Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
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Impediments to forest recovery in bracken-dominated clearings in the African Highlands

Einstape i afrikanske høylandsområder: hvordan bregner hindrer gjenvekst av skog

Fredrick Ssali

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“Every complex problem has a solution which is simple, direct, plausible—and wrong.”

Adapted from H. L. Mencken.

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Paper II

Ssali, F., Moe, S. R. and Sheil, D. (2018). Tree seed rain and seed removal, but not the seed bank, impede forest recovery in bracken (*Pteridium aquilinum* (L.) Kuhn) dominated clearings in the African highlands. *Ecology and Evolution*, **00**, 1–13. https://doi.org/10.1002/ece3.3944

Paper III

Ssali, F., Moe, S. R. and Sheil, D. The differential effects of bracken (*Pteridium aquilinum* (L.) Kuhn) on germination and seedling performance of tree species in the African tropics. *Submitted.*

Paper IV

Ssali, F., Moe, S. R. and Sheil, D. Damage to artificial seedlings across a disturbed Afromontane forest landscape. *Submitted.*

Summary

Vegetation dynamics in disturbed forested landscapes remain incompletely understood. Considerable areas with stalled forest recovery occur worldwide and may reflect the effects of dense and persistent understorey plants including bracken fern *Pteridium aquilinum* (L.) Kuhn. Bracken is a long-lived clonal plant which can form monodominant stands that may affect tree seedling establishment.

In the East African Highlands persistent bracken thickets already cover hundreds of square kilometres and are associated with failed forest recovery. Studies elsewhere, most of them from temperate and neotropical regions, have suggested various interference mechanisms and it is unclear which are involved in tropical Africa.

This thesis consists of a series of studies from a tropical montane forest in Uganda. The main aim of these studies was to examine why forest recovery in bracken-dominated areas is so limited and slow. Such understanding is potentially valuable for forest restoration. I explored how vegetation structure varies across the forest-bracken boundary and highlighted the potential factors affecting the ability of woody species to re-colonise bracken (Paper I). I also investigated processes that can contribute to recruitment limitation in bracken-dominated clearings by examining if differences in seed rain, soil seed bank or seed removal can, individually or in combination, explain the differences in tree regeneration found between bracken dominated areas and the neighbouring forest (Paper II). I carried out a manipulative experiment where I examined how bracken affects seed germination, seedling survival and growth of forest trees (Paper III). Using artificial seedlings, I determined how the intensity and pattern of damage varies across the landscape in different contexts including bracken dominated areas. These are the first ecological studies of bracken in tropical Africa.

Key among the findings is that bracken-dominated clearings are locally abundant and persistent and that recruitment is limited by seed arrival and rapid removal. When comparing forest and nearby bracken I found that tree seedling densities averaged 3.0 times higher in the forest than in bracken (34,515 ± 6066 versus 11,557 ± 5482 seedlings ha^{-1}). I also found roughly similar stem-size density ratios both in forest and bracken and a markedly lower ratio of saplings to large seedlings in bracken than in forest. The difference for tree seed rain was 1.7 times (forest 1605 ± 335 versus bracken 949 ± 582 versus tree seeds m^{-2} yr^{-1}), and for the seed bank was 0.9 times (264 ± 99 versus 304 ± 236 viable tree seeds m^{-2}). The difference for seed persistence rates was 2.0 times (59.4 ± 2.4% versus 29.9 ± 2.4% per three-day period) though much greater contrasts would arise when these losses are compounded over longer periods. I also recorded markedly higher rodent densities in bracken versus forest (25.7 ± 5.4 vs. 5.0 ± 1.6 rodents per 100 trapping sessions) and observed that rodents were the most frequent visitors to locations where seeds were placed. These numbers and observations indicate that tree seed arrival and low tree seed persistence (likely removal by rodents) can explain the limited recovery of forest vegetation in bracken.

I also found that the effects of bracken on seed germination, seedling survival and growth of forest trees are both facilitative and inhibitory (Paper III). These results are from a replicated multi-block field experiment where I examined both pioneer and late successional tree species in six treatments: 1) undisturbed ferns control (‘‘Bracken’’), 2) fern fronds cut and removed but litter left intact (‘‘Cut’’), 3) ferns and coarse litter removed “Cut and litter removed”, 4) fern fronds pinned down ‘‘Bent’’, 5) bracken and soil removed and replaced with forest soil “Forest soil” and 6) bracken and rhizomes removed but soil returned “Bracken soil”. While pioneer species generally performed better in bracken-free plots, late-successional species germinated better and had better seedling survival in full bracken. Taken together these studies imply that bracken hinders establishment of pioneer species but favours late-successional species. This ecological filter appears to be determined by shade and by soil mediated processes and contributes to stalled succession as most seed inputs are from pioneers.

Furthermore, I found that damage to artificial seedlings in Bwindi's disturbed areas surpasses the damage frequency reported in other montane forests, likely reflecting the density of large vertebrates in our site. While most damage was attributable to animals, most of the variation among sites was due to plant debris. As seen in Papers I and II, seedling densities in these open areas are low due in part to limited seed rain and low seed persistence. In these circumstances a 61.3% non-species specific damage rate will further slow recovery.

With these studies, I have investigated the multiple factors influencing forest recovery in bracken-dominated areas in the African Highlands. These are the first ecological studies of bracken in equatorial Africa. Taken together the studies show that poor regeneration in bracken-dominated areas reflects multiple factors operating in concert. These include distance (dispersal) limitation, lack of perches, seed predation, shading, soil mediated processes, vertebrate damage and suppression by climbers. Low seed arrival, seed predation and poor seedling establishment and growth in particular appear sufficient to constrain forest recovery.

Synopsis

Introduction

The taxonomy, distribution and ethnobotany of bracken ferns

TAXONOMY

Bracken ferns have had a long, complex and controversial taxonomic history. The ferns were first named *Pteris aquilina* (Linnaeus, 1753) and later renamed *Pteridium aquilinum* (Kuhn, 1879). The ensuing debates gave rise to over 135 variants of bracken until the study of Tryon (1941) which reduced the variants into a single species *Pteridium aquilinum* (L.) Kuhn, two subspecies and 12 varieties (Page, 1976; Marrs & Watt, 2006; Thomson, 2004). While Tryon's study settled the debate on bracken's classification at the genus level, the subordinate taxa sparked controversy and continue to attract attention (Ashcroft & Sheffield, 1999; Page, 1989; Schwartsburd, 2018; Zhou *et al*., 2014).

The genus *Pteridium* can be differentiated from other Pteridophytes based on morphological characters such as rhizome hairs, frond colour, frond size, hairiness of the lower surface of fronds and laminar architecture (Tryon 1941; Marrs & Watt, 2006). The ferns have an extensive repeatedly branched underground rhizome, sometimes bearing hundreds of fronds which can grow up to 4 m tall (Marrs & Watt, 2006; Roos *et al*., 2010). Sub-taxa within the genus *Pteridium* can also be differentiated based on morphological characters. For instance, *Pteridium arachnoideum* has shortened, thickened, bent and tuberculate hairs on and between veins while *Pteridium caudatum* has generally simple sparse hairs on veins (Thomson & Alonso-Amelot, 2002). The fronds of *Pteridium arachnoideum* are also generally darker while those of *Pteridium caudatum* have lighter green colouration (Alonso-Amelot & Rodulfo-Baechler, 1996). However, due to high phenotypic plasticity, few diagnostic characters and high potential for intermediates between the described taxa (see Marrs & Watt, 2006), morphological characters may not be sufficient for a clear differentiation of sub-generic taxa.

Recent taxonomic studies have avoided this problem by employing molecular approaches (Der *et al.*, 2009; Speer, 2008; Thomson, 2012; Zhou *et al.*, 2014; Wolf *et al.*, 2015).

Bracken in Sub-Saharan Africa belongs to two sub-species of *Pteridium aquilinum* i.e. *Pteridium aquilinum* ssp *centrali-africanum* or ssp *capense* (Der *et al.*, 2009; Marrs & Watt, 2006; Thomson *et al*., 2005).

DISTRIBUTION

Bracken occurs throughout the world with the exception of arctic (and antarctic), alpine and desert regions and the southern tip of South America (Holm *et al*., 1997; Marrs & Watt, 2006; Page, 1976). It is the most widely distributed pteridophyte and ranks among the five most common vascular plants in the world (den Ouden, 2000; Marrs & Watt, 2006). Bracken plants can outcompete other vegetation and survive physical damage, wildfire and drought due to the fern's physiological and morphological properties, including large and deep rhizomes, high productivity, deep litter and efficient water use (den Ouden, 2000; Marrs & Watt, 2006; Marrs *et al*., 2000).

Bracken is generally considered a forest species though it is common in open environments (Marrs & Watt, 2006). It grows in a wide range of soils (Marrs & Watt, 2006; Watt, 1940). Bracken is mycorrhizal though the relationships remain poorly characterised (e.g., Cooper, 1976; see also Marrs & Watt, 2006). Bracken spreads and disperses both through spores (sexual) and through clonal growth of the perennial rhizome (asexual) (see Marrs & Watt, 2006).

In the East African Highlands bracken already forms stands over large areas where it is widely believed to impede forest recovery and reduces local conservation values (Masozera, 2004; Plumptre *et al*., 2002; Ssali *et al*., 2017). Bracken stands are likely to expand in the African equatorial Highlands in future as human disturbance, droughts and fire are predicted to increase (IPCC, 2014).

ETHNOBOTANY

Several vernacular names have been given to bracken: *Anuhe* in New Zealand, *Einstape* in Norway, *Olulele* in Tanzania, *Samambaia* in Brazil, *Umbewe* in South Africa and *Warabi* in Japan (Gil da Costa *et al*., 2012; Kisangau *et al*., 2011; Leach 2003; Måren, 2009; Maroyi, 2014). Even in English several common names have been used: Bracken, Brake, Hog Brake, Upland Fern, Eagle Fern, Umbrella Fern, Erne Fern and Turkey-foot Fern (Weatherby, 1952). The name 'bracken' derives from the German word *brache* or *brache-feld*, meaning land yet uncultivated or left 'open' following fallow years (Rymer, 1976).

Bracken has been valued for food, medicine and other cultural aspects in various parts of the world (McGlone *et al*., 2005; Marrs & Watt, 2006; Rymer, 1976). For instance, bracken used to be a staple for the Maori communities in New Zealand (McGlone *et al*., 2005; Leach, 2001; Leach, 2003) and the Batwa in Uganda—who used to eat young croziers when they still lived in Bwindi forest (ITFC unpublished data). Young croziers are still eaten in Indonesia and Japan and in many African countries (D. Sheil pers. comm., Hirono *et al*., 1972; Maroyi, 2014). Bracken has also been used as packaging material for fruits and for wrapping heads of curing cheese in Venezuela (Mitich, 1999; Tryon, 1982). It has also been used as an ingredient in beer brewing in Norway (Fernandes & Orita, 1991). As a medicine, bracken has been used to cure several ailments including rickets, nose bleeding, wounds, oral candidiasis and tuberculosis in Tanzania and in the UK (Kisangau *et al*., 2011; Rymer, 1976).

Bracken fern has also been used for mulching, basket making, soap making and glass making. The fronds have been used as thatching for houses and bedding for livestock and as fuel in brick making, brewing and heating (Rymer, 1976; Taylor & Thomson, 1998; Tryon, 1941).

However, bracken ferns are toxic to humans and most animals including cattle, sheep, pigs and horses (Hopkins, 1990; McGlone *et al*., 2005; Wilson *et al*., 1998). Even young fronds, though widely consumed (see e.g. Maroyi, 2014; Rymer, 1976), contain high concentrations of toxic compounds (Gil da Costa *et al*., 2012). The toxic compounds can be passed through milk, meat and water (Gil da Costa *et al*., 2012; Pamucku *et al*., 1978).

Bracken ferns and stalled forest succession

Considerable areas with stalled succession occur in forested regions worldwide (for a review see Royo & Carson, 2006). These areas likely result from various exogenous and endogenous factors including dispersal limitation, interference from dominant herbaceous plants and recurrent damage to regrowth (Boyes *et al*., 2011; Gunaratne *et al*., 2014; Royo & Carson, 2006; Thrippleton *et al*., 2018). Succession—defined as a long-term directional change in community composition, structure and function following a disturbance event (see Ghazoul & Sheil, 2010; Glenn-Lewin & van der Maarel, 1992)—may be delayed or stalled in bracken-dominated clearings due to factors associated with bracken itself or other influences within the ecosystem.

The succession of forest communities is usually initiated and maintained by forest cover expanding into nearby deforested areas. During this process stem numbers increase through tree colonization until canopy space is filled and then decrease as larger trees increasingly become dominant (Eggeling, 1947; Ghazoul & Sheil, 2010; Glenn-Lewin & van der Maarel, 1992). Ferns, herbs, shrubs and climbers typically form the initial ground cover and later give way to woody colonists—usually pioneer trees—which establish and become dominant. This early woody regeneration is derived primarily from the seed rain, soil seed bank and sprouts of remnant trees or from the nearby forest patch (Esaete *et al*., 2014; Ghazoul & Sheil, 2010; Long *et al*., 2015). However, succession may be delayed or even stalled if disturbance events extensively remove the vegetation and soil seed banks and if the remnant forest patches or seed trees are far away (Boyes *et al*., 2011; Marques & Burslem, 2015; Pickett *et al*., 1999). Studies have suggested that stalled succession can result from interference by herbaceous vegetation (see George & Bazzaz 1999a; 1999b; Meiners, 2014; Royo & Carson, 2006), but in many contexts—including equatorial Africa—the mechanisms involved remain unclear.

In this thesis (Papers I-IV), I investigated the mechanisms and factors which prevent regeneration of forest tree species at different life stages (Fig. 1). I examined if processes at early life-cycle stages are influenced by the presence of bracken and if this influence is dependent on the bracken canopy, litter, rhizome or soil mediated processes (Papers I and III). I also examined if the limited forest regeneration in bracken compared to forest is related to differences in recruitment limitation (namely seed arrival, persistence and predation) and if this limitation reflects perching animals as dispersal agents (Papers I and II). Furthermore, I explored if fire, stem damage and climber interference are involved (Paper I). Lastly, I assessed the intensity and pattern of seedling damage in different contexts including bracken dominated clearings (Paper IV).

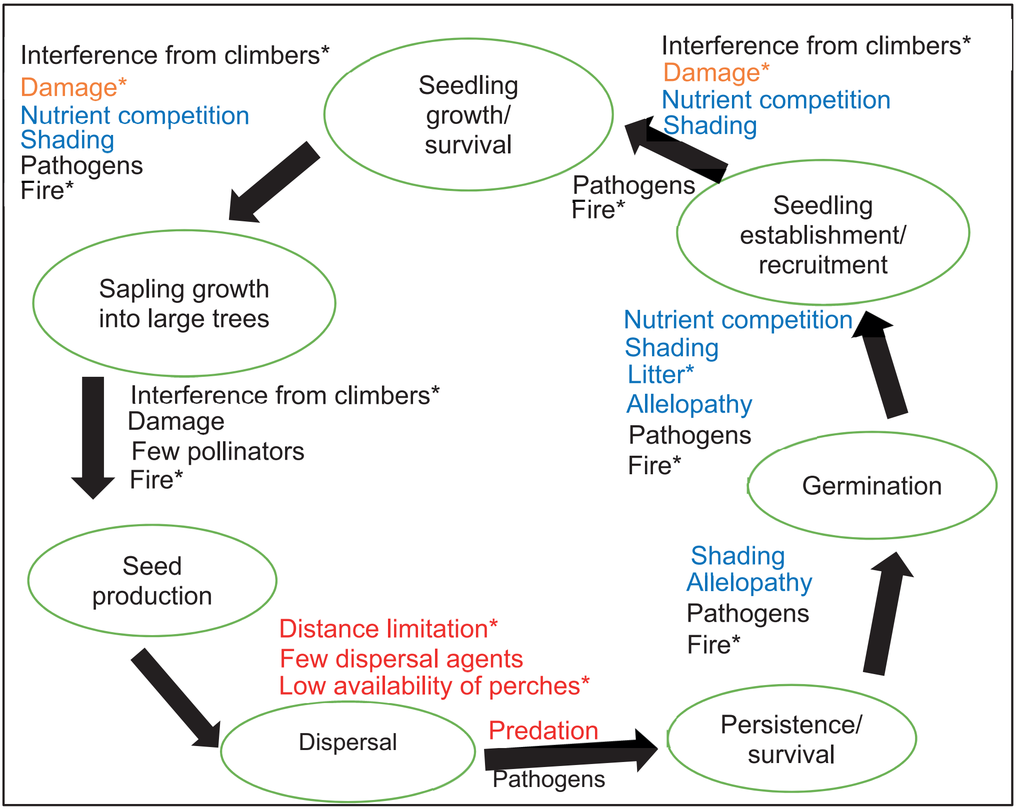

Figure 1. Mechanisms and factors that might explain the influence of bracken on tree regeneration at different life stages. The mechanisms and factors examined in this thesis are denoted in red (Paper II), blue (Paper III), orange (Paper IV) and with asterisks (Paper I).

Materials and methods

Study area

Bwindi Impenetrable National Park (henceforth "Bwindi") is a UNESCO World Heritage site located at 0°53'–1°08' S, 29°35'–29°50' E near the equator in South-West Uganda (Fig. 2a). The park spans 1,160–2,607 m asl and is one of the most important forests for biodiversity conservation in East Africa, containing many endemic and threatened species (Butynski, 1984; Hamilton *et al*., 2000). Bwindi's main vegetation has been classified as moist lower montane forest (Hamilton, 1982; Howard, 1991). The climate is tropical with two rainfall peaks from March to May and September to November. Annual rainfall ranges from 1,130 to 2,390 mm and the mean temperature ranges between 7°C and 29°C determined primarily by elevation (Kasangaki *et al*., 2012). The driest months are December-January and July-August.

