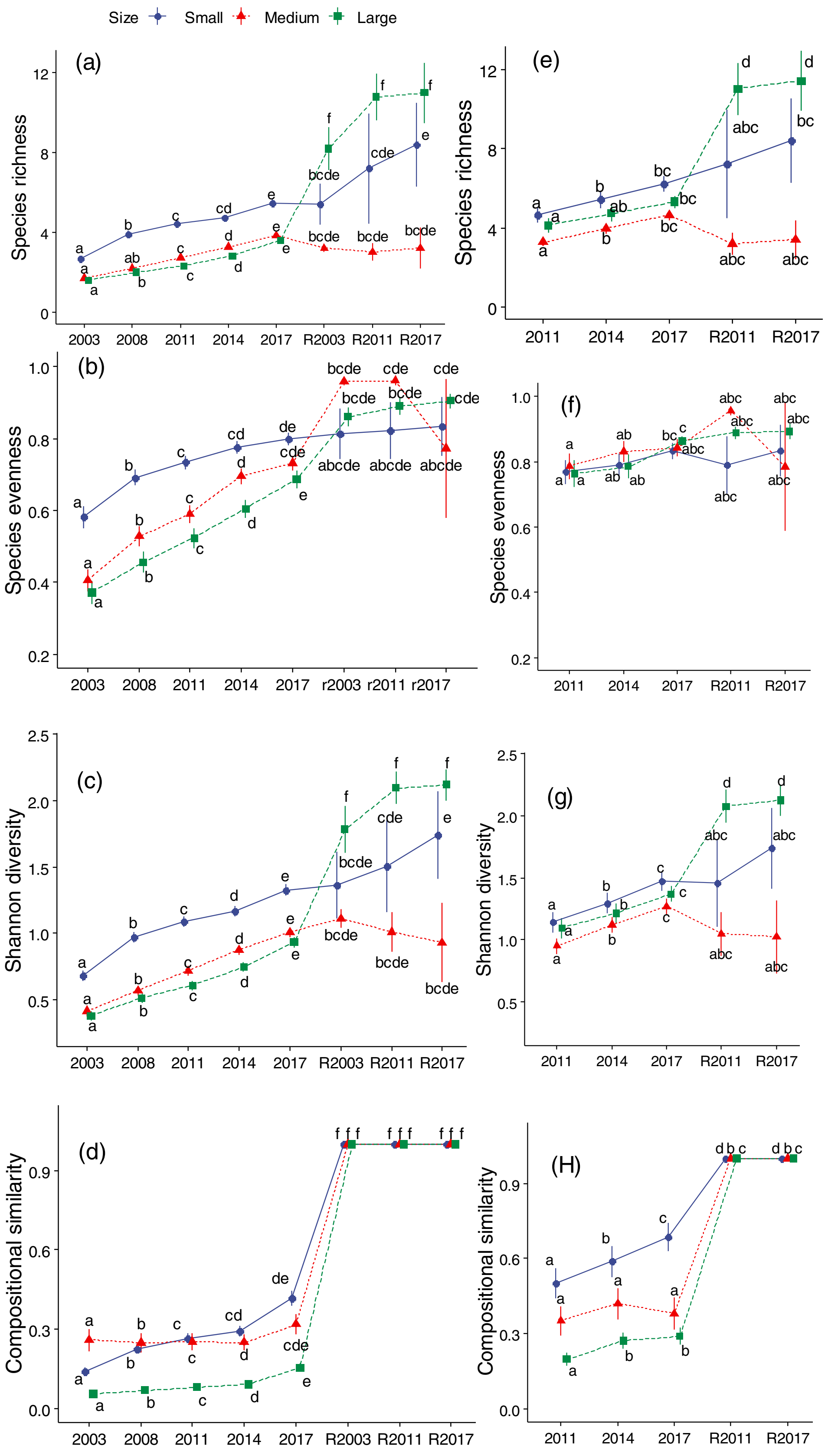

FIGURE 2 Variation of mean species richness, evenness, Shannon–Wiener diversity, and compositional similarity to the old-growth forest of small (dbh ≥ 5 cm), medium (≥15 cm), and large trees (≥30 cm) with sampling year in restoration plantings (a–d) and regrowth forests (e–h) in Kibale National Park, Uganda. R2003, R2011, and R2017 represent sampling years for the old-growth forest. Different letters show significant differences between sampling years and error bars show ±95% confidence intervals for the mean.