Bwindi has a steep and rugged topography, with extensive clearings in some areas of the forest, which were created by past fires, logging, mining and human settlements prior to the establishment of the national park (Babaasa *et al*., 2004; Olupot *et al*., 2009; Ssali *et al*., 2017). In many areas, these clearings are dominated by bracken fern *Pteridium aquilinum* ssp *centrali-africanum* or ssp *capense* (Marrs & Watt, 2006; Ssali *et al*., 2017; Thomson *et al*., 2005). The African mountain bamboo *Yushania alpina* (K. Schum.) Lin. and various Acanthaceae including the thicket-forming *Mimulopsis solmsii* Schweinf. and *Mimulopsis arborescens* C.B. Clarke also dominate other areas both in the continuous forest and in the open clearings (Sheil, 2012). The forest is home to several large mammals including elephant *Loxodonta africana* Blumenbach, mountain gorilla *Gorilla beringei beringei* Matschie (see Fig. 2 b-c), bush pig *Potamochoerus larvatus* F. Cuvier, black-fronted duiker *Cephalophus nigrifrons* Thomas and yellow-backed duiker *Cephalophus silvicultor* Afzelius (Olupot & Sheil, 2010, Ssali, *et al*., 2012, Mugerwa *et al*., 2013).

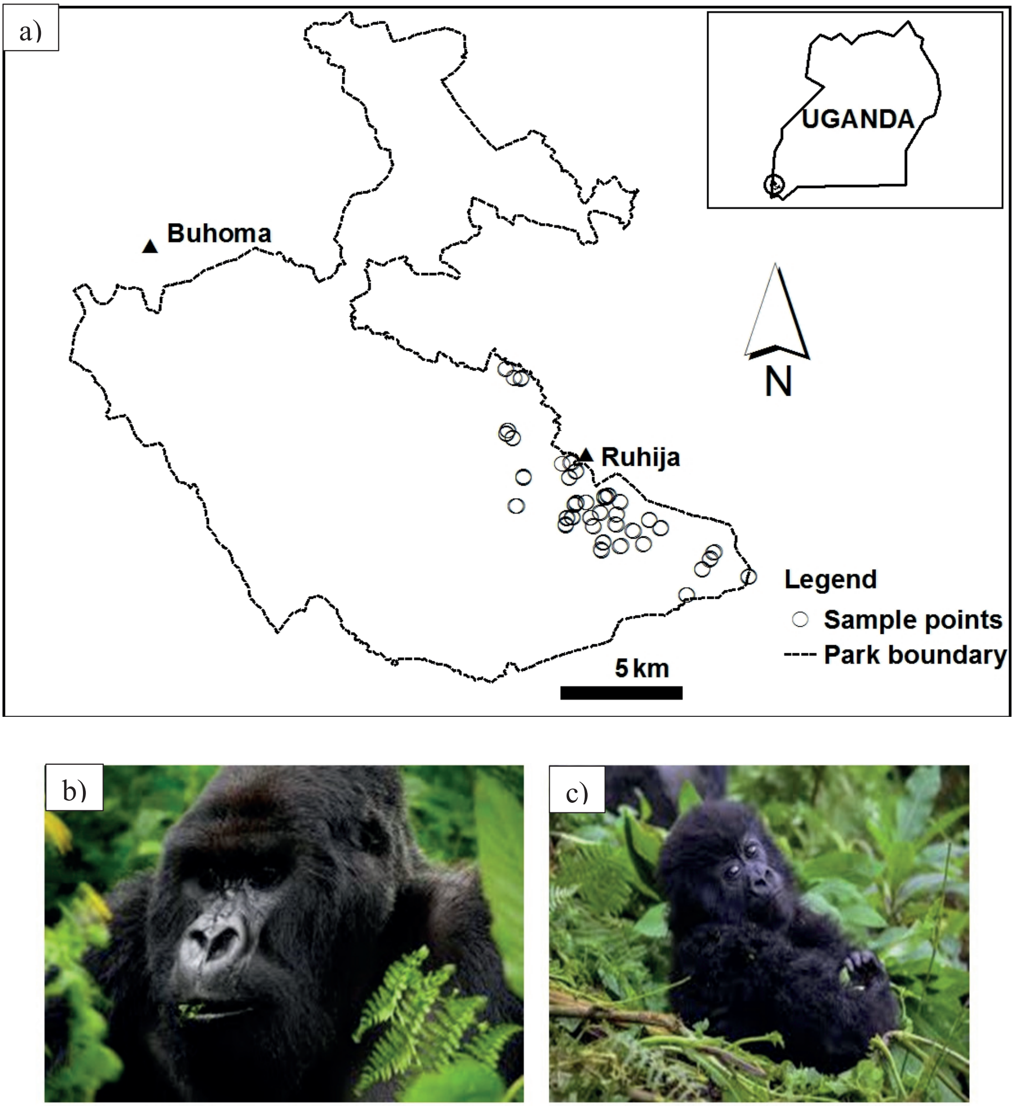

Figure 2 a) The location of sample plots in the Bwindi Impenetrable National Park, Uganda; **b-c)** mountain gorillas in Bwindi's bracken-dominated vegetation. Photos: D. Sheil.

Methods specific to Paper I

Data collection

In **Paper I**, we made a start at examining how bracken interferes with forest recovery at the bracken-forest interface. We selected 40 bracken-dominated clearings (see Fig. 3) and placed one 50 × 5-m transect in each clearing across the forest-bracken boundary with the 25-m point at the interface and 25 m extending into both the bracken patch and forest. In each transect, we recorded all woody stems and the number of bracken fronds in 1-m^2 quadrats established every 5 m. We interviewed local informants, who had worked in these forests for many years, about the history of each site. Site history data collected per transect were: occurrence of past logging, landslides and fire (we also asked the key informants to estimate the first and last years when each site was burnt). We also recorded site data: litter depth, canopy openness, basal area, density of herbaceous plants, elevation, inclination and bracken patch size. After initial exploration of the data, we measured seed size and bark thickness for each of the 25 most abundant tree species.

Statistical analyses

We used non-parametric tests to examine stem abundance in each third of a 50-m transect, i.e. forest (40 83.5-m^2 plots), edge (40 83.5-m^2 plots) and bracken (40 83.5-m^2 plots) and also estimated patterns over each 25 m^2 5 m-transect segment. Given the variation in the accuracy and precision of our explanatory variables we avoided multivariate approaches that are known to be sensitive to these differences (Biggs *et al.* 2009).

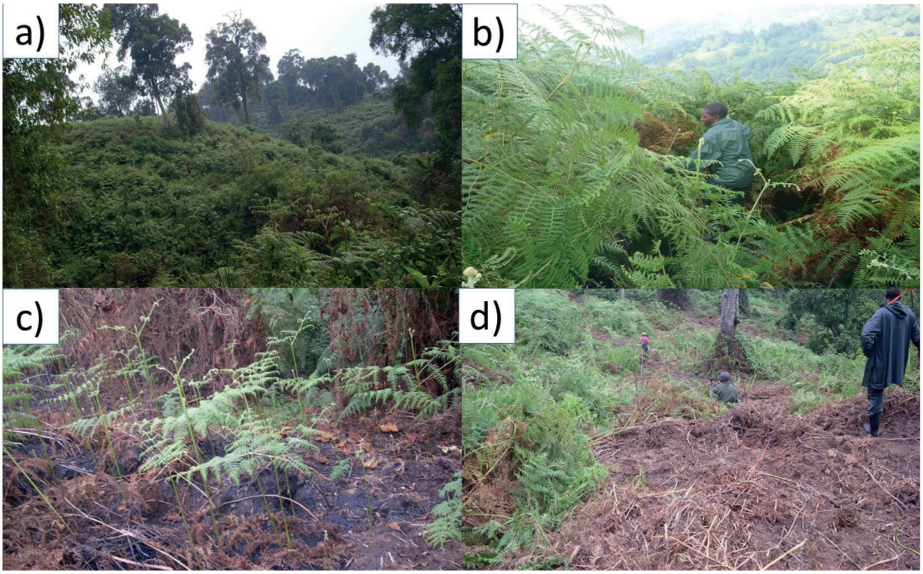

Figure 3 a) A landscape view of a bracken-dominated clearing in the Bwindi Impenetrable National Park, Uganda; **b)** dense and tall bracken in a clearing; **c)** bracken regenerating in a burnt area; **d)** bracken-dominated clearing trampled by elephants. Photos: F. Ssali.

Methods specific to Paper II

Data collection

In **Paper II**, we examined if differences in seed rain, soil seed bank or seed removal can, individually or in combination, explain the differences in tree regeneration found between bracken dominated areas and the neighbouring forest. We assessed seed rain by placing seed traps along ten transects established at the forest-bracken interface. Seed traps were visited every two weeks and the trapped material collected and processed at the research station. To assess the soil seed bank, we collected soil samples in the forest, at the edge and in bracken along each of the ten transects. The soil samples were washed to separate soil from seeds, spread in trays and placed in a transparent polythene shelter for 6 months. The trays were watered and checked for emerging seedlings every 2 days. To assess seed removal, we placed wooden trays, each with 13 different seed species, in eleven locations along each of the ten transects. We recorded the number of seeds removed every 3 days in ten-census periods. Furthermore, we used Sherman live traps to assess rodents: the traps were placed at eleven 5-m positions along the transects. Species and weight of each rodent were recorded before release. We also attempted to identify the animals implicated in seed removal by deploying camera traps along seven transects during the last three days of the seed removal study (see Fig. 4).

Statistical analyses

We examined stem abundance, seed rain, soil seed bank and seed removal in three segments of the 50 x 5-m transects, i.e. "forest", "edge" and "bracken". To examine whether seedling densities, seed rain and soil seed bank differed between forest and bracken, we calculated the degree of dissimilarity between the abundance of each common woody species in bracken versus that in the forest using a modified Bray-Curtis dissimilarity index (Bray-Curtis, 1957).

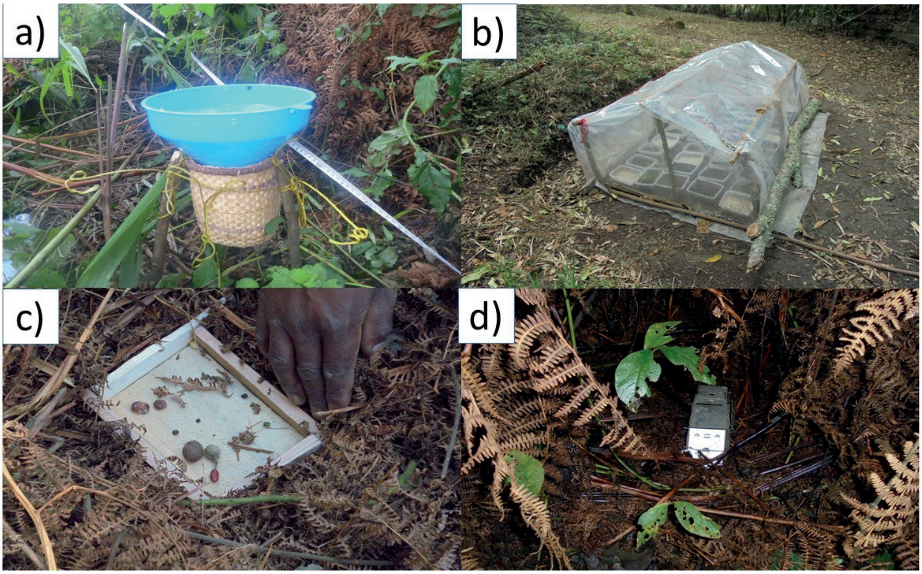

Figure 4 a) One of the seed traps used to assess seed rain; **b)** trays containing washed soil samples and seed-free sand placed in a transparent polythene shelter; **c)** one of the wooden trays used to assess seed removal; **d)** a Sherman live trap set in a bracken-dominated area. Photos: F. Ssali.

Methods specific to Paper III

Data collection

In **Paper III**, we experimentally examined tree seed germination, seedling survival, and seedling growth under field conditions in 120 1 x 1-m plots spread across five sites. Each site had four sets of six treatments: 1) ferns left undisturbed as a control (‘‘Bracken’’), 2) ferns removed by cutting fronds and leaving the litter intact (‘‘Cut’’), 3) ferns and all the coarse litter removed by cutting fronds and raking the litter “Cut and litter removed”, 4) fern fronds bent toward the edges of plots to reduce bracken shade ‘‘Bent’’, 5) bracken removed with the surrounding soil and replaced with soil from non-bracken areas “Forest soil” and 6) bracken removed by cutting fronds and digging and incorporating rhizomes into the soil “Bracken soil” (see Fig. 5).

To examine seed germination, we placed seeds of 14 woody species in all experimental plots. Plastic containers, open at both ends and covered on top with a 5 x 5-mm wire-mesh to keep out rodents, were placed in two 50 x 50-cm stations within each plot. We used a funnel to deposit 10 seeds (for the 10 small-seeded species) or 5 seeds (for the four large-seeded species) in each open container to avoid crowding. An additional open container was placed at each station to control for any seed rain. We then covered each seed station with a wire-mesh tied to wooden sticks with flexible wire. Each site was checked every two weeks between June 2015 and December 2015 and the number of germinated seeds recorded.

Seedling survival and growth were assessed by monitoring forest tree seedlings (n = 8 species) transplanted into the experimental plots. We watered all the seedlings on the day of planting, two days after planting and two weeks after planting to avoid desiccation. Seedling growth, damage and mortality were recorded every month for a period of one year. The height of each seedling was measured with a ruler from the base of the stem to the apical meristem. Height measurements made within three days after planting were used as initial height.

Statistical analyses

To examine the effect of bracken on seed germination and seedling survival, we tested for differences in the proportion of germinated seeds and surviving seedlings by fitting binomial generalised linear mixed-effects models (GLMM). We used the function *glmer* from package lme4 (Bates *et al*., 2015) to fit the GLMMs and selected the most parsimonious models following Crawley (2013) and Zuur *et al*. (2013). To examine whether seedling performance was affected by bracken, we tested for differences in relative seedling growth rates between the treatments by fitting a linear mixed effects model (LME) using the function *lme* and the R package lme4.

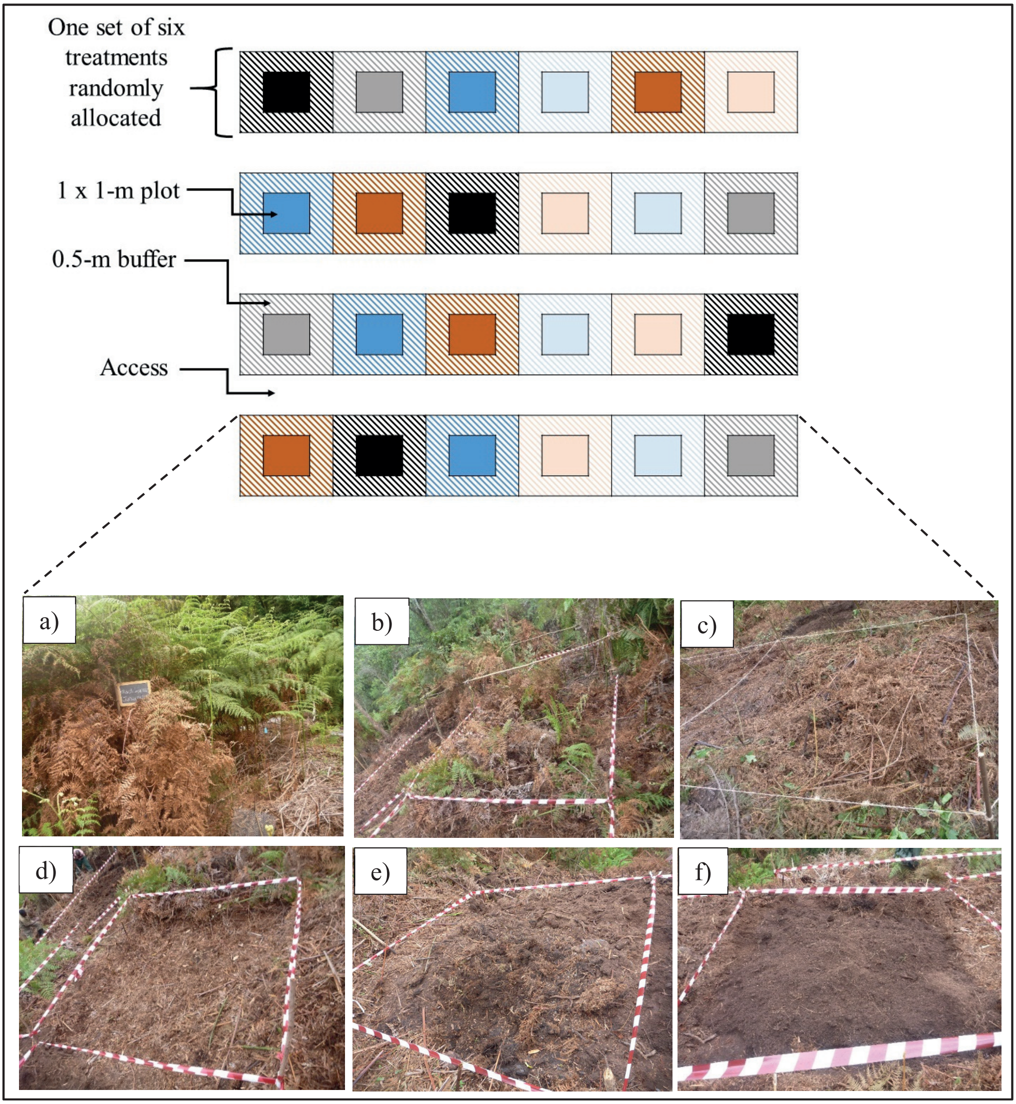

Figure 5: Layout of bracken-removal treatments replicated in five study sites: a) Bracken, b) Bent, c) Cut, d) Cut and litter removed, e) Bracken soil and f) Forest soil. Photos: F. Ssali.