we fitted generalized linear models with richness, evenness, Shannon–Wiener diversity, crown width, basal area, height, and stem density each pooled for all tree size classes as response variables (Pinheiro et al., 2014). For compositional similarity (Bray–Curtis index), we fitted beta regression models with a logit link function. For

TABLE 1 Likelihood ratio test (χ^2, *df* = degrees of freedom) for the variation of diversity, composition, and structure of small (dbh ≥ 5 cm), medium (≥15 cm), and large trees (≥30 cm) over the sampling period for restoration plantings and regrowth forests in Kibale National Park, Uganda

		Restoration plantings		**Regrowth forests**	
		χ^2 (*df* = 7)	*p*	χ^2 (*df* = 4)	*p*
Species richness	Small trees	261.41	<.001 ***	16.72	.002 **
	Medium trees	245.45	<.001 ***	15.28	.004 **
	Large trees	230.09	<.001 ***	15.17	.004 **
Species evenness	Small trees	117.22	<.001 ***	4.82	.306
	Medium trees	179.28	<.001 ***	5.40	.248
	Large trees	180.09	<.001 ***	10.33	.035 *
Shannon diversity	Small trees	375.25	<.001 ***	38.68	<.001 ***
	Medium trees	389.51	<.001 ***	30.86	<.001 ***
	Large trees	386.30	<.001 ***	28.53	<.001 ***
Compositional similarity	Small trees	365.51	<.001 ***	25.17	<.001 ***
	Medium trees	66.00	<.001 ***	11.01	.026 *
	Large trees	288.04	<.001 ***	70.78	<.001 ***
Stem density	Small trees	41.93	<.001 ***	790.26	<.001 ***
	Medium trees	122.66	<.001 ***	574.25	<.001 ***
	Large trees	293.00	<.001 ***	321.97	<.001 ***
Basal area	Small trees	104.42	<.001 ***	9.51	.049 *
	Medium trees	258.90	<.001 ***	27.05	<.001 ***
	Large trees	290.66	<.001 ***	36.18	<.001 ***
Height	Small trees	118.98	<.001 ***	8.54	.074
	Medium trees	255.60	<.001 ***	35.20	<.001 ***
	Large trees	328.11	<.001 ***	53.55	<.001 ***
Crown width	Small trees	135.74	<.001 ***	16.24	.003 **
	Medium trees	234.91	<.001 ***	42.01	<.001 ***
	Large trees	310.16	<.001 ***	53.31	<0.001 ***

Note: Values are significant at $p < .05$.
Abbreviation: dbh, diameter at breast height.
*$p < .05$; **$p \leq .01$; ***$p \leq .001$.

each response, a maximal model was created with distance to old-growth forest, and proportion of banana plants, shrubs, and short grass as explanatory factors and then stepwise model reduction was carried out using Akaike Information Criteria. Similar error structures, link functions, and model validation techniques as in 2.3.1 were applied.

RESULTS

We recorded 28,758 individuals in the restoration plantings (i.e., active restoration), 6198 in regrowth forests (i.e., passive restoration), and 730 in the old-growth forest over the sampling period. We found 79 species restricted to the restoration plantings, 26 species to regrowth forests, and 17 species to the old-growth forest whereas 34 species were found in the three forest types (Table S2). The species accumulation curves indicated adequate sampling effort for the restoration plantings and regrowth forests, however the old-growth forest could support more species than we recorded (Figure S3).

Variation in diversity, composition, and structure over time

The species richness, evenness, Shannon–Wiener diversity, and compositional similarity to the old-growth forest (i.e., biodiversity attributes) of small, medium, and large trees in restoration plantings significantly increased

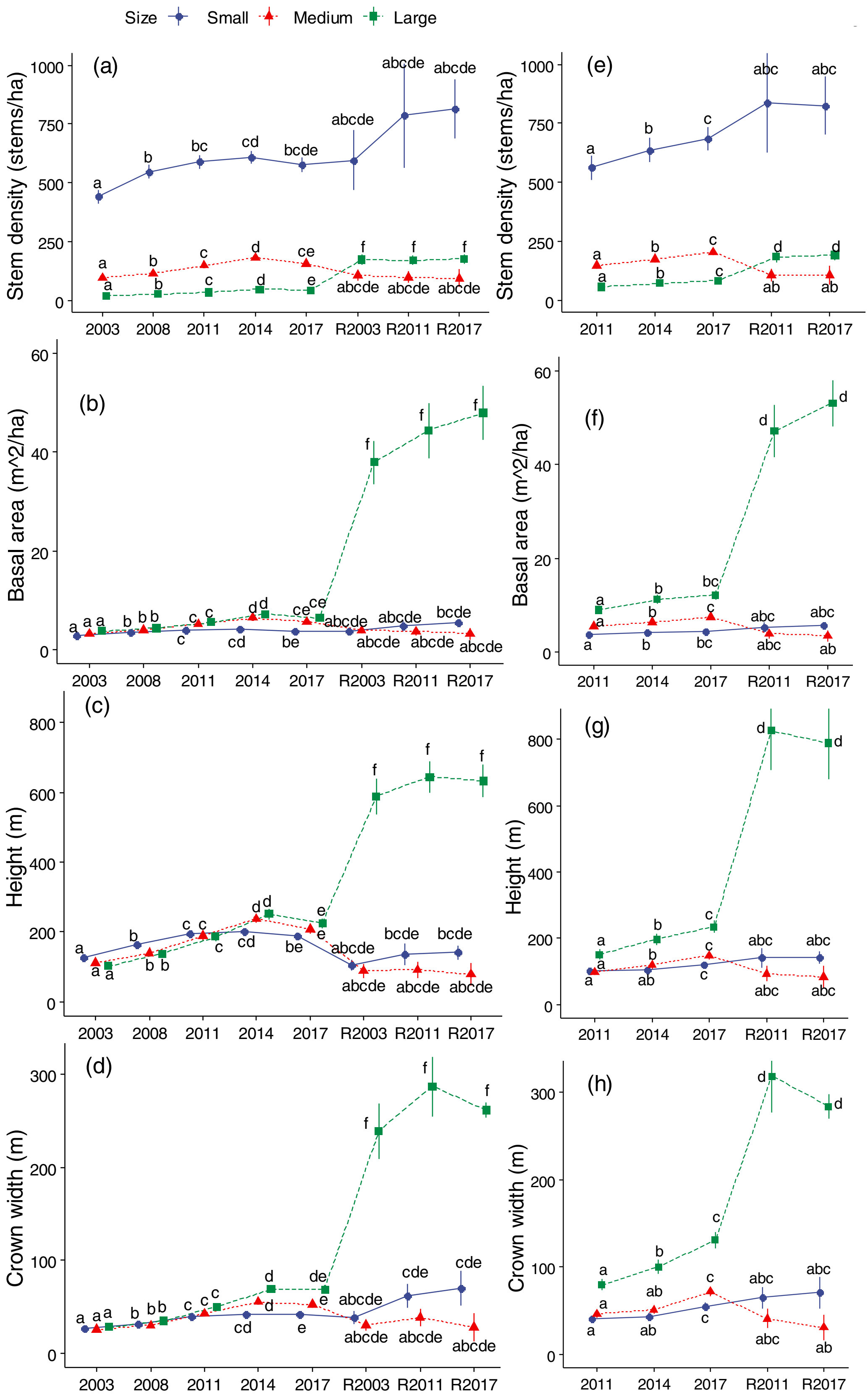

FIGURE 3 Variation of mean stem density, basal area, height, and crown width of small (dbh ≥ 5 cm), medium (≥15 cm), and large trees (≥30 cm) with sampling years in restoration plantings (a–d) and regrowth forests (e–h) in Kibale National Park, Uganda. R2003, R2011, and R2017 represent sampling years for the old-growth reference forest. Different letters show significant differences between sampling years and error bars show ±95% confidence intervals for the mean. dbh, diameter at breast height