Methods specific to Paper IV

Data collection

In **Paper IV**, we used artificial seedlings to determine how much damage occurs and how it varies with location following the approach developed by Clark and Clark (1989). We located the artificial seedlings in 106 slope-based plots. In each plot, we recorded slope position, GPS coordinates and dominant understorey plants. We measured or estimated: 1) canopy openness, 2) basal area, 3) slope angle, 4) elevation, 5) number of trees supporting large masses of climbers and 6) distance from the nearest bracken clearing. We also determined the shortest horizontal distance between each plot and park boundary, motorable road and water source from the Bwindi GIS database using ArcGIS 10.5 (ESRI, 2011). The ‘seedlings’ were relocated and examined every month from July 2011 to February 2013. For comparison with other studies, three categories of damage were recorded: damage due to vertebrates, damage due to plant debris and the damage due to unknown agents (see Fig. 6).

We conducted a second smaller study to assess which animals might be impacting the artificial seedlings in and around bracken-dominated areas. We did this by deploying camera traps for 30 days along eight additional transects in the forest (25 m), at the edge (0 m) and in bracken (25 m). Ten artificial seedlings were placed 1-m apart within view of each cameras. Both the cameras and ‘seedlings’ were relocated in April 2015, after 30 days of the study. Unlike in the first study, we did not classify damage. Taxonomy follows Wilson and Reeder (2005).

Statistical analyses

We evaluated the factors associated with damage to artificial seedlings (a binary response: damage or not damaged) by fitting generalized linear models (GLMs) with negative binomial errors. We used the function *glm.nb* from the R “MASS” package (Venables & Ripley, 2002) to fit the GLMs and selected the best models by first fitting saturated models with fixed effects and two-way interactions and sequentially removing the least significant terms starting with the interactions using the update function (Crawley, 2013; Zuur *et al*., 2013). To permit comparisons, we also calculated annual rates using a modified formula from Sheil *et al*., (1995): $100\,(1-(1-(N_t/N_0)/100)^{12})$, where N_0 and N_t are the number of artificial seedlings at the start and the number of damaged artificial seedlings at the end of each monthly census, respectively.

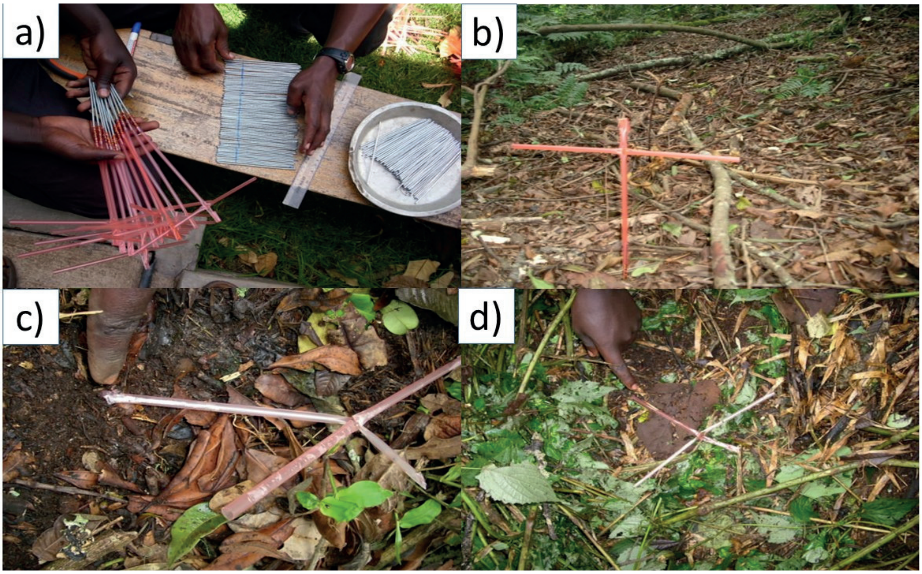

Figure 6 **a)** Newly manufactured artificial seedlings; **b)** an artificial seedling planted near fallen plant debris; **c)** an artificial seedling damaged by unknown agents; **d)** an artificial seedling damaged by a young elephant (note the size of the elephant dung). Photos: F. Ssali.

Results and discussion

Taken together, the studies presented here indicate that bracken-dominated clearings in Bwindi are long-lived and locally abundant and that low seed arrival and persistence (high rates of seed removal), poor seedling establishment and growth and high frequency of seedling damage can explain the reduced regeneration in bracken. Specifically, in **Paper I** we found that multiple factors impede forest recovery in the presence of bracken. Dispersal limitation, damage by vertebrates and suppression by climbers all offered plausible explanation for poor tree regeneration in bracken. In **Paper II** we found that recruitment limitation due to limited seed arrival and low persistence of unburied seeds contributes to both the slow recovery of forest in bracken dominated areas and to the composition of the tree species that occur. In **Paper III**, we found that bracken acts as an ecological filter that removes early successional species from the seedling community by hampering their germination, survival and growth through shading and soil mediated processes. In **Paper IV**, we found that damage surpasses 60% per stem per year suggesting that damage contributes to reduced regeneration in areas already depleted by low seed arrival and poor seedling establishment and growth.

3.1 Plausible mechanisms for impeded regeneration in bracken

Our exploratory investigation (**Paper I**) indicated that bracken-dominated clearings are persistent and have near-negligible regeneration. Distance limitation, lack of perches, damage by vertebrates and suppression by climbers all offer potential explanations of impeded regeneration in bracken. We found that bracken thickets had substantially lower densities of woody plants at all life stages than the nearby forest. The lower density of juvenile trees in bracken versus forest, in particular, indicates that progression from seed production to seedling establishment is impeded. We also found that all our bracken clearings had been affected by fire. In Bwindi many areas were burnt before the forest became a National Park in 1991 (Butynski, 1984). Since gazettement, fire occasionally occurred following droughts especially near the Park boundary (Olupot *et al*., 2009). We found that large trees regenerating in bracken (**Paper I**, Fig. 4b) had thicker bark than those in the forest, suggesting tree species that are better protected against fire are favoured over those that are less well defended (Pausas, 2015; Pellegrini *et al*., 2017).

We also found that seedlings and saplings in bracken and at the forest edge, suffer a greater burden of climbers than stems growing in forest (**Paper I**, Fig. 4f). Climbers compete for light, water and nutrients, suppress growth and are known to increase mortality and retard forest succession (Schnitzer *et al*., 2004; Tobin *et al*., 2012). From this we infer that regeneration in bracken, and at the forest edge, is likely hindered by climbers. Furthermore, woody species present in bracken, and at the forest edge, had a greater proportion of damaged stems than those in the forest (**Paper I**, Fig. 4e). We believe that this is due to animals (as seen in Paper IV). Studies show that trees in more open habitat tend to suffer greater damage (Laws *et al*., 1975, Ssali *et al*., 2012). Such damage appears to impede regeneration of trees in bracken and is a topic we examine in greater detail in Paper IV.

3.2 Low seed arrival and high rates of seed removal limit recruitment in bracken-dominated areas

Paper II results show that when compared to the neighbouring forest, bracken thickets not only had fewer seedlings, saplings and large trees but also received fewer seeds and any unburied seeds were more likely to be removed (reduced persistence). Both the limited seed arrival and the low persistence of unburied seeds appear sufficient to limit establishment of tree seedlings in bracken-dominated clearings. The low density of seeds in the soil seed bank, which is similar across the forest and bracken, plays no major role in generating the differences in regrowth, though it is clearly important for the local abundance of the treelet *Clutia abyssinica* (**Paper II**, Fig. 2c). The proportion of seeds removed over 3 days was considerably higher in bracken than in the forest with rates of removal for some tree species like *Neoboutonia macrocalyx* and *Olinia rochetiana* differing by a factor of two or three, with these differences accentuated by compounding over longer periods (**Paper II**, Fig. 3). The per-species relative abundance of seedlings in the forest versus bracken had a significant positive relationship with the per-species relative abundance of the seed rain but had no relationship with the per-species relative abundance of viable seeds in the soil. The low persistence of seeds in bracken is likely related to the high densities of rodents. Taken together, these findings indicate that recruitment limitation contributes to the limited establishment of trees in bracken, and that these factors differ among species and thus influence species composition.

3.3 Dominant interactions limiting seed germination and seedling survival and growth in bracken

We tested the hypothesis that bracken affects seed germination and survival and growth of seedlings through a range of interference processes (**Paper III**). Seed germination and seedling survival of late-successional species such as *Syzygium guineense* and *Vepris nobilis* were higher in full bracken than in bracken-removal plots (**Paper III,** Fig. 3; Fig. 5). This implies that bracken and litter play an important role in moderating the conditions for germination and seedling establishment. In contrast most pioneer species such as *Macaranga capensis* and *Ficalhoa laurifolia* consistently germinated, survived and grew better in bracken-removal plots than in full bracken. Thus, it seems clear that the effects of bracken hamper establishment and progression of pioneer species to later life-cycle stages. Taken together, and acknowledging that most seeds arriving in bracken are likely to be pioneers (see Ssali *et al*., 2017), these results imply that the filtering imposed by bracken will slow or prevent forest recovery.

Bracken's negative impact on the germination and survival of early successional species, versus the positive influence on late successional species is striking. Others have noted that allelopathy—here defined as the direct plant-plant interference mediated by allelochemicals produced by bracken—appears to play a greater role in the ecological relationships of pioneer versus shade tolerant species (Meiners, 2014). In the study of bracken elsewhere both negative (interference) and positive (facilitating) responses have been observed (Dolling, 1996; Günter *et al*., 2009; Gallegos *et al*., 2015; Marrs *et al*., 2000), but we believe that ours is the first to record both within one community. This may reflect growth potential or more complex interactions via the soil (Mariotte *et al*., 2018; Meiners, 2014). The ecological, evolutionary, and practical implications of these differences warrant further evaluation.

This study (**Paper III**) provides evidence of both inhibition and facilitation by bracken. While pioneer species performed better in bracken-free plots, late-successional species germinated better and had better seedling survival in full bracken. Bracken acts as an ecological filter that removes early successional species from the seedling community by hampering their germination, survival and growth through shading and soil mediated processes.

3.4 The role of damage in limiting forest recovery

In **Paper IV**, we found that the mean likelihood of a seedling experiencing damage (i.e., 61.3% per stem per year) was higher than that reported in other tropical montane forests but lower than the damage rates in several lowland sites (**Paper IV,** Table 4). Most of the damage in our site was attributable to animals while most of the variation was due to plant debris. Artificial seedlings experienced a higher frequency of damage in more (versus less) open areas, farther (versus nearer) from roads and on relatively gentle (versus steep) slopes. The observed increase in damage frequency with canopy openness appears to reflect a higher abundance of falling plant debris and foraging animals in open versus closed forest. The frequency of vertebrate damage increased with distance from the nearest road and this likely reflects the combined influence of traffic and sharp habitat edges. Further, damage frequency declined with progression from lower-slope to mid-slope to hilltop sites, likely indicating that animals are more abundant in these lower slope habitats.

Though artificial seedlings located in bracken suffered less damage compared to some other vegetation types, such as the short understorey herbs (damage per year was 47.0 ± 10.7% in bracken vs 60.1 ± 2.6% in the short understorey herbs), the damage appears sufficient to further impede the slow forest recovery seen in these areas. Indeed the herbivore activity seen at the forest edge in these areas seems likely to counteract much of the regrowth that might otherwise occur. Though it did not occur at our monitored locations, our informal observations show that elephants feed in these clearings: they pull up bracken plants and cut the rhizomes from the ground with their toes, swinging their front feet from side-to-side, a process leaving bare soil that is soon recolonised by bracken but devoid of seedlings.

Our results have implications for tree regeneration. First, seedlings, particularly those of slower growing shade tolerant species, are vulnerable to high damage frequency since they remain many years in the understorey. We thus predict that the seedlings that reach large size will be those that grow quicker and escape from vulnerable to less vulnerable (larger) sizes (see Sheil & Salim, 2004). Second, frequently disturbed areas may take long to recover due in part to a high frequency of debris damage and a perpetuating cycle in which disturbed vegetation maintains and attracts further disturbance. Finally, as seen in our studies of bracken-dominated clearings in and around Bwindi, seedling densities in these open areas are low (Ssali *et al*., 2017), due in part to limited seed rain and low seed persistence (Ssali *et al*., 2017, Ssali *et al*., 2018), and thus a 61.3% damage rate implies that such intensity of non-species specific damage will contribute to further slow recovery.

Conclusions and future perspectives

This is the first ecological study of bracken in the African tropics. Our results show that forest regeneration in bracken-dominated areas is low due to a number of factors including distance limitation, few dispersal agents, lack of perches, seed predation, shading, soil mediated processes, vertebrate damage and suppression by climbers (**Papers I-IV**). While each of the processes in the plant life cycle is important (see Fig. 1), seeds and seedlings represent the initial and most vulnerable stages. Thus, our findings indicate that forest recovery in bracken dominated areas is primarily hampered by low seed arrival and poor seedling establishment and growth. Species with readily dispersed seeds, well protected seeds and seedlings and long-term seed dormancy are best suited to establish in bracken.

The management of bracken-dominated clearings in African forests will likely become more challenging in future given that droughts and fire are predicted to increase (IPCC, 2014). The drier conditions will likely impose stronger constraints to tree seedling establishment and growth in bracken. In contrast, bracken stands will likely expand since bracken plants can cope better with dry conditions and can survive fire. Future studies need to identify effective strategies for restoration and management of bracken-dominated clearings. I have some provisional suggestions that I hope might be evaluated in the future. First, branched cuttings of figs may be planted in bracken to serve as perches for enhancing the dispersal of zoochorous species (**Paper I**). Second, bracken fronds in fenced plots—exclosures to deter rodents and large herbivores—may be cleared periodically and seeds and seedlings of shade-tolerant and light-demanding tree species added to facilitate seedling establishment (**Papers II-IV**). Third, interviewing local people about the value and significance of bracken and their practices and strategies for its control may provide alternative restoration techniques.

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Appendix: Papers I-IV

Paper I

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A first look at the impediments to forest recovery in bracken-dominated clearings in the African Highlands

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ABSTRACT

Areas dominated by bracken, *Pteridium aquilinum*, occur on every continent except Antarctica. These fern thickets appear to retard forest recovery and thus reduce forest diversity and carbon values. We examined how bracken inhibits forest recovery in the Bwindi Impenetrable National Park, Uganda. We established 40 50 × 5-m transects across the forest-bracken interface. On average, we recorded 596 ± 64 large trees (stems ha^{-1} ± 1 SE), 1440 ± 159 saplings, 33580 ± 8860 large seedlings and 31003 ± 8854 small seedlings in the forest and 45 ± 16 large trees, 114 ± 28 saplings, 7015 ± 2268 large seedlings and 6317 ± 2240 small seedlings in bracken. All bracken clearings had been affected by fire. The density of bracken was 4.9 ± 0.3 fronds m^{-2}. Our results suggest that distance limitation, lack of perches, damage by vertebrates and suppression by climbers all offer potential explanations of impeded regeneration in bracken. The sparser woody vegetation that occurred in bracken typically had smaller-seeded and thicker-barked tree species than the nearby forest and also included more pioneers and fewer animal dispersed species. Interestingly we detected a negative relationship between proximity to bracken plants and woody regeneration within the forest. Several key explanatory variables including canopy cover, litter depth, distance to forest and bracken density are correlated and hard to separate.

1. Introduction

Areas dominated by bracken *Pteridium aquilinum* (L.) Kuhn occur on every continent except Antarctica and appear to impede forest recovery (Der et al., 2009; Marrs and Watt, 2006; Marrs et al,. 1997, Page 1976). In the East African Highlands such fern thickets tend to result from droughts, fires and other disturbance processes (landslides, abandoned cultivation etc.), and already cover hundreds of square kilometres of previously forested habitat (DS pers. obs., Holm et al., 1997; TGC, 2011; Verdcourt, 1999). Bracken thickets are likely to expand in tropical Africa in future as droughts and fire are predicted to increase (IPCC, 2014).

Temperate studies indicate that common bracken, *Pteridium aquilinum* (L.) Kuhn, interferes with forest regrowth (Den Ouden, 2000; Dolling, 1996; Facelli and Picket, 1991; Gaudio et al., 2011; Priewasser, 2013). However, various interference mechanisms have been suggested and it is unclear which of these, if any, are involved in the highlands of equatorial Africa. In the Bwindi Impenetrable National Park (Bwindi), a UNESCO World Heritage site, bracken thickets are already locally abundant and appear persistent: retarding forest recovery and reducing forest biodiversity and carbon values.

There have been few ecological studies of how bracken and forest interact in the tropics. Most publications relating to bracken in Africa focus on taxonomy or control (Masozera, 2004; Thomson et al., 2005; TGC, 2011, but see Adie et al., 2011). Even outside Africa, forest boundaries adjacent to bracken-dominated clearings have received little attention despite a considerable literature on forest-edge dynamics (see Haddad et al., 2015; Harper et al., 2005; Porensky and Young, 2013 for reviews). In this paper, we examine how bracken interferes with forest recovery at the forest-bracken interface in and around Bwindi in the equatorial highlands of Western Uganda. To our knowledge, this is the first ecological study of bracken in tropical Africa.