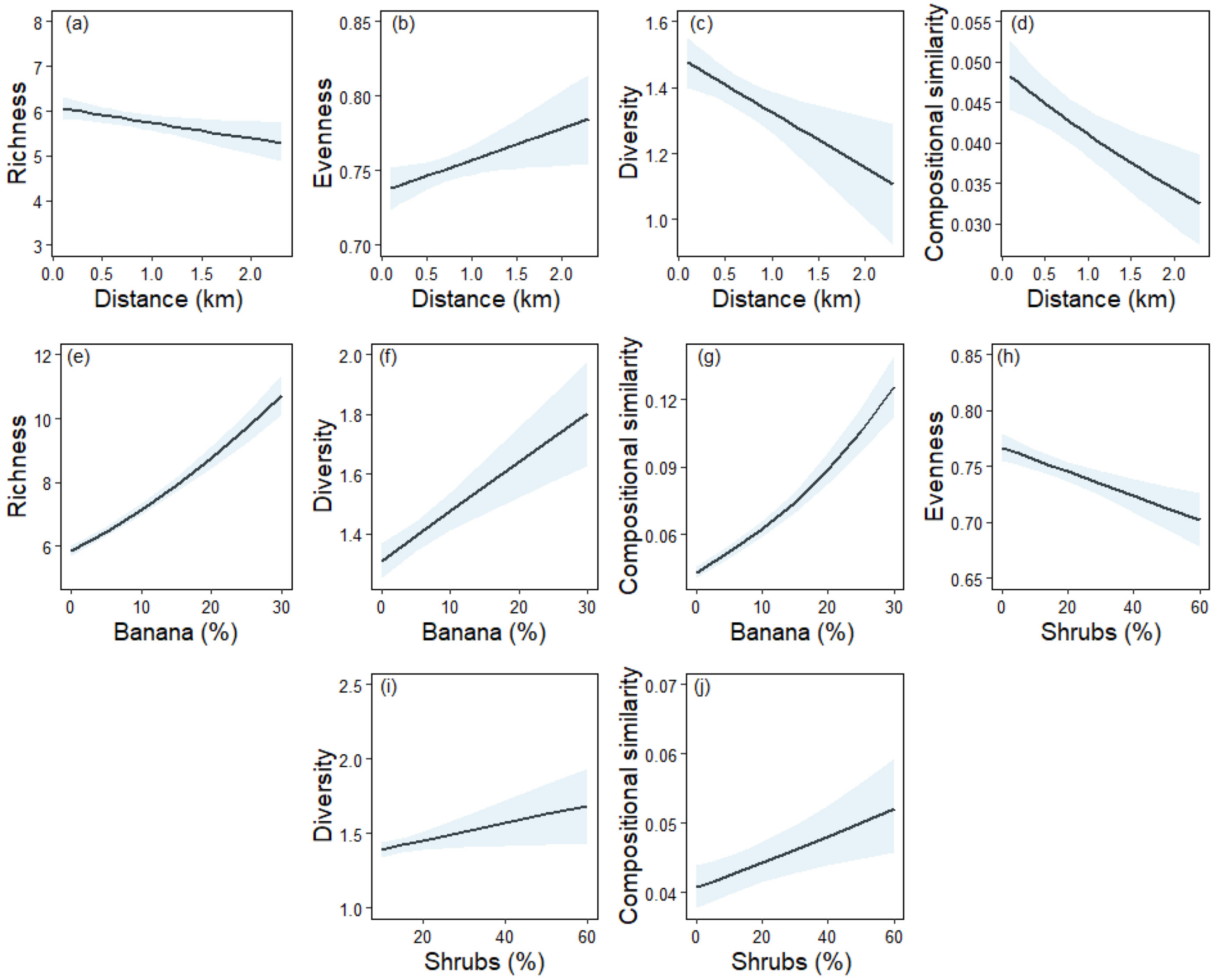

FIGURE 4 Effect of initial site conditions on species richness, evenness, Shannon–Wiener diversity, and compositional similarity to the old-growth forest each measured per plot in Kibale National Park, Uganda. Site conditions include: distance to old-growth forest (a–d), proportion of remnant banana plants (e–g), and shrubs (h–j). Regression lines are drawn with 95% confidence intervals for the mean

towards the levels in the old-growth forest over time in the period 2003–2017 (Figure 2a–d, Table 1). The general increase in these biodiversity attributes was consistent for sites of different planting years (Figure S4a–d). Similarly, the species richness, Shannon–Wiener diversity, and compositional similarity to the old-growth forest of small, medium, and large trees in regrowth forests increased significantly over time in the period 2011–2017 (Figure 2e–h, Table 1). Species evenness increased significantly for large trees and not significantly for small and medium trees in regrowth forests (Figure 2e–h, Table 1).

The structural attributes of restoration plantings and regrowth forests increased towards those of the old-growth forest. The stem density (stems/ha), basal area (m^2/ha), height, and crown width of small, medium, and large trees in restoration plantings increased significantly towards the old-growth forest over time during the sampling period (Figure 3a–d, Table 1). The general increase in structural attributes was also consistent for sites of different planting years (Figure S4e–h). However, the structural attributes of older restoration plantings (i.e., 1995, 1996, and 1997 planting years) tended to decline between 2014 and 2017 (Figure S4e–h). Equally in regrowth forests, the stem density, basal area, and crown width of small, medium, and large trees increased significantly towards those of the old-growth forest over time during the sampling period (Figure 3e–h, Table 1). Height increased significantly for medium and large trees and not significantly for small trees in regrowth forests (Figure 2e–h, Table 1). There was no significant variation in biodiversity and structure in the old-growth forest during the sampling period (Figures 2 and 3).

Restoration success

Generally, the restoration plantings were younger (i.e., 3–8 years old) in 2003 with significantly lower species richness, evenness (small and large trees), and Shannon–Wiener diversity than the old-growth forest (Figure 2a–d, Table S3). However, they already exhibited similar stem density, basal area, height, and crown width of small and medium trees as the old-growth forest (Figure 3a–d, Table S3). Subsequently, the restoration plantings consistently exhibited similar species richness and Shannon–Wiener diversity of small and medium trees as the old-growth forest and were substantially different in terms of the large trees (Figure 3a–d). Also, the regrowth forests first measured at 16 years in 2011 showed similar patterns of species richness and Shannon–Wiener diversity of small, medium, and large trees (Figure 3e–h, Table S4). Species evenness in restoration plantings and regrowth forests recovered to levels in the old-growth forest irrespective of the tree size class (Figure 2). The species composition of small and medium trees was more similar to that of the old-growth forest compared to the species composition of trees. Despite the positive trend in compositional similarity, restoration plantings and regrowth forests were still markedly different from the old-growth forest in terms of species composition (Figure 2d and h, Tables S3 and S4). Our results also showed that with temporal development, the restoration plantings and regrowth forests reached similar levels of stem density, basal area, height, and crown width of small and medium trees as those of the old-growth forest and were different from the old-growth forest in terms of the large trees (Figure 3).