Our objectives were to: (1) describe vegetation structure across the forest-bracken boundary, (2) determine the potential factors affecting the ability of woody species to re-colonise bracken, and thus (3) provide an initial exploration of mechanisms that might explain how bracken slows forest regrowth. Our observations and review of the literature suggested many mechanisms might be operating and that bracken might be both the cause or the consequence of impeded forest recovery (Fig. 1; see also Marrs and Watt, 2006 for a review). Crucially, these mechanisms might be operating alone or in combination so we sought to avoid misleading simplifications (see Evans et al., 2013; Hilborn and Stearns, 1982). For this exploratory investigation, we developed simple hypotheses, and predictions, associated with a subset of the candidate

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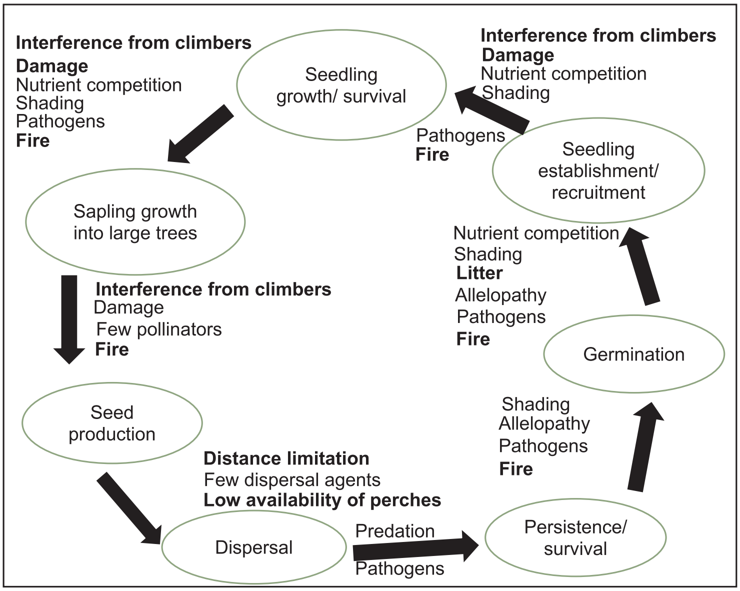

Fig. 1. Mechanisms and factors that might explain the influence of bracken on tree regeneration at different life stages. The mechanisms and factors examined in this study are denoted in bold.

mechanisms. If seed dispersal (seed limitation i.e. failure of seeds to arrive in bracken) is involved we expect a decline in regeneration with distance from seed sources, while if this limitation reflects perching animals as dispersal agents, regeneration will vary with perch availability (Saavedra et al., 2015). If bracken plants directly interfere with seed survival or germination, or with seedling establishment and growth, then we expect a negative relationship between the density of bracken and the density of woody species (den Ouden, 2000; Priewasser, 2013). If a thick litter layer impedes seedling establishment and survival (Xiong and Nilsson, 1999), we expect larger-seeded species to be relatively better represented than smaller-seeded species in the seedling population in bracken. We knew that some bracken areas had burned previously and wondered if fire was responsible for generating these areas and for keeping them open. If fire generates these areas we expect confirmation that they had all burned. If it maintains them we would expect that time since the last fire would be positively correlated with the density of woody species, and that given this rate of recovery fires would be sufficiently frequent to explain the low abundance of woody stems. Furthermore if fire plays a major role we predicted that it would be selective and that thicker-barked species would be relatively more common than thinner-barked species in affected areas due to their better survival (Pausas, 2015; Pellegrini et al., 2017). If stem damage is involved, we expect greater damage (per stem) in bracken than in forest due to higher incidence of damage in more open habitats (Ssali et al., 2012). If interference from climbers is involved (Schnitzer et al., 2004; Tobin et al., 2012), we expect stems in bracken to suffer a greater burden of climbers than those growing in forest.

2. Methods

The study took place in the Bwindi Impenetrable National Park a UNESCO World Heritage site “Bwindi” in South-West Uganda. The park is one of the most important forests for biodiversity conservation in East Africa, containing many endemic and threatened species (Butynski, 1984; Hamilton et al., 2000). Bwindi spans a range of elevations (1160–2607 m asl) and is located 0 °53′–1 °08′ S, 29 °35′–29 °50′ E near the equator and has been included in various larger regions including the “Kigezi Highlands”, the “Greater Virunga Landscape” and the “Albertine Rift Valley” (Butynski, 1984; Butynski and Kalina, 1993; Plumptre et al., 2007; Taylor, 1990). Bwindi’s vegetation is classified as moist lower montane forest (Hamilton, 1982; Howard, 1991). The forest is home to half of the world’s critically endangered mountain gorillas *Gorilla beringei beringei* Matschie. The objective of park management is the protection, restoration and improvement of the forest’s conservation value, which was affected by logging, fire and mining before it became a National Park in 1991 (Uganda Wildlife Authority: BINP General Management Plan 2014-2024).

Fieldwork was conducted between July 2015 and January 2016. We selected 40 bracken-dominated clearings with abrupt and noticeable changes in woody vegetation along the forest-bracken boundary and accessible from the ITFC research station at Ruhija (2355 m asl, see Fig. 2). To select a clearing, we searched for open areas within a day’s travel from the research station using satellite images and experienced local guides. In total we surveyed 40 bracken patches and in each we placed one 50 × 5-m transect across the forest-bracken boundary with the 25-m point at the interface and 25 m extending into both the bracken patch and forest.

In each transect, we recorded all woody stems and the number of bracken fronds in 1-m^2 quadrats established every 5 m along the transect. We also measured site data and interviewed local informants who had worked in these forests for many years about the history of each site. The site data measured were: (1) litter depth (cm, using a ruler in the centre of a 1-m^2 quadrats placed every 5 m along the transect), (2) canopy openness (%, using a densiometer in the middle and at each end of the transect), (3) basal area (m^2 ha^{-1}, using a ‘relascope’ in the middle and at each end of the transect), (4) density of herbaceous plants (number m^{-2}, visually estimated every 5 m along the transect), (5) elevation (m, using a GPS in the middle and at each end of the transect), (6) inclination (°, using a clinometer in the middle and at each end of the transect), and bracken patch size (ha, visually estimated for each transect). Site history data collected per transect were: occurrence of past logging, landslides and fire (we also asked the key informants to estimate the first and last years when each site was burnt).

In our initial exploration of the data, we determined the 25 most abundant tree species. For each of these species we subsequently

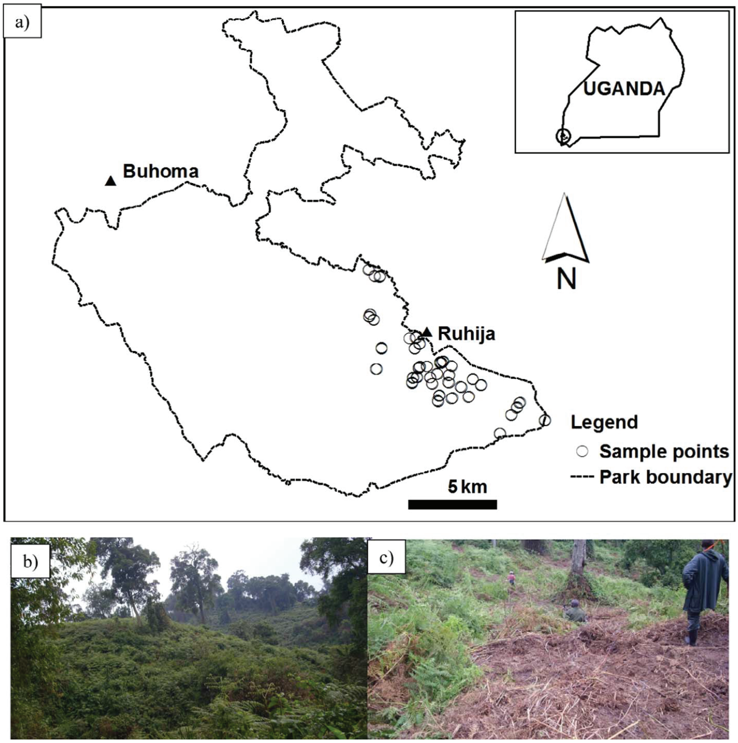

Fig. 2. (a) The 40 transects in Bwindi Impenetrable National Park, Uganda; (b) A landscape view of a bracken-dominated clearing; (c) bracken-dominated clearing trampled by elephants.

collected, dried and measured ten seeds (longest seed dimension, mm, using a caliper). To determine bark thickness, we extracted portions of the bark from four stems of each of these species (two stems 2–10 cm dbh and two that are larger than 10 cm dbh). We used a chisel at 1.3 m height and measured the fresh-cut thickness (mm) with a caliper. We used linear regressions of bark thickness versus stem diameter for each species and used this to estimate bark thickness at a reference diameter of 10 cm (see Appendix 4). We omitted one species that does not attain a diameter over 10 cm (*Clutia abyssinica*).

2.1. Analyses

Woody plants were categorized as large trees (dbh ≥ 10 cm), saplings (dbh 2–9.9 cm), large seedlings (basal diameter < 2 cm and > 30 cm tall) and small seedlings (< 30 cm tall). We also assigned the 25 most abundant tree species to successional guild (here pioneer versus non-pioneer) and dispersal types (animal dispersed “zoochorous” versus non-zoochorous) following Protabase (www.prota.org) with some additions from other references (Hamilton, 1991; Katende et al., 1995, Sheil et al., 2000). Data were analysed using R (R Core Team, 2016). Using non-parametric tests we examined stem abundance in each third of a 50-m transect, i.e. forest (40 83.5-m^2 plots), edge (40 83.5-m^2 plots) and bracken (40 83.5-m^2 plots) and also estimated patterns over each 25 m^2 5 m-transect segment. During data characterisation and checking, we performed various graphical examinations, including scatter graphs, correlations, regressions and multivariate analyses. The purpose was to characterise patterns and identify suitable analyses (Zuur et al., 2010). Given the variation in the accuracy and precision of our explanatory variables we avoided multivariate approaches that are known to be sensitive to these differences (Biggs et al., 2009). As our study is primarily exploratory rather than hypothesis-driven, we quote uncorrected P-values (Nakagawa and Cuthill, 2007).

3. Results

3.1. Clearings, stem densities and litter depth

Our bracken-dominated clearings ranged from about 0.1 ha to over 700 ha and their slope ranged between 6° and 44°. According to local informants all 40 clearings had been affected by fire, two had been last burned as recently as 2008, 14 in the 1990s, and the remainder (24) up to four decades previously (1970s and 1980s). Out of 40 clearings, 37 had been impacted by timber cutting and extraction, nine by landslides and seven by other human activity (settlements and related). On average (± 1 SE), bracken canopy in the clearings was 1.9 ± 0.05 m in height.

We recorded 21,807 woody plants comprising 19,233 small seedlings, 1617 large seedlings, 680 saplings and 277 large trees of 83 species in the 50-m transects (n = 40, Appendix 1). Dividing the 50-m transect into thirds: forest, edge and bracken (open bracken-dominated areas), on average (± 1 SE) we recorded 0.3 ± 0.1 bracken fronds m^{-2} in the forest, 2.8 ± 0.2 fronds m^{-2} at the edge and 4.9 ± 0.3 fronds m^{-2} in the bracken-dominated areas. Litter depth averaged 5.8 ± 0.4 cm in the forest, 9.7 ± 0.6 cm at the edge and 14.0 ± 1.1 cm in the bracken. The density of large trees, saplings and seedlings decreased with increasing distance from the forest, increasing bracken density, and increasing litter depth (Fig. 3). In bracken, seedling density was generally greater in transects where large trees occurred (nine of 40) than those without them though this was not significant (i.e. 11,590 ± 8543 versus 4787 ± 1556 small seedlings ha^{-1}; Mann Whitney test, W = 130, P = 0.771). Much of the difference was due to

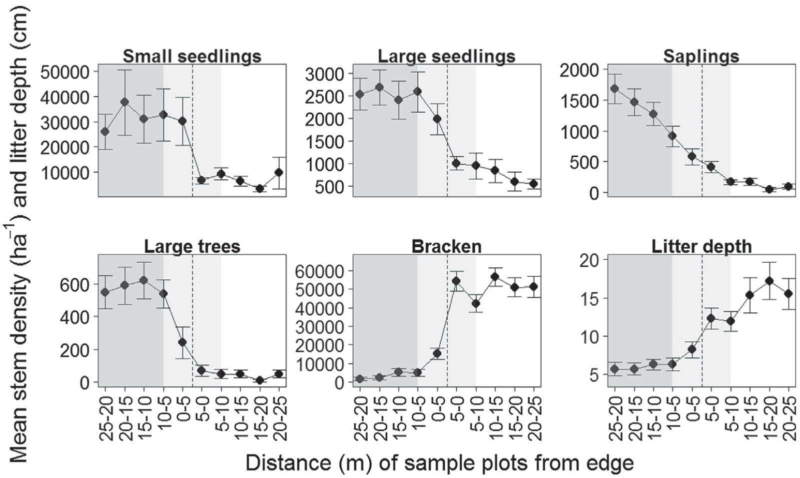

Fig. 3. Density of trees (stems ha^{-1} ± 1 SE), density of bracken (fronds ha^{-1} ± 1 SE) and litter depth plotted relative to the edge between the forest and bracken. Distance classes are successive 25 m^2 5 m-transect segment with the forest dark grey, the edge grey and the bracken-dominated area unshaded.

the animal-dispersed species which comprised the majority of seedlings when larger trees were present, though again there was no significant difference in our small sample (9940 ± 8539 versus 2163 ± 884 small seedlings ha^{-1}; W = 163, P = 0.443). Most seedlings of animal-dispersed species observed in bracken where larger trees occurred (eight transects) were not the same species as these trees (10,240 ± 9696 versus 629 ± 629 small seedlings ha^{-1}; W = 10.5, P = 0.015).

We were interested to examine whether the clearings were expanding or contracting, and hypothesised that this would be apparent from the stem-sizes in the forest edge communities, but we found no relationship between the last time a clearing had burned and the densities or size of stems in the forest edge community (for small seedlings: Kendall's correlation, $\tau = 0$, P = 1; large seedlings: $\tau = -0.04$, P = 0.733; saplings: $\tau = -0.04$, P = 0.757; large trees: $\tau = -0.1$, P = 0.435). But interestingly when we examined animal-dispersed species alone we did detect a significant negative correlation between the last time a clearing had burned and the density of small seedlings (but not of large seedlings, saplings and large trees, i.e. for small seedlings: $\tau = -0.29$, P = 0.022; large seedlings: $\tau = -0.02$, P = 0.861; saplings: $\tau = 0.05$, P = 0.707; large trees: $\tau = -0.13$, P = 0.379). We detected no significant relationship between the last time a clearing had burned and the mean bark thickness of the most abundant species though all relationships were positive (data not shown).

3.2. Species characteristics

Common species (i.e. the ten most abundant species in each segment) represent more than two thirds of all seedlings and large trees and at least 40% of saplings per segment (Table 1). The density of common woody species (all individuals included) differed substantially among the forest, edge and bracken segments. Compared to the forest and edge, fewer seedlings were present in bracken. Among the species occurring in each of the three segments, *Rytigynia ruwenzoriensis* (De Wild.) Robyns declined most between forest and bracken (i.e. a more than twenty-fold difference) while *Macaranga capensis* (Baill.) Sim declined least (i.e. a two to three-fold difference). On average, there were 557 ± 29 (stems ha^{-1} ± SE) saplings of common species in the forest, 174 ± 12 saplings at the edge and 57 ± 6 saplings in bracken compared to 1015 ± 49 large seedlings in the forest, 973 ± 43 large seedlings at the edge and 587 ± 43 large seedlings in bracken.

We explored the ratios among life stages as a potential indicator of differences in relative transition rates. Considering all stems in the 40 transects (see Appendix 1), the ratio of small to large seedlings in forest versus bracken was similar (1.08 versus 1.11), that from large seedlings to saplings was about a third (0.043 versus 0.016) and from saplings to large trees was again similar (0.414 versus 0.395).

Of the most abundant species (Appendix 2), bracken typically had a lower proportion of stems of larger-seeded species (for small seedlings: Mann Whitney test, W = 1000, P = 0.0003; large seedlings: W = 895.5, P = 8.3×10^{-6}; saplings: W = 368, P = 0.025; large trees: W = 202, P = 0.021), a lower proportion of stems of thicker-barked species (for small seedlings: W = 741, P = 0.839; large seedlings: W = 475, P = 0.01; saplings: W = 326, P = 0.043; large trees: W = 81, P = 0.092) and fewer animal-dispersed species (for small seedlings: W = 1271, P = 6.5×10^{-8}; large seedlings: W = 935, P = 4.7×10^{-7}; saplings: W = 127, P = 0.004; large trees: W = 229, P = 0.001) than those in the forest (Fig. 4). They also had more stems of pioneer species (for small seedlings: W = 1049, P = 0.002; large seedlings: W = 609, P = 0.417; saplings: W = 411, P = 0.001; large trees: W = 165, P = 0.269), a higher proportion of damaged stems (for large seedlings: W = 1132, P = 0.0009; saplings: W = 1225, P = 5.0×10^{-6}; large trees: W = 897.5, P = 0.087) and a higher proportion of stems with climbers (for large seedlings: W = 881, P = 0.236; saplings: W = 1122, P = 0.0002; large trees: W = 880, P = 0.041).