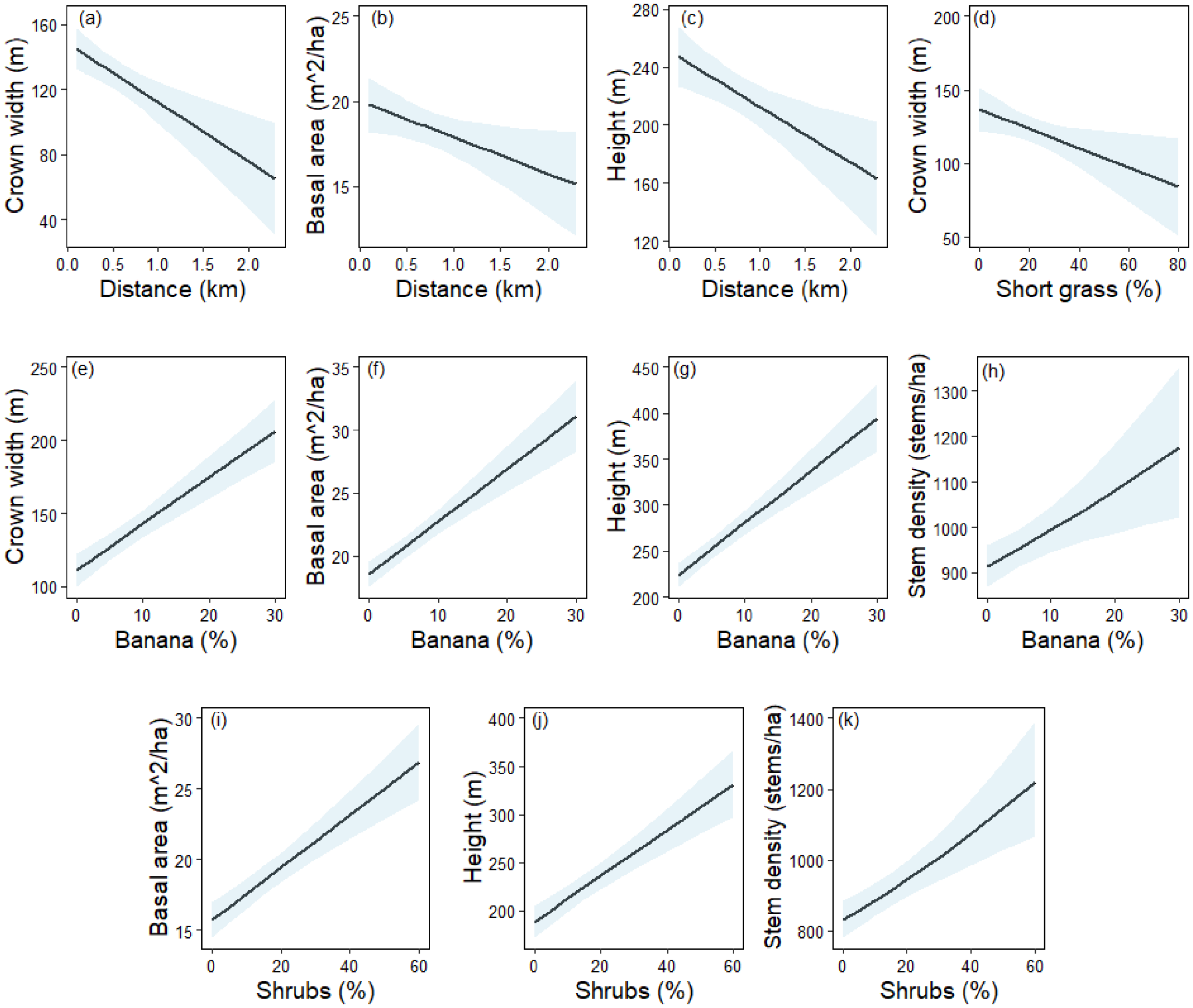

FIGURE 5 Influence of initial site conditions on crown width, basal area, height, and stem density each measured per plot in Kibale National Park, Uganda. Site conditions include: distance to old-growth forest (a–c), proportions of short grass (d), remnant banana plants (e–h), and shrubs (i–k). Regression lines are drawn with 95% confidence intervals for the mean