3.3. Relationships between variables

Various relationships occur among site variables and plant densities in the forest, at the edge and in bracken (Table 2). Notably, there were significant correlations between bracken density, canopy openness, basal area, litter depth and herbaceous plant density (Table 3). An examination of scatterplots and residuals (i.e. observed values subtracted from mean values per transect segment) of seedlings versus bracken density, litter depth and bracken proximity generally failed to indicate clear relationships. However, we noted that seedling and sapling densities declined with increasing litter depth in forest, edge and bracken (though only saplings in forest declined significantly) and that they also show a decline with bracken density in forest (only saplings in forest and edge had a significant decline) and have no relationship in bracken (Fig. 5; Table 2). We also found that the density of saplings per 25 m^2 5 m-segment of each transect in the forest was positively rank-correlated with distance from the nearest 25 m^2 5 m-segment containing any bracken plants indicating a negative relationship between proximity to

Table 1
List of the 10 most common woody species (all individuals included) in the forest, at the edge and in bracken showing mean density (stems ha^{-1} ± 1 SE) of their seedlings, saplings and large trees as recorded in 40 50 × 5-m transects between 2085 and 2538 m asl in the Bwindi Impenetrable National Park.

Species	Small seedlings	Large seedlings	Saplings	Large trees
Forest				
Olea capensis L.	15694 ± 8393	51 ± 19	21 ± 9	21 ± 9
Rytigynia ruwenzoriensis (De Wild.) Robyns	2886 ± 1055	252 ± 71	198 ± 47	18 ± 8
Psychotria mahonii C.H.Wright	2626 ± 667	66 ± 18	42 ± 20	63 ± 29
Macaranga capensis (Baill.) Sim	1386 ± 977	69 ± 15	54 ± 22	84 ± 32
Galiniera saxifraga (Hochst.) Bridson	1329 ± 474	54 ± 39	12 ± 6	15 ± 10
Clutia abyssinica Jaub. & Spach	1012 ± 800	228 ± 90	24 ± 11	0
Psychotria kirkii Hiern	799 ± 261	201 ± 56	153 ± 56	0
Allophylus abyssinicus (Hochst.) Radlk.	964 ± 462	57 ± 20	33 ± 13	18 ± 11
Faurea saligna Harv.	731 ± 447	9 ± 9	0	27 ± 16
Syzygium guineense (Willd.) DC.	572 ± 335	30 ± 13	21 ± 10	18 ± 8
% All species in the forest	92.7%	43.4%	42.6%	53.8%
Edge				
Olea capensis L.	6060 ± 3346	21 ± 9	3 ± 3	9 ± 7
Galiniera saxifraga (Hochst.) Bridson	3461 ± 2454	111 ± 46	6 ± 4	21 ± 11
Rytigynia ruwenzoriensis (De Wild.) Robyns	2503 ± 1802	99 ± 26	42 ± 19	3 ± 3
Psychotria mahonii C.H.Wright	2395 ± 625	96 ± 39	0	12 ± 7
Macaranga capensis (Baill.) Sim	2138 ± 1268	153 ± 48	57 ± 23	27 ± 18
Clutia abyssinica Jaub. & Spach	1243 ± 461	434 ± 96	39 ± 17	0
Faurea saligna Harv.	434 ± 246	6 ± 4	0	3 ± 3
Olinia rochetiana Juss.	305 ± 233	0	6 ± 4	12 ± 9
Psychotria kirkii Hiern	183 ± 90	36 ± 12	6 ± 6	0
Polyscias fulva (Hiern) Harms	177 ± 88	0	0	3 ± 3
% All species at the edge	95.5%	63.5%	40.4%	60.3%
Bracken				
Olea capensis L.	2126 ± 1915	0	3 ± 3	0
Macaranga capensis (Baill.) Sim	635 ± 275	216 ± 113	12 ± 7	6 ± 6
Psychotria mahonii C.H.Wright	805 ± 255	24 ± 11	15 ± 8	6 ± 4
Faurea saligna Harv.	793 ± 667	0	0	6 ± 6
Clutia abyssinica Jaub. & Spach	335 ± 99	299 ± 75	3 ± 3	0
Polyscias fulva (Hiern) Harms	554 ± 530	0	0	6 ± 6
Maesa lanceolata Forssk.	273 ± 190	3 ± 3	3 ± 3	3 ± 3
Rytigynia ruwenzoriensis (De Wild.) Robyns	117 ± 52	30 ± 16	12 ± 9	3 ± 3
Croton macrostachyus Hochst. ex Delile	117 ± 74	0	0	12 ± 7
Ekebergia capensis Sparrm.	123 ± 120	0	0	0
% All species in bracken	96.2%	82.4%	39.5%	73.3%

bracken plants and woody regeneration (Kendall's tau Appendix 3).

4. Discussion

Our data show that bracken-dominated clearings are persistent with some being older than 40 years. Compared to nearby forest, bracken thickets had substantially lower densities of woody plants at all life stages (i.e. seedlings to large trees). When considering the life-cycle of woody plants (Fig. 1), the low density of seedlings in bracken versus forest indicates that progression from seed production to seedling establishment is impeded. Some size class ratios appear roughly similar in forest and bracken (i.e. large versus small seedlings at 1.1, and larger trees to saplings at 0.4 in both): notably however, the ratio of saplings to large seedlings is much lower in bracken than in forest (0.016 versus 0.043) suggesting an increased mortality to growth ratio, in bracken.

Our exploratory evaluations supported several predictions, though in each case further research would be required to verify the implied mechanisms. The decline in regeneration with distance from the forest indicates that dispersal limitation is involved. The increased regeneration of animal-dispersed species where trees are present suggests that perches and perching animals are potentially important too.

We found that all our bracken clearings had been affected by fire. In Bwindi many areas were burnt before the forest became a National Park in 1991 (Butynski, 1984). Since gazettement, fire occasionally occurred following droughts especially due to numerous activities near the Park boundary (Olupot et al., 2009). Bracken rhizomes survive fire and produce a dense, low canopy soon after fire (Marrs et al., 2000; Roos et al., 2010). We found that large trees regenerating in bracken (Fig. 4b) had marginally thicker bark than those in the forest, suggesting tree species that are better protected against fire are favoured over those that are less well defended (Pausas, 2015; Pellegrini et al., 2017). Furthermore, we found that, rather than increasing, the density of animal dispersed seedlings declined with time since burning—we lack an explanation though it may indicate that seed predation for these species increases with time. While fire has impacted all the bracken clearings fires appear too infrequent to make fire alone a plausible mechanism for impeded regeneration and the limited woody vegetation observed in our transects.

We see that seedlings and saplings in bracken and at the forest edge, suffer a greater burden of climbers than stems growing in forest (Fig. 4f). Climbers compete for light, water and nutrients, suppress growth and are known to increase mortality and retard forest succession (Schnitzer et al., 2004; Tobin et al., 2012). From this we infer that regeneration in bracken, and at the forest edge, is likely hindered by climbers.

Woody species present in bracken, and at the forest edge, had a greater proportion of damaged stems than those in the forest (Fig. 4e). We believe that this is due to animals. In African rain forests, various large herbivores, including elephant *Loxodonta africana* Blumenbach, bush pig *Potamochoerus larvatus* F. Cuvier, black-fronted duiker *Cephalophus nigrifrons* Thomas, yellow-backed duiker *Cephalophus silvicultor* Afzelius, gorilla *Gorilla beringei beringei* Matschie and monkeys damage trees (Laws, 1970; Plumptre, 1993; Sheil and Salim, 2004; Struhsaker et al., 1996; Ssali et al., 2012; Tweheyo et al., 2013). Studies show that trees in more open habitat tend to suffer greater damage (Laws et al., 1975; Ssali et al., 2012). The reasons for such impacts are

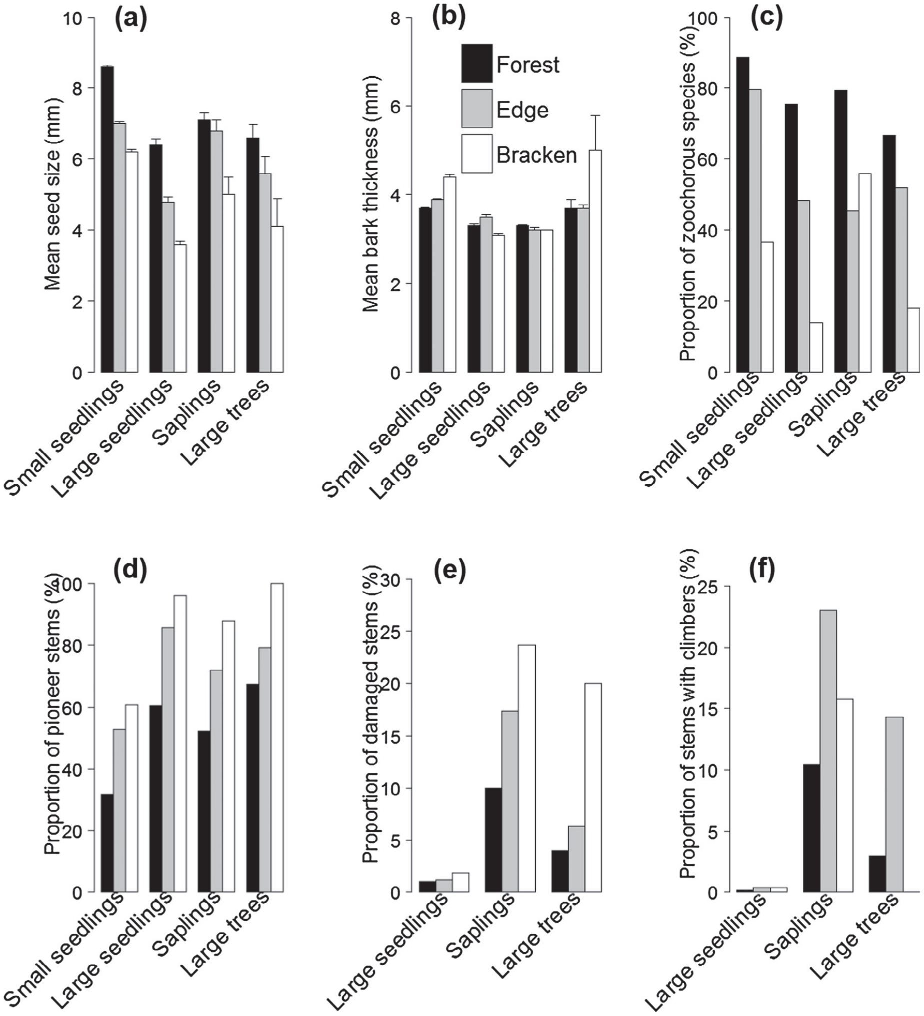

Fig. 4. Mean seed size (± 1 SE), mean bark thickness (± 1 SE) and proportion of zoochorous species, pioneer species, damaged stems and stems with climbers at each life stage in the forest, at the edge and in bracken for common species (a–d) and all species (e–f). From (a) to (d), the number of stems are: 9908 small seedlings in the forest, 6607 small seedlings at the edge, 2060 small seedlings in bracken, 505 large seedlings in the forest, 412 large seedlings at the edge, 202 large seedlings in bracken, 314 saplings in the forest, 114 saplings at the edge, 25 saplings in bracken, 144 large trees in the forest, 48 large trees at the edge and 11 large trees in bracken. From (e) to (f), the number of stems are: 861 large seedlings in the forest, 523 large seedlings at the edge, 233 large seedlings in bracken, 481 saplings in the forest, 161 saplings at the edge, 38 saplings in bracken, 199 large trees in the forest, 63 large trees at the edge and 15 large trees in bracken.

uncertain but it has been suggested that animals visit open areas and use them as social spaces (Midgley et al., 2005; Ssali et al., 2012). Few animals eat bracken, but elephants and bush pigs are both known to excavate and eat bracken rhizomes (Babaasa et al., 2004; Seydack, 2013). Our own observations suggest that feeding elephants do not kill the ferns, which regenerate from remaining rhizome fragments, but the behaviour does break and clear other plants. Pigs also cause extensive disturbance and soil turnover which leads to local clearings that are readily (re)colonised by bracken (F.S. *pers. obs.* similar to the processes reported with feral pig, *Sus scrofa*, in Australia, Choquenot et al., 1996). Such damage appears to impede regeneration of trees in bracken.

One prediction that we failed to confirm was that larger-seeded species would become better represented than smaller-seeded species due to the selective impact of shade and deep litter on establishment and initial survival. We found no such response. Indeed we found a decline in mean seed size from smaller to larger seedlings, and that this trend was also present in the forest (where we would also expect large seeds to increase survival). Nonetheless, the thick litter layer associated with bracken, which is almost three times thicker than the litter in forest, remains striking and is, we believe, likely to interfere with seed germination and survival though this influence remains undemonstrated.

Our data also show that some woody plants, especially pioneer species, do establish in bracken (Fig. 4). This again suggests that dispersal is involved but also indicates that species with longer seed dormancy and greater growth potential (Ghazoul and Sheil, 2010) are better suited to progress through stages vulnerable to bracken interference. This may indicate that occasional short-lived opportunities for

Table 2
Kendall's correlations between main response and explanatory variables for tree regeneration in the forest, edge and bracken. Significant values ($P < 0.05$) are denoted in bold.

Segment	Small seedlings		Large seedlings		Saplings		Large trees		All size classes	
	τ	P	τ	P	τ	P	τ	P	τ	P
Bracken stem density										
Forest	−0.16	0.191	−0.21	0.090	−0.39	**0.002**	−0.40	**0.002**	−0.2	0.117
Edge	0.11	0.342	0.07	0.549	−0.24	**0.039**	−0.14	0.244	0.11	0.342
Bracken	0.03	0.788	0.02	0.879	−0.13	0.284	−0.10	0.441	0.03	0.762
Percentage canopy openness										
Forest	−0.11	0.305	−0.19	0.086	−0.21	0.060	−0.12	0.295	−0.14	0.208
Edge	0.30	**0.006**	−0.02	0.843	−0.36	**0.002**	−0.18	0.144	0.26	**0.018**
Bracken	0.12	0.289	−0.07	0.565	−0.25	**0.044**	−0.28	**0.027**	0.06	0.616
Local basal area										
Forest	0.12	0.889	0.12	0.299	0.21	0.055	0.32	**0.006**	0.03	0.762
Edge	0.16	0.136	0.07	0.521	0.27	**0.018**	0.65	**6.6e−8**	0.19	0.087
Bracken	0.12	0.293	0.31	**0.007**	0.66	**1.0e−7**	0.56	**1.5e−5**	0.18	0.113
Mean litter depth										
Forest	−0.16	0.19	−0.19	0.090	−0.29	**0.011**	−0.08	0.488	−0.25	**0.027**
Edge	0.11	0.342	−0.14	0.199	−0.08	0.480	−0.19	0.117	−0.19	0.089
Bracken	−0.15	0.180	−0.03	0.814	−0.09	0.494	−0.18	0.163	−0.13	0.234
Herbaceous plant density										
Forest	−0.18	0.103	0.221	**0.046**	0.07	0.513	0.04	0.698	−0.14	0.192
Edge	0.09	0.395	0.10	0.363	−0.09	0.445	−0.18	0.126	0.09	0.428
Bracken	0.01	0.963	0.03	0.796	−0.02	0.857	0.004	0.974	−2.6e−3	0.981

woody plants to establish do occur. We note that pioneer species predominate in the forest areas studied. This may indicate recent disturbance or that late successional species have problems in establishing perhaps due to a lack of seed sources in the nearby forest.

Our results show that regeneration is not just limited in the open clearings, but that sapling density declines markedly with proximity to such clearings and is still increasing with distance at 25 m into the forest (Fig. 3). This is in contrast to what is expected at most forest edges where increased light typically results in denser woody vegetation (Didham and Lawton, 1999). We have no ready explanation for this spatial pattern. Possibilities include the influence of climbers and damage from animals. One interesting suggestion is that an increased density of seed predators may be associated with the ground cover provided by bracken, and that these predators will range into the neighbouring forest as observed in bracken in Netherlands (den Ouden, 2000). Such a relationship is also supported by our observation that per-transect sapling density tends to increase with distance from bracken plants.

There is a perception among our local informants that some bracken clearings are being colonised by forest at the forest edge, and are thus reducing in size, yet our data show no evidence of such a general spatial process, i.e. we detect no relationship between time since the last fire in the clearing and the structure and density of woody vegetation at the forest edge. We note that all our clearings had to be of sufficient size to contain a transect and that this eliminated the smallest bracken clearings which are also those that people report seeing reduce in extent (various local informants pers. comm.).

Shade remains a plausible explanation for impeded regeneration in bracken-dominated areas. We know from studies in other parts of the world that bracken is an aggressive competitor that shades out other vegetation (George and Bazzaz, 1999; Hartig and Beck, 2003; Priewasser, 2013). While observations in the Neotropics have suggested that bracken can sometimes facilitate the regeneration of woody species (Gallegos et al., 2015) we found no indications of such

Table 3
Pairwise correlation coefficients and p-values of explanatory variables for tree regeneration in forest, edge and bracken. Significant values ($P < 0.05$) are denoted in bold.

Segment	Bracken density		Canopy openness		Local basal area		Litter depth		Herbaceous plant density
	τ	P	τ	P	τ	P	τ	P	τ
Forest									
Bracken density	1.0								
Canopy openness	0.25	**0.048**	1.0						
Local basal area	−0.25	**0.047**	−0.13	0.243	1.0				
Litter depth	0.24	0.054	0.19	0.088	−0.12	0.263	1.0		
Herbaceous plant density	0.1	0.441	0.08	0.499	−0.1	0.385	0.06	0.592	1.0
Edge									
Bracken density	1.0								
Canopy openness	0.22	0.054	1.0						
Local basal area	−0.13	0.270	−0.12	0.289	1.0				
Litter depth	0.1	0.366	−0.02	0.852	−0.19	0.087	1.0		
Herbaceous plant density	−0.07	0.549	0.15	0.176	−0.16	0.159	−0.19	0.089	1.0
Bracken									
Bracken density	1.0								
Canopy openness	0.15	0.187	1.0						
Local basal area	−0.13	0.233	−0.27	**0.014**	1.0				
Litter depth	0.32	**0.004**	−0.04	0.701	−0.11	0.333	1.0		
Herbaceous plant density	−0.12	0.294	−0.02	0.880	0.04	0.744	−0.29	**0.008**	1.0

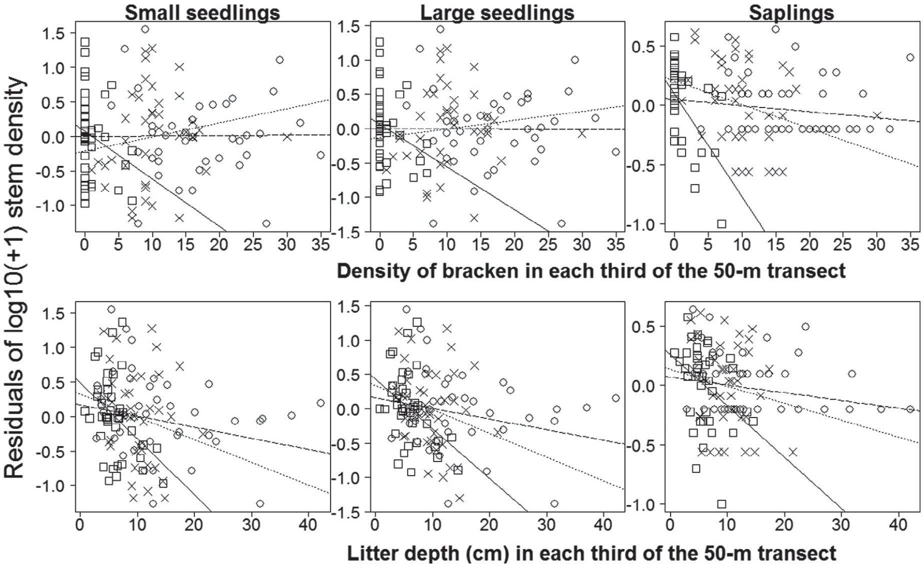

Fig. 5. Residuals of seedlings and saplings versus bracken density and litter depth for each third of a 50-m transect segment. Open squares and solid lines represent the forest, crosses and dotted lines represent the edge and open circles and long dash lines represent the bracken-dominated area.

interactions—i.e., no positive relationship between bracken and sapling densities.

Overall, our results are consistent with forest regrowth in bracken being impeded in multiple ways including distance limitation, lack of perches, damage by vertebrates and climber interference. Many other potential factors, including seed predation, allelopathy, competition, fire, litter and pathogens are not ruled out.

That multiple factors impede forest recovery in the presence of bracken is important given that several potential explanations are associated with correlated variables (Freckleton, 2002). In our case, distance from seed sources, bracken density, canopy cover, litter depth and the densities of woody plants cannot be separated readily. Since these variables underlie established ecological mechanisms determining regeneration (Ghazoul and Sheil, 2010), and these variables have been assessed with differing accuracy, simple analyses appear inadequate to weigh and assess additional mechanisms related with these variables with confidence (Biggs et al., 2009). Additional studies are needed.

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Appendix A

A.1. Appendix

Number of stems of the 25 most abundant woody species (of a total of 83) in all transects regenerating in the forest (FO), the edge (ED) and bracken (BR).

Species	Small seedlings			Large seedlings			Saplings			Large trees		
	FO	ED	BR	FO	ED	BR	FO	ED	BR	FO	ED	BR
Olea capensis L.	5242	2024	710	17	7	0	7	1	1	7	3	0
Psychotria mahonii C.H.Wright	877	800	269	22	32	8	14	0	4	21	4	2
Rytigynia ruwenzoriensis (De Wild.) Robyns	964	836	39	84	33	5	66	14	1	6	1	0
Galiniera saxifraga (Hochst.) Bridson	444	1156	27	18	37	4	4	2	1	5	7	0
Macaranga capensis (Baill.) Sim	463	714	212	23	51	72	18	19	4	28	9	2
Clutia abyssinica Jaub. & Spach	338	415	112	76	145	100	8	13	1	0	0	0
Faurea saligna Harv.	244	145	265	3	2	0	0	0	0	9	1	2
Psychotria kirkii Hiern	267	61	0	67	12	1	51	2	1	0	0	0
Allophylus abyssinicus (Hochst.) Radlk.	322	38	7	19	5	1	11	4	1	6	1	0
Polyscias fulva (Hiern) Harms	5	59	185	0	0	0	0	0	0	4	1	0
Syzygium guineense (Willd.) DC.	191	25	3	10	1	0	7	3	0	6	0	0
Maesa lanceolata Forssk.	73	21	91	4	6	1	1	2	1	6	5	1

Olinia rochetiana Juss.	89	102	2	1	0	0	1	2	0	1	4	0
Allophylus africanus (Gilg) Verdc.	109	11	0	63	7	4	1	0	0	0	0	0
Xymalos monospora (Harv.) Baill.	80	14	0	23	23	0	18	8	0	13	2	0
Chrysophyllum pruniforme Pierre ex Engl.	82	52	0	15	3	0	7	1	0	8	0	0
Rytigynia kigeziensis Verdc.	51	45	8	13	9	3	19	3	0	4	2	0
Bridelia micrantha (Hochst.) Baill.	42	8	10	32	31	6	4	4	4	0	0	0
Gymnosporia acuminata (L.f.) Szyszyl.	80	2	1	37	9	0	7	2	0	1	0	0
Neoboutonia macrocalyx Pax	5	8	10	18	8	1	36	28	5	5	6	0
Vepris nobilis (Delile) Mziray	38	8	1	28	5	0	25	3	1	7	0	0
Symphonia globulifera L.f.	44	9	1	24	11	1	15	3	0	4	0	0
Podocarpus latifolius (Thunb.) R.Br. ex Mirb.	33	8	1	29	1	0	14	2	0	8	0	0
Croton macrostachyus Hochst. ex Delile	1	42	39	0	1	0	0	0	0	0	2	4
Ekebergia capensis Sparrm.	21	15	41	1	0	0	3	3	0	0	0	0
Total for abundant species	10,118	6622	2037	650	453	213	345	127	27	149	48	11
Total for all species	10,355	6768	2110	861	523	233	481	161	38	199	63	15

A.2. Appendix

Characteristics of the most abundant woody species (i.e., 23 out of a total of 83).

Species	Seed size (mm)	Bark thickness (mm)	Successional guild	Dispersal type
Allophylus abyssinicus (Hochst.) Radlk.	2.6	2.4	Pioneer	Zoochorous
Bridelia micrantha (Hochst.) Baill.	5	2.8	Pioneer	Zoochorous
Chrysophyllum pruniforme Pierre ex Engl.	19	2.5	Non-pioneer	Zoochorous
Clutia abyssinica Jaub. & Spach	2.7	N/A	Pioneer	Non-zoochorous
Croton macrostachyus Hochst. ex Delile	7	4.6	Pioneer	Non-zoochorous
Ekebergia capensis Sparrm.	13	5.1	Non-pioneer	Zoochorous
Faurea saligna Harv.	1.1	10.1	Pioneer	Non-zoochorous
Galiniera saxifraga (Hochst.) Bridson	3.9	4.8	Pioneer	Zoochorous
Macaranga capensis (Baill.) Sim	4.1	2.9	Pioneer	Non-zoochorous
Maesa lanceolata Forssk.	0.5	3.1	Pioneer	Zoochorous
Neoboutonia macrocalyx Pax	7.6	2.9	Pioneer	Non-zoochorous
Olea capensis L.	11.3	3.7	Non-pioneer	Zoochorous
Olinia rochetiana Juss.	10	3.7	Non-pioneer	Zoochorous
Psychotria kirkii Hiern	2.8	5.1	Pioneer	Zoochorous
Podocarpus latifolius (Thunb.) R.Br. ex Mirb.	9.5	2.7	Non-pioneer	Zoochorous
Polyscias fulva (Hiern) Harms	4	3.4	Pioneer	Zoochorous
Psychotria mahonii C.H.Wright	3.2	3.7	Pioneer	Zoochorous
Rytigynia kigeziensis Verdc.	8	2.0	Non-pioneer	Zoochorous
Rytigynia ruwenzoriensis (De Wild.) Robyns	9.5	3.0	Non-pioneer	Zoochorous
Symphonia globulifera L.f.	17.5	1.9	Non-pioneer	Zoochorous
Syzygium guineense (Willd.) DC.	10.1	3.7	Non-pioneer	Zoochorous
Vepris nobilis (Delile) Mziray	5.5	3.2	Non-pioneer	Zoochorous
Xymalos monospora (Harv.) Baill.	11.9	4.1	Pioneer	Zoochorous

A.3. Appendix

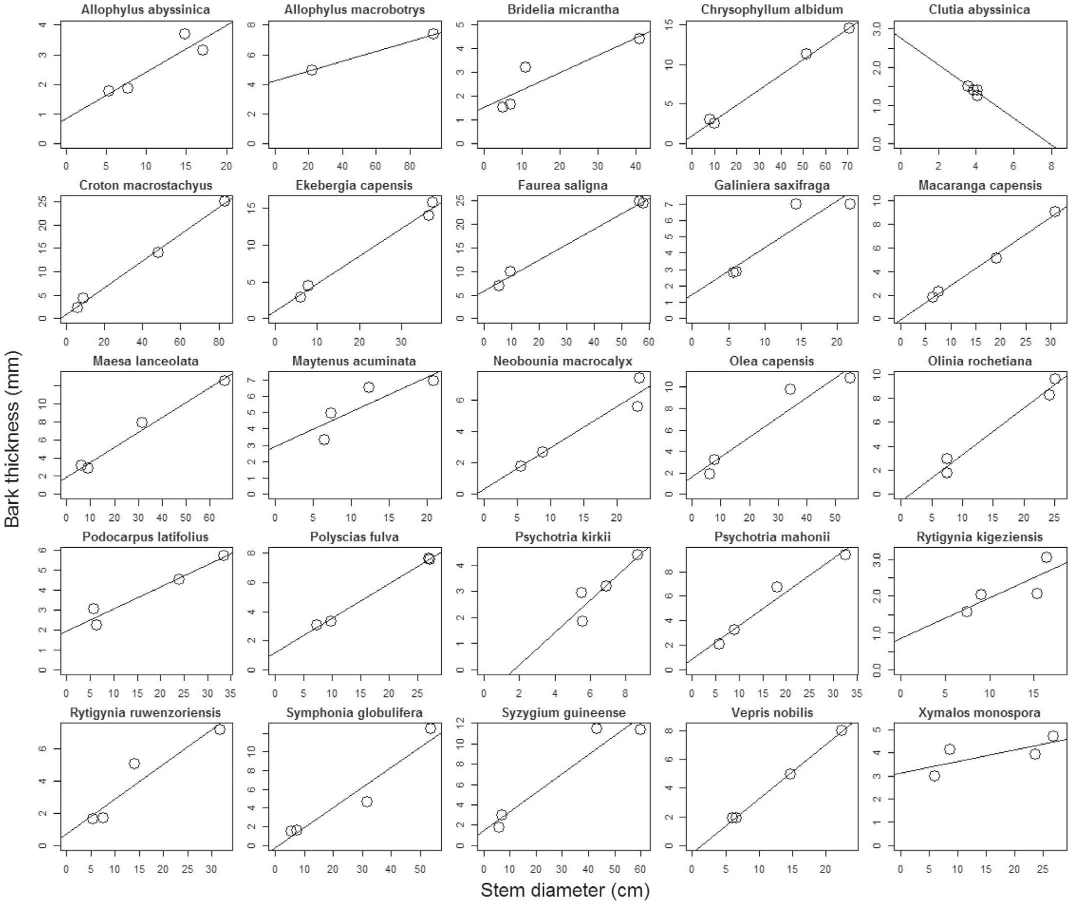
Kendall's correlations between stem densities per 25 m^2 5 m-transect segment and distance of the plot from the nearest 25 m^2 5 m-transect segment containing bracken. Significant values ($P < 0.05$) are denoted in bold.

Size class	Plot	τ	P
Small seedlings	0–5 m	0.04	0.728
Small seedlings	5–10 m	0.25	**0.036**
Small seedlings	10–15 m	0.14	0.235
Small seedlings	15–20 m	0.10	0.411
Small seedlings	20–25 m	0.00	1.000
Large seedlings	0–5 m	0.07	0.573
Large seedlings	5–10 m	0.24	**0.045**
Large seedlings	10–15 m	0.16	0.179
Large seedlings	15–20 m	0.09	0.462
Large seedlings	20–25 m	0.01	0.913
Saplings	0–5 m	0.18	0.154

Saplings	5–10 m	0.21	0.099
Saplings	10–15 m	0.32	**0.011**
Saplings	15–20 m	0.26	**0.047**
Saplings	20–25 m	0.40	**0.005**

A.4. Appendix

Bark thickness versus stem diameter of the most abundant woody species (i.e., 23 out of a total of 83).



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ORIGINAL RESEARCH

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Tree seed rain and seed removal, but not the seed bank, impede forest recovery in bracken (*Pteridium aquilinum* (L.) Kuhn)-dominated clearings in the African highlands

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Abstract

Considerable areas dominated by bracken *Pteridium aquilinum* (L.) Kuhn occur worldwide and are associated with arrested forest recovery. How forest recovery is impeded in these areas remains poorly understood, especially in the African highlands. The component processes that can lead to recruitment limitation—including low seed arrival, availability and persistence—are important determinants of plant communities and offer a potential explanation for bracken persistence. We investigated key processes that can contribute to recruitment limitation in bracken-dominated clearings in the Bwindi Impenetrable National Park, Uganda. We examined if differences in seed rain (dispersal limitation), soil seed bank, or seed removal (seed viability and persistence) can, individually or in combination, explain the differences in tree regeneration found between bracken-dominated areas and the neighboring forest. These processes were assessed along ten 50-m transects crossing the forest–bracken boundary. When compared to the neighboring forest, bracken clearings had fewer seedlings (bracken 11,557 ± 5482 vs. forest 34,515 ± 6066 seedlings/ha), lower seed rain (949 ± 582 vs. 1605 ± 335 tree seeds m^{-2} $year^{-1}$), comparable but sparse soil seed bank (304 ± 236 vs. 264 ± 99 viable tree seeds/m^2), higher seed removal (70.1% ± 2.4% vs. 40.6% ± 2.4% over a 3-day interval), and markedly higher rodent densities (25.7 ± 5.4 vs. 5.0 ± 1.6 rodents per 100 trapping sessions). Camera traps revealed that rodents were the dominant animals visiting the seeds in our seed removal study. *Synthesis*: Recruitment limitation contributes to both the slow recovery of forest in bracken-dominated areas, and to the composition of the tree species that occur. Low seed arrival and low persistence of unburied seeds can both explain the reduced density of seedlings found in bracken versus neighboring forest. Seed removal, likely due to rodents, in particular appears sufficient to constrain forest recovery and impacts some species more severely than others.

KEYWORDS
Afro-tropical forest, Bwindi, forest-bracken edge, invasive species, *Pteridium aquilinum*, recruitment limitation, seed rain, seed removal, soil seed bank

1 | INTRODUCTION

The role of clearings dominated by bracken fern *Pteridium aquilinum* (L.) Kuhn in retarding forest recovery is a worldwide concern. Areas dominated by such fern thickets occur on every continent except Antarctica and cover thousands of square kilometers of previously forested habitat (Holm, Doll, Holm, Pancho, & Herberger, 1997; Marrs & Watt, 2006; Verdcourt, 1999). Temperate studies have suggested that bracken, *Pteridium aquilinum*, interferes with forest regrowth due to the effects of shade, pathogens, allelopathy, deep litter or perhaps seed removal (den Ouden, 2000; Dolling, 1996; Facelli & Pickett, 1991; Gaudio et al., 2011; Ghorbani, Duc, Mcallister, Pakeman, & Marrs, 2007; Priewasser, 2013). However, how these factors and mechanisms might operate singly or in combination has seldom been examined especially in equatorial Africa (but see Ssali, Moe, & Sheil, 2017).

Recruitment limitation—failure of a species to arrive and establish—is an important determinant of plant communities. This limitation can arise from multiple processes including low seed production, seed dispersal, or persistence (Marques & Burslem, 2015). Crucially, little is known about the role of recruitment limitation in explaining bracken persistence although previous temperate studies have shown that seed addition can sometimes increase tree regeneration in bracken-dominated areas (Ghorbani et al., 2007; Pakeman, Le Duc, & Marrs, 2002). Studies elsewhere have shown that recruitment failure in deforested areas can be the result of seed limitation and/or establishment limitation (see, e.g., Muscarella et al., 2013; van Eck, de Steeg, Blom, & de Kroon, 2005). Here we focus on the early life-history stages where recruitment limitation can be manifested, that is, seed arrival, seed persistence (and viability), and seed removal.