Effect of initial site conditions on active restoration

Among the site conditions studied, the proportion of remnant banana plants was the major driver of biodiversity and structural characteristics of the restored forests due to its larger effect size compared to the distance from the old-growth forest, and proportion of remnant shrubs and short grasses. Species richness ($p = .013$), Shannon–Wiener diversity ($p = .002$), and compositional similarity to the old-growth forest ($p < .001$) declined with distance to the old-growth forest (Figure 4, Table S5). However, evenness increased with distance to the old-growth forest ($p = .022$, Figure 4, Table S5). There was a significant positive effect of the proportion of banana plants on richness ($p < .001$), Shannon–Wiener diversity ($p < .001$), and compositional similarity ($p < .001$; Figure 4, Table S5). The proportion of shrubs substantially increased Shannon–Wiener diversity ($p = .027$) and compositional similarity ($p = .002$) but reduced evenness ($p < .001$; Figure 4, Table S5).

Our results also revealed that increasing distance from the old-growth forest reduced basal area ($p = .025$), crown width ($p < .001$), and height ($p = .002$; Figure 5, Table S5). The proportion of banana plants increased basal area ($p < .001$), crown width ($p < .001$), height ($p < .001$), and stem density ($p = .002$; Figure 5, Table S5). A high proportion of shrubs substantially enhanced basal area ($p < .001$), height ($p < .001$), and stem density ($p < .001$; Figure 5, Table S5). Crown width declined with increasing proportion of short grass ($p = .019$; Figure 5, Table S5).

DISCUSSION

By disaggregating data according to tree size classes (i.e., small, medium, and large trees), we reveal long-term successional patterns for restoration plantings (i.e., active restoration) and regrowth forests (i.e., passive restoration) over a 15-year and 7-year monitoring period, respectively. We found a progressive increase towards the old-growth forest in the biodiversity and structural attributes in both restoration plantings and regrowth forests which corroborates observations from previous studies in our sites (Omeja et al., 2011, 2016; Wheeler et al., 2016), and supports the prediction of the gradual continuous model of succession that successional communities gradually drift, becoming similar to the ecosystem before disturbance (Suganuma & Durigan, 2015). Species richness, evenness, Shannon–Wiener diversity, and compositional similarity to the old-growth forest of small, medium, and large trees increased overtime which reiterates the role of active and passive restoration interventions in increasing the biodiversity conservation value of human-modified tropical landscapes (Gilman et al., 2016; Wheeler et al., 2016). Although species composition of restoration plantings and regrowth forests continued to progress towards the old-growth forest during the sampling period, it was still markedly different from that of the old-growth forest. This difference in composition may be linked to the restoration plantings and regrowth forests being dominated by highly abundant early-successional species like *Shirakiopsis elliptica* (Euphorbiaceae), *Cassia spectabilis* (Fabaceae), *Ravolfia vomitaria* (Apocynanceace), and *Erythrina abyssinica* (Papilionaceae) which were not recorded in the old-growth forest. Besides, the old-growth forest was dominated by late-successional species like *Mimusopsis kummel* (Annonaceae) and *Chrysophyllum gorungosum* (Apocynanceace) which were not encountered in the restoration plantings and regrowth forests.

The progressive increase in stem density, basal area, height, and crown width of small, medium, and large trees suggests increasing structural complexity due to restoration that is potentially beneficial to forest wildlife by increasing habitat availability (Staples et al., 2020). However, our results revealed that the structural attributes of stem density, basal area, height, and crown width in the older planting years (i.e., 1995, 1996, and 1997 planting years) tended to decline between 2014 and 2017 sampling years which might be interpreted as an indication of post-restoration disturbance. Although not tested in this study, we attribute the post-restoration disturbance to elephants as they have been reported to damage small and large trees in restoration sites in Kibale (Lawes & Chapman, 2006; Omeja et al., 2016) with preference for actively-restored to passively-restored sites (Ssekuubwa et al., 2018). There is a need to investigate the causes of the decline in structural complexity and implement measures to avoid a substantial deviation from the desirable trajectory towards old-growth forests.