Successful establishment requires the arrival and persistence of viable seeds, germination, and seedling survival. Our initial exploration showed that bracken-dominated areas are persistent and indicated that species with longer seed dormancy and greater growth potential are better suited to establish in bracken than are species lacking these characteristics (Ssali et al., 2017). However, how seed limitation and establishment limitation, that is, seed rain, soil seed bank, and seed removal, influence tree regrowth in bracken clearings remains poorly understood despite the existing literature (from temperate and neotropical regions, see Marrs & Watt, 2006; Priewasser, 2013; Royo & Carson, 2006).

Dispersal limitation (i.e., low seed arrival) in open areas adjacent to tropical forest has attracted much attention (e.g., Barnes & Chapman, 2014; Duncan & Chapman, 1999; Wijdeven & Kuzee, 2000). Notably, Duncan and Chapman (1999) found that seed rain in deforested habitats decreases rapidly with distance from the forest. The nonzoochorous tree species, especially early successional species, tend to produce numerous small seeds that can be transported by wind, but most tropical forest tree species depend on frugivorous animals for dispersal (Ghazoul & Sheil, 2010). Observations in the neotropics have indicated that the seed rain of animal-dispersed species is influenced by the availability of food and of perching sites (e.g., Saavedra, Hensen, & Schleuning, 2015). Studies in African forests have also found that the arrival of large-seeded species depends on large mammals including elephants and primates (Babweteera, Savill, & Brown, 2007; Beaune, 2015; Gross-Camp, Masozera, & Kaplin, 2009). Indeed, in the forest adjacent to bracken clearings in the Bwindi Impenetrable National Park in Uganda, animal-dispersed species comprise approximately 80% of the common tree species (Ssali et al., 2017).

Following dispersal, the seeds may be incorporated into the soil where they can persist for months before germinating (Ghazoul & Sheil, 2010). However, temperate studies have found that bracken fronds and litter impede the incorporation of seeds into the soil (Ghorbani, Le Duc, McAllister, Pakeman, & Marrs, 2006; Pakeman & Hay, 1996). Further, temperate and neotropical studies have found that the soil seed bank in bracken may be negatively affected by predation, allelopathy, or trampling by large mammals (De Jesus Jatoba et al., 2016; Ghorbani et al., 2007). Furthermore, species with longer seed dormancy may possess greater potential to survive bracken interference and can thus dominate the seed bank in bracken (Ssali et al., 2017).

Seed removal studies in the tropics have shown that few seeds persist if they arrive in thick undergrowth (Blackham & Corlett, 2015; Razafindratsima, 2017). Typically, the main agents of seed removal are rodents (Hulme, 1998), although other animals can be involved, for example, insects (Gallegos, Hensen, & Schleuning, 2014), birds (Cordeiro, Ndangalasi, McEntee, & Howe, 2009), and large mammals (Beaune, Bollache, Fruth, & Bretagnolle, 2012; Feer, 1995). Once removed, seeds may experience different fates including predation or being scatter-hoarded by rodents which may then fail to retrieve them (Aliyu, Adamu, Moltchanova, Forget, & Chapman, 2014; Forget, 1991; Janzen, 1970; Traveset, Heleno, & Nogales, 2014).

In the Bwindi Impenetrable National Park ("Bwindi") in Uganda, forest recovery in bracken-dominated clearings is slow (Ssali et al., 2017). Our hypothesis here is that the limited forest recovery in bracken compared to forest is related to differences in recruitment limitation (namely seed arrival, persistence, and predation). Thus, in this study, using a series of integrated field studies, we explored the role of recruitment limitation in explaining the difference in regeneration between bracken and neighboring forest environments by examining seedling densities, seed rain, soil seed bank, and seed removal rates (and rodent densities). Given that these limitations will favor or filter species in a manner that may shed light on the underlying processes, we are interested in both the implications for overall woody regeneration and the differences that arise among individual species.

2 | MATERIALS AND METHODS

The study was conducted in the Bwindi Impenetrable National Park (henceforth "Bwindi") a UNESCO World Heritage site in South-West Uganda. Bwindi is located at 0°53′–1°08′ S, 29°35′–29°50′ E near the equator and spans a wide range of elevations (1,160–2,607 m asl). The park's main vegetation is classified as moist lower montane forest (Hamilton, 1982; Howard, 1991). The climate is tropical with two rainfall peaks from March to May and September to November. Annual rainfall ranges from 1,130 to 2,390 mm and the mean temperature ranges between 7 and 29°C. The driest months are December-January and July-August. Bwindi is relatively rich in species owing to high rainfall, range of elevations, and likely proximity to Pleistocene refugia (Hamilton, 1982).

Bwindi is rugged, steep, and divided by cliffs, with a remarkably dense understorey. The forest canopy is open in many areas due in part to extensive clearings dominated by bracken fern *Pteridium aquilinum* (Ssali et al., 2017). The clearings have been created by past fires, landslides, timber cutting, and cultivation (Babaasa, Eilu, Kasangaki, Bitariho, & McNeilage, 2004; Olupot, Barigyira, & Chapman, 2009; Ssali et al., 2017). Other understorey species dominate other areas both in the continuous forest and in the open clearings. Many of the common understorey species form extensive stands and flower only every few decades before seeding and dying en masse. Examples include the African mountain bamboo *Yushania alpina* (K. Schum.) Lin. and various Acanthaceae including the thicket-forming *Mimulopsis solmsii* Schweinf. and *Mimulopsis arborescens* C.B. Clarke. Along with other understorey species, these monocarpic species are key food plants for mountain gorillas *Gorilla beringei beringei* Matschie (Sheil, 2012).

Our field observations were conducted between June 2015 and December 2016. We selected 10 bracken-dominated clearings accessible from the Institute of Tropical Forest Conservation (ITFC)—a research station at Ruhija (2,355 m asl). Within each clearing, we established one 50 × 5-m transect across the forest-bracken boundary with the 25-m mid-point at the forest edge and 25 m extending one way into the bracken and the other into the forest. We recorded all woody stems and the number of bracken fronds in eleven 1-m^2 quadrats established 5-m apart along each of the 10 transects. We also measured slope (° using a clinometer) in the middle and at each end of the transect and interviewed local informants who had worked in these forests for many years about the history of each site.

We assessed the seed rain by placing 11 seed traps at 5-m intervals along each transect. Each trap consisted of a high-density polyethylene funnel (diameter = 27 cm) mounted on wooden poles 40 cm above the ground with the spout resting on a small basket which contained a collection bag. The traps were visited every 2 weeks and the trapped material collected and then processed at the research station. Seeds were lost occasionally (eight of 4,422 trap visits) when the traps were knocked down by African bush elephant *Loxodonta africana* Blumenbach and when the collection bags were removed (possibly by L'Hoest's monkey *Cercopithecus l'hoesti* P. Sclater or Olive baboon *Papio anubis* Lesson). Seeds were identified at ITFC with references (Hamilton, 1991; Katende, Birnie, & Tengnäs, 1995), voucher specimens in ITFC's herbarium or by identifying parent trees where seeds were still attached. Nomenclature follows Global Plants (http://plants.jstor.org/).

To assess the soil seed bank, along each transect we collected and combined five 10.2-cm-wide and 10-cm-deep soil cores 1-m apart in the forest (−25 m), at the edge (0 m) and in bracken (25 m). The soil samples were kept in paper bags and processed at the ITFC research station. Each soil sample was spread on a fine mesh (2 mm) and washed to separate soil from seeds. The washed samples, which mainly comprised fibrous matter and seeds, were spread in trays and placed in a transparent polythene shelter—a well-illuminated environment where viable seeds were germinated. In addition, trays containing seed-free sand were placed among the sample trays to control for any dispersal of seeds into the germination shelter. All the trays were kept moist and were watered and checked for emerging seedlings every 2 days. We also mixed the remaining material every month to ensure the remaining seeds were exposed to light. No seedlings emerged from the trays containing sand in the 6 months of the study. Seedlings were identified by ITFC's botanical staff and removed as they emerged.

We assessed seed removal by placing wooden trays, each with 13 different seed species, in eleven above-ground locations 5-m apart along each of the 10 transects. Litter was removed to make space for the seed stations. The 13 species were the trees *Strombosia scheffleri*, *Chrysophyllum pruniforme*, *Allophylus abyssinicus*, *Macaranga capensis*, *Neoboutonia macrocalyx*, *Polyscias fulva*, *Clutia abyssinica*, *Faurea saligna*, *Psychotria mahonii*, and *Olinia rochetiana*, and also the crops *Oryza glaberrima*, *Arachis hypogaea*, and *Zea mays*. The first 10 are common near the research station and regularly produce seeds between June and August (ITFC unpublished data), while the last three are common crops in the villages neighboring the park. All tree seeds were stored in paper bags and placed out in their fruits except for seeds of *Chrysophyllum pruniforme* which were manually separated from their fleshy arils. We recorded the number of seeds removed after 3 days over 10-census periods carried out in June-August 2016 (n = 1,430 seeds). During each census, we replaced any removed or damaged seeds with fresh ones.

To assess rodents, we placed Sherman live traps (H. B. Sherman Inc., Tallahassee, Flor. 8 × 8 × 23 cm) at 5-m positions along the 10 transects. Traps were set on the ground. For bait, we combined sweet bananas, maize flour, and roasted powdered groundnuts and left them to ferment overnight following Isabirye-Basuta and Kasenene (1987) and Kasangaki, Kityo, and Kerbis (2003). The traps were inspected twice daily for five consecutive days (late July and early August 2016): early in the morning for nocturnal species and late in the evening for diurnal species. Species and weight were recorded before release. We also attempted to identify the animals implicated in seed removal by deploying camera traps (Reconyx model RM45; http://www.reconyx.com) preset with a 1-s delay between subsequent images in two locations along seven transects during the last 3 days of the seed removal study. We count and analyse "events" as one or more sequences of images separated by no more than one minute. Nomenclature follows Wilson and Reeder (2005).

2.1 | Analyses

Woody plants were categorized as large trees (dbh ≥ 10 cm), saplings (dbh 2–9.9 cm), large seedlings (basal diameter <2 cm and >30 cm tall), and small seedlings (<30 cm tall). We examined stem abundance, seed rain, soil seed bank, and seed removal in three segments of the 50 × 5-m transects, that is, "forest" (ten 83.5-m^2 plots), "edge" (ten 83.5-m^2 plots), and "bracken" (ten 83.5-m^2 plots).

To examine whether seedling densities, seed rain, and soil seed bank differed between forest and bracken, we calculated the degree of dissimilarity between the abundance of each common woody species in bracken versus that in the forest using a modified Bray-Curtis dissimilarity index (Bray & Curtis, 1957):

$$y_{B,F} = \left[\frac{(m_{iB}+0.5)-(m_{iF}+0.5)}{(m_{iB}+0.5)+(m_{iF}+0.5)}\right] \times 100$$

where $y_{B,F}$ denotes the dissimilarity index, m_{iB} the abundance of the ith common woody species in bracken, and m_{iF} the abundance of the ith common woody species in the forest. We obtained the dissimilarity index by subtracting the number of seeds per-species in each transect segment of forest from the corresponding number of seeds in bracken and divided the outcome by the sum of seeds for the forest and bracken transect segments combined. We added a half to the number of seeds in both forest and bracken transect segments to avoid the occurrence of zero values in the denominator and multiplied the result by 100. All analyses used R (R Core Team, 2016).

3 | RESULTS

3.1 | Clearings, bracken, and seedlings

Our 10 transects intersected bracken-dominated clearings ranging in area from 0.1 ha to 2.5 ha and with slopes from 12 to 35°. According to local informants, the 10 clearings had been affected by fire (one had last burned in 1998 and the other nine in the 1980s). Of the 10 clearings, eight had been impacted by past timber cutting and extraction, two by landslides and two by other human activity (settlements and related). On average (±1 *SE*), bracken density in the clearings was 3.0 ± 0.3 fronds/m^2. The bracken-dominated area typically had fewer seedlings, saplings, and large trees as well as markedly higher rodent density than the nearby forest (Figure 1). When comparing trees at different life stages, the ratio of small to large seedlings in forest versus bracken was similar (1.187 vs. 1.089, i.e., 0.99 times), that from large seedlings to saplings was about nine times (0.093 vs. 0.01, i.e., 9.37 times) and from saplings to large trees was again similar (0.397 vs. 0.4, i.e., 1.09 times).

3.2 | Seed rain

We collected 12,997 seeds of 39 woody species (trees, treelets, and woody climbers) over 18 months from the seed traps. The seeds comprised 34 woody species (*n* = 5,536 seeds) in the forest, 29 woody species (*n* = 4,251 seeds) at the edge, and 20 woody species (*n* = 3,210 seeds) in bracken (Appendix S1). Trees comprised 97.3% of these seeds in the forest, 97.7% at the edge, and 99.9% in bracken. The remainder of the seeds belonged to woody climbers and treelets (i.e., free standing woody plants with one or more stems that seldom have stem diameters or overall height exceeding 5 cm or 5 m, respectively). On average (±1 *SE*) seed rain density (tree seeds m^{-2} $year^{-1}$) was 1604.7 ± 334.6 in the forest, 1625.3 ± 708.1 at the edge, and 948.5 ± 581.8 in bracken. The average abundance of seeds declined significantly with distance from the forest into bracken-dominated clearings, except for small-seeded species (i.e., for larger (≥5 mm) seeds of trees: Kendall's correlation, $\tau = -0.67$, $p = .003$; for smaller (<5 mm) seeds of trees: $\tau = -0.27$, $p = .283$; seeds of treelets and lianas: $\tau = -0.62$, $p = .009$; $n = 11$ in all cases; see Figure 1).

At species level, seed density declined significantly with distance from the forest interior into bracken clearings for nine of the 16 most common woody species (see Appendices S2 and S3). In addition, of the 12 tree species with four or more occurrences in the forest and bracken combined (edge excluded) seven species had significantly greater relative abundance in the forest while only one species, *Maesa lanceolata*, had significantly greater relative abundance in bracken (Figure 2a). We found a significant positive relationship between seed rain dissimilarity index and the dissimilarity index of seedlings (Kendall's rank correlation, $\tau = 0.3$, $n = 12$, $p = .025$) and no significant correlation between seed rain dissimilarity index and mean seed size of common tree species ($\tau = 0.12$, $n = 12$, $p = .582$). In bracken, seed rain density of four of seven common tree species was positively correlated with seedling density but only *Nuxia congesta* had a significant correlation ($\tau = 0.75$, $n = 10$, $p = .013$).

3.3 | Soil seed bank

A total of 6,953 seeds germinated and emerged from the soil samples (and none from the controls). Five hundred and fifty were seedlings belonging to a total of 15 woody species, 5,905 plants belonged to nonwoody species while 498 could not be identified (Appendix S1). Of the 15 woody species, 12 emerged from soil collected in the forest, nine species from the edge, and seven from bracken. On average, the density of viable seeds in the soil (tree seeds/m^2) was 264.4 ± 99.3 in the forest, 181.2 ± 65.9 at the edge and 303.5 ± 236.1 in bracken. Seeds of the treelet *Clutia abyssinica* were significantly more abundant in bracken (dissimilarity index = 11.7 ± 7.8) while *Maesa laceolata* was significantly more abundant in the forest (dissimilarity index = 26.7 ± 21.3; Figure 2b, despite a considerably greater abundance of *Maesa laceolata* in bracken than in the forest at one transect; see Appendix S1). We found no significant correlation between seed bank dissimilarity index and the dissimilarity index of seedlings of common tree species ($\tau = 0.08$, $n = 9$, $p = .798$). In bracken, seed bank density of three of four common species was positively correlated with seedling density but none reached significance (all *p* values >.1).