In terms of restoration success, our results showed that restoration plantings and regrowth forests recovered the species richness, evenness, Shannon–Wiener diversity, stem density (stems/ha), basal area (m^2/ha), height, and crown width of small and medium trees in the old-growth forest. By contrast, these attributes differed substantially for large trees being higher in the old-growth forest than in restorations plantings and regrowth forests. In addition, the species composition of small and medium trees in both restoration plantings and regrowth forests tended to be closer to that of the old-growth forest unlike for the larger trees. We suggest that studies measuring smaller trees only may overestimate recovery capacities of ecosystems as attributes of smaller trees recover relatively faster while studies measuring large trees only may not detect early successes as attributes of larger trees take longer to recover. We propose that in order to achieve a holistic measure of restoration, studies monitoring restoration need to include different size classes or growth stages and disaggregate data according to size/growth stage. Restoration monitoring calls for long-term commitment by all stakeholders especially if it takes decades to reach the final goal (Greipsson, 2011). Therefore, it is preferable for short-term monitoring to include attributes of smaller plant sizes or younger growth stages, since they recover faster, as interim goals that act as "milestones" of the final goal. Using milestones aids in the evaluation of a restoration project at regular intervals and can facilitate stakeholder acceptance of the entire project. Long-term monitoring can be used to assess attributes of larger plant sizes or older growth stages as the endpoint of restoration (Greipsson, 2011). Our results should be interpreted cautiously as the fewer plots surveyed in the old-growth forest compared to the restoration sites could underestimate old-growth conditions as species accumulation curves showed that there could be more species in the old-growth forest than we recorded. Nonetheless, our results are still relevant to tropical forest restoration as they are based on long-term observations.

We found that increasing distance from active restoration sites to the old-growth forest reduced species richness, Shannon–Wiener diversity, compositional similarity to the old-growth forest, crown width, basal area, and height probably because away from the old-growth forest, dispersal limitations reduce seed arrival (Holl et al., 2000) and microsite limitations impede tree recruitment beneath the restoration plantings (Duncan & Duncan, 2000). The increase in evenness with distance to the forest could be linked to the inverse relationship between richness and evenness (Stirling & Wilsey, 2001). A high proportion of banana plants and remnant shrubs increased Shannon–Wiener diversity, compositional similarity, crown width, basal area, height, and stem density which may be attributed to bananas and shrubs facilitating tree recruitment by providing perches for seed dispersers (bats and birds), thereby increasing seed rain into the soil seed bank (Lins et al., 2020). When the bananas are cleared during restoration, the seed bank facilitates tree recruitment under the restoration plantings. Retaining the remnant shrubs among restoration plantings helps to provide a suitable microclimate for tree growth (Myster, 2003). In contrast, a high proportion of short grasses reduced crown width probably due to competition for light and soil nutrients between younger trees and grasses (Elliott et al., 2013). We suggest that areas with dense grasses at the on-set of active restoration may require frequent weeding to control grasses and enhance crown width (Elliott et al., 2013).

In conclusion, we found that the biodiversity and structural attributes in restoration plantings and regrowth forests increased over time towards those in the old-growth forest. Restoration success varied for small, medium, and large trees under active and passive interventions. We suggest that practitioners could incorporate the effect of plant size when evaluating restoration using vegetation-based indicators in order to obtain a holistic assessment of the efficacy of restoration. We have also shown that forest recovery under restoration plantings increases with the proportion of banana plants and remnant shrubs, and closer to mature forests. These factors need to be considered during the planning and implementation of restoration projects.

AUTHOR CONTRIBUTIONS

Enock Ssekuubwa and Mnason Tweheyo conceived the ideas; Wouter van Goor, Martijn Snoep, Kars Riemer, and Fredrick Wanyama collected data; Enock Ssekuubwa, Daniel Waiswa, Fred Yikii, and Mnason Tweheyo conducted statistical analyses and wrote the paper. All authors contributed to editing and approved the final version of the manuscript.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and R code for reproducing all results and figures are available in Zenodo.org at http://doi.org/10.5281/zenodo.5084757 (Ssekuubwa et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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