3.4 | Seed removal

The mean proportion of seeds of woody species removed over 3 days was 40.6% ± 2.4% in the forest, 67.5% ± 2.4% in the edge and 70.1% ± 2.4% in bracken. *Polyscias fulva* had the highest proportion of seeds removed in both the bracken area (92.0% ± 2.4%) and forest (67.7% ± 2.4%) per 3 days followed by *Strombosia*

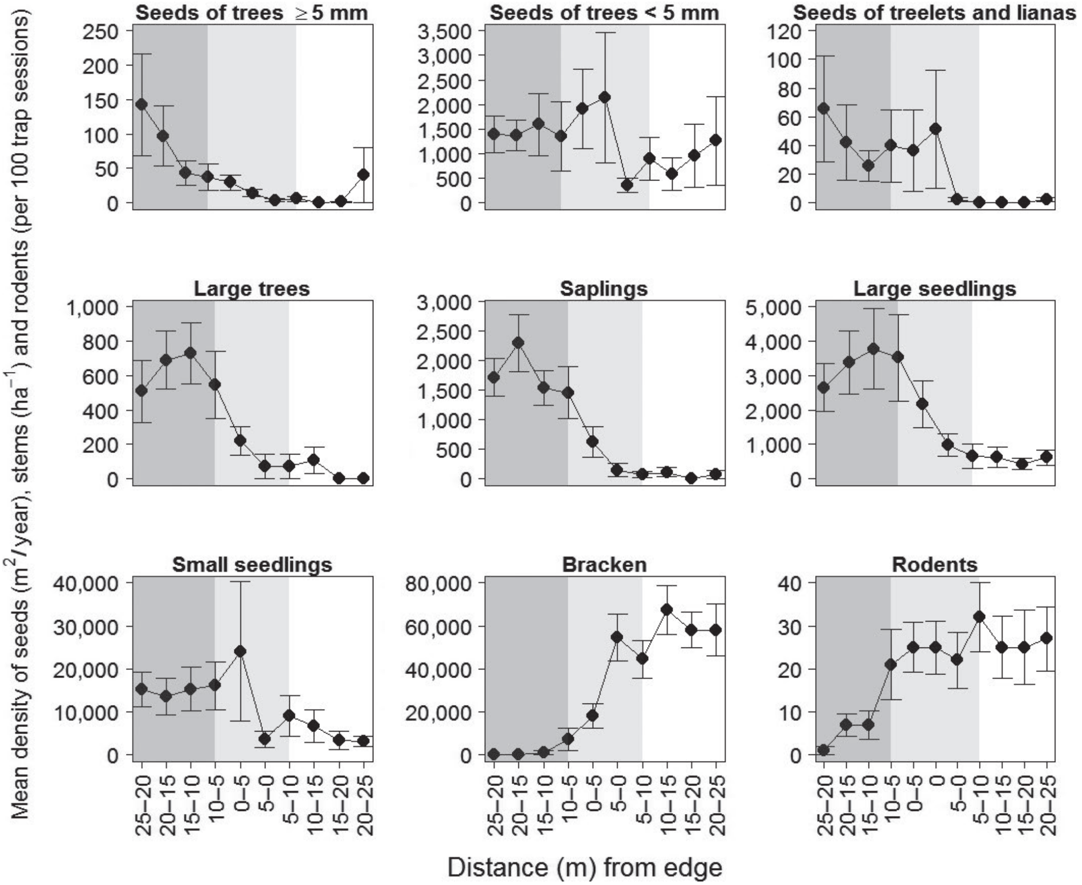

FIGURE 1 Seed rain density (seeds m^{-2} year^{-1} ± 1 *SE*), density of trees (stems/ha ±1 *SE*) and density of rodents (per 100 trap sessions ±1 *SE*) plotted relative to the edge between the forest and bracken. Distance classes are successive 25 m^2 5 m-transect segment with the considered "forest" marked dark gray, the "edge" in lighter gray, and the bracken-dominated area unshaded. Treelets are here defined as free standing woody plants with one or more stems that seldom have stem diameters or overall height exceeding 5 cm or 5 m respectively (see Appendix S1 for a full species list)

scheffleri with removal rates of 83.5 ± 2.4% and 67.0% ± 2.4% in bracken and the forest, respectively (Figure 3). *Neoboutonia macrocalyx* was removed the least with removal rates of 34.5% ± 2.4% and 12.0% ± 2.4% per 3 days followed by *Olinia rochetiana* with removal rates of 44.7% ± 2.4% and 16.2% ± 2.4% in bracken and the forest, respectively. All seeds of woody species included in the study had lower rates of removal than all three grain crops, which also showed high rates of removal in the forest (see Figure 3). We found a significant positive correlation between removal rates of woody species in forest and the removal rates of woody species in bracken ($\tau = 0.87$, $n = 10$, $p = .0001$), between the removal rates in forest and at the edge ($\tau = 0.82$, $n = 10$, $p = .0004$), and between the removal rates at the edge and in bracken ($\tau = 0.82$, $n = 10$, $p = .0004$). We detected no significant correlation between mean seed size and seed removal per 3 days of woody species in forest ($\tau = 0.1$, $n = 10$, $p = .728$), at the edge ($\tau = -0.02$, $n = 10$, $p = 1$), in bracken ($\tau = 0.16$, $n = 10$, $p = .601$), and in all segments combined ($\tau = 0.06$, $n = 10$, $p = .862$).

3.5 | Rodent captures

A total of 217 rodents were captured on the 10 transects in 1,100 trapping sessions (550 days, morning and evening). Captures occurred approximately five times more frequently in the bracken than in the forest (Table 1). We found a significant positive relationship between rodent captures and the density of bracken fronds (Kendall's rank correlation, $\tau = 0.89$, $n = 10$, $p = .001$). Assuming that captures are proportional to densities we estimated rodent biomass to be around six times higher in bracken than in the forest due to the large species *Lophuromys flavopunctatus* and

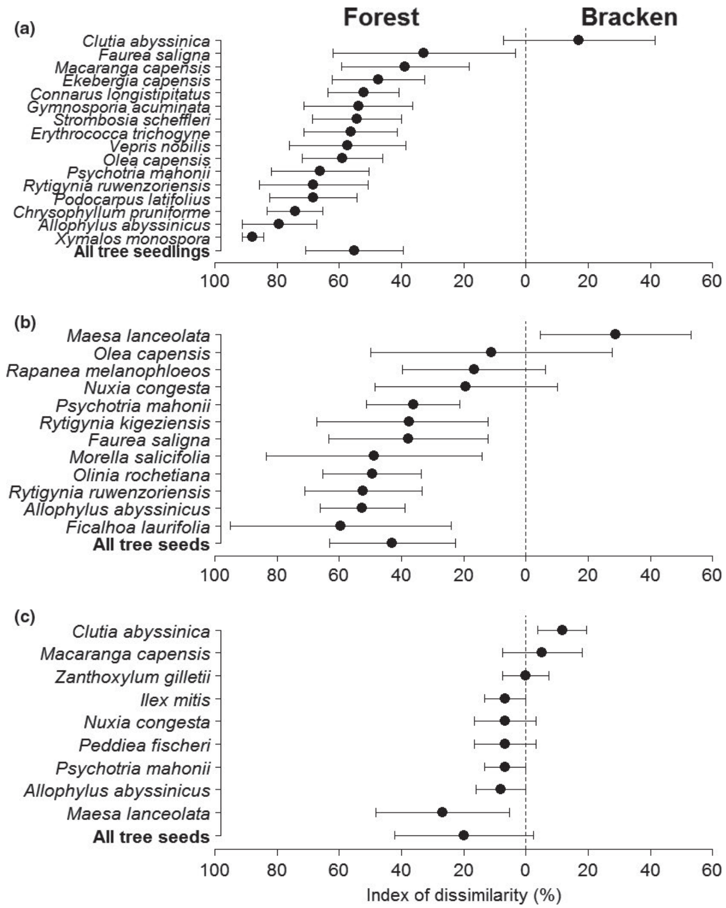

FIGURE 2 Forest versus bracken dissimilarity index (absolute values ±1 *SE*) of common tree species in the (a) seedlings, (b) seed rain, and (c) soil seed bank. The selected common tree species had (a) five or more occurrences in the seedling population, (b) four or more occurrences in seed rain, and (c) two or more occurrences in soil seed bank in the forest and/or bracken

Lophuromys woosnami representing the majority of the rodent biomass in bracken and the smaller *Praomys* spp representing about half of the rodent biomass in the forest (Table 1). The images from the camera traps selectively employed in seven transects (n = 544 images) were not always readily identified (either the animal or its activity) due to problems of visibility (and activation of the motion detector particularly in the thicker vegetation outside the forest: 62 of 211 images in the forest were clearly discernible compared to only 40 of just 202 images in bracken). While bracken-dominated sites averaged 65% fewer images of rodents removing seeds than the forest sites, these same bracken sites had a 78% higher rate of seed removal (Appendix S4). The number of clear rodent "events" (sequences of observations of specific species separated by less than one minute) and proportion of seeds removed were not significantly correlated (τ = 0.1, n = 10, p = .717). Nonetheless, these "events" indicated that most of the species captured in the live traps along with other rodents including large ones like *Cricetomys emini* and *Funisciurus carruthersi* that were too large to trap, visited locations where they could remove seeds (Table 2).

3.6 | Role of woody cover and perches

We examined if the local abundance of trees influenced key variables (potential sources of seeds and perches for birds and bats). We compared the local abundance of large trees and basal area with seedlings, seed rain and soil seed bank in the forest, edge, and bracken (Appendix S1). None of these relationships achieved significance although the correlation between tree basal area in all segments and seed rain in bracken and that between basal area in bracken and seed rain in bracken were borderline (p < .1).

4 | DISCUSSION

4.1 | Synthesis and overview

Our data show that when compared to the neighboring forest, bracken thickets not only had fewer seedlings, saplings, and large trees but also received fewer seeds in the seed rain and any unburied seeds were more likely to be removed (reduced persistence). Both

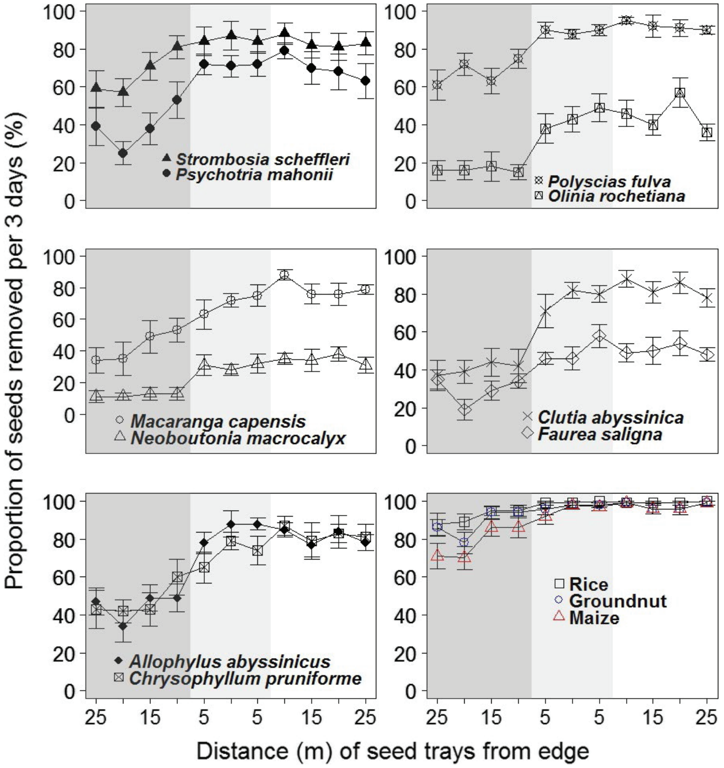

FIGURE 3 Proportion of seeds removed by location. Trays are placed every 5-m starting in the forest and ending in bracken. The area termed "forest" is dark gray, "edge" is gray, and the bracken-dominated area is unshaded. The forest species (in bold italic) are common tree species within the park that had a substantial number of seeds during the census while the grain crops (in bold) were used as a way to assess removal for attractive seeds

the limited seed arrival and the low persistence of unburied seeds can limit establishment of tree seedlings in bracken-dominated clearings. The low density of seeds in the soil seed bank, which is similar across the forest and bracken, plays no major role in generating the differences in regrowth, although it is clearly important for the local abundance of the treelet *Clutia abyssinica*. The proportion of seeds removed over 3 days was considerably higher in bracken than in the forest with rates of removal for some tree species like *Neoboutonia macrocalyx* and *Olinia rochetiana* differing by a factor of two or three (Figure 3). This marked difference in seed removal will be higher when compounded over longer periods. The per-species relative abundance of seedlings in the forest versus bracken had a significant positive relationship with the per-species relative abundance of the seed rain but had no relationship with the per-species

TABLE 1 Abundance and biomass of rodents (mean ± 1 *SE*) per 100 trapping sessions in the forest, edge, and bracken and their feeding classification based on Happold (1996)

	Rodent abundance			Rodent biomass (g)			
Species	Forest	Edge	Bracken	Forest	Edge	Bracken	Feeding classification
Lophuromys flavopunctatus Thomas, 1888	0	7.0 ± 2.7	12.3 ± 4.9	0	290.0 ± 99.3	479.0 ± 186.5	Omnivore
Lophuromys woosnami Thomas, 1906	0.3 ± 0.3	3.7 ± 1.9	6.0 ± 1.7	12.0 ± 12.0	140.1 ± 70.3	222.3 ± 63.0	Omnivore
Praomys spp.	2.3 ± 1.1	2.3 ± 0.9	4.7 ± 1.9	77.0 ± 42.7	84.0 ± 31.1	159.7 ± 63.0	Granivore
Hybomys univittatus (Peters, 1876)	1.3 ± 0.7	7.3 ± 2.7	1.3 ± 0.7	51.0 ± 27.6	295.7 ± 108.6	65.7 ± 35.8	Omnivore
Hylomyscus vulcanorum Lönnberg & Gyldenstolpe, 1925	1.0 ± 0.7	2.0 ± 0.7	0.7 ± 0.4	15.7 ± 11.3	45.7 ± 17.7	25.7 ± 18.2	Granivore
Praomys jacksoni (de Winton, 1897)	0	1.3 ± 0.7	0	0	59.0 ± 32.3	0	Granivore
Mus bufo (Thomas, 1906)	0	0.3 ± 0.3	0.3 ± 0.3	0	4.0 ± 4.0	1.7 ± 1.7	Granivore
Unknown species (escaped)	0	0	0.3 ± 0.3	–	–	–	
All rodent species	5.0 ± 1.6	24.0 ± 4.2	25.7 ± 5.4	155.7 ± 62.4	918.4 ± 158.4	979.4 ± 195.4	

TABLE 2 Number of identified rodent "events" and estimated rodent biomass (mean ± 1 SE) in the forest, edge and bracken.

	Events over 3 days			Estimated rodent biomass (g) over 3 days		
	Forest	Edge	Bracken	Forest	Edge	Bracken
N cameras over 3 days	5	4	5			
Species						
Lophuromys spp.	1	6	7	7.8 ± 7.8	58.4 ± 46.4	54.5 ± 45.4
Hybomys univittatus (Peters, 1876)	0	0	3	0	0	24.5 ± 24.5
Praomys spp.	23	8	32	186.1 ± 105.2	80.9 ± 49.5	258.9 ± 182.1
Hylomyscus vulcanorum Lönnberg & Gyldenstolpe, 1925	11	5	0	52.1 ± 52.1	29.6 ± 29.6	0
Cricetomys emini Wroughton, 1910	0	0	1	0	0	247.0 ± 247.0
Funisciurus carruthersi Thomas, 1906	13	0	0	1662.7 ± 1023.2	0	0
Unidentified rodents	2	15	4	–	–	–
All rodent species	50	34	47	318.1 ± 167.3	28.2 ± 3.2	97.5 ± 38.8

relative abundance of viable seeds in the soil. The low persistence of seeds in bracken is likely related to the high densities of rodents. Taken together, these findings indicate that recruitment limitation contributes to the limited establishment of trees in bracken, and that these factors differ among species and thus influence species composition.

When comparing forest and bracken, we found that tree seedling densities were ~ 3.0 times higher in the forest than in bracken (34,515 ± 6066 vs. 11,557 ± 5482 seedlings/ha). We also found roughly similar stem-size density ratios in both forest and bracken in our 10 transects and a markedly lower ratio of saplings to large seedlings in bracken than in forest. The low abundance of seedlings appears to be largely a result of limited recruitment or poor survival rather than rapid development as the abundance of more mature life stages is lower or similar to those seen in forest (see also Ssali et al., 2017). The difference for tree seed rain was 1.7 times (forest 1605 ± 335 vs. bracken 949 ± 582 vs. tree seeds m^{-2} year^{-1}), and for the seed bank was 0.9 times (264 ± 99 vs. 304 ± 236 viable tree seeds/m^{2}). The difference for seed persistence rates was 2.0 times (59.4% ± 2.4% vs. 29.9% ± 2.4% per 3-day period). These numbers indicate that tree seed arrival and low tree seed persistence can explain the limited recovery of forest vegetation in bracken.

When we examined tree species (the most common plus those used in the seed removal study, see Table 3), we found similar results in most cases although there were some exceptions. Three species *Nuxia congesta*, *Psychotria mahonii*, and *Maesa lanceolata* had higher seed rain in bracken than in the forest, for example. *Nuxia congesta* produces small hairy capsules containing many seeds that are easily transported by wind (Katende et al., 1995) while *Psychotria mahonii* and *Maesa lanceolata* produce numerous small fleshy fruits which are eaten and dispersed by primates or birds (Graham, Moermond, Kristensen, & Mvukiyumwami, 1995; Gross-Camp et al., 2009; Sun, Ives, Kraeuter, & Moermond, 1997). The three most abundant tree seedlings that occurred in bracken were *Faurea saligna*, *Psychotria mahonii* and *Rytigynia ruwenzoriensis*. These species also ranked highly in the local seed rain in bracken (2nd, 3rd, and 5th, respectively) but had no seed bank. *Faurea saligna* produces small hairy nutlets that lose viability in 1 month (Katende et al., 1995) while *Rytigynia ruwenzoriensis* also produces fleshy fruits and is dispersed by animals, including primates (Rothman, Nkurunungi, Shannon, & Bryer, 2014). *Clutia abyssinica*, which has gravity dispersed seeds capable of dormancy (Katende et al., 1995; Shehaghilo, 1989), was significantly more abundant in the soil seed bank in bracken than in the forest (see Figure 2b) and was the only common woody species whose seedlings were more abundant in bracken. The link between seed rain and seedling abundance in explaining the difference between forest and bracken is further underlined by the correlation between the dissimilarity indices for the most common species.

Seed removal rates although generally high varied among species. For example, *Strombosia scheffleri* and *Polyscias fulva* had higher seed removal rates per 3 days both in the forest and in bracken than *Neoboutonia macrocalyx*, *Olinia rochetiana*, and *Faurea saligna*. Of these species, the only one that is found relatively frequently as a seedling in bracken is *Faurea saligna* which also appears to be a well defended and common seed in the seed rain. Overall our results suggest that species with readily dispersed seeds, well-protected seeds, and long-term seed dormancy are best suited to establish in bracken.

4.2 | Processes

Our finding that seed rain in bracken is only around 59% of that in the nearby forest reflects the generally low seed rain found by other studies in tropical rain forests in open areas adjacent to the forest. For instance, in Ngel Nyaki Forest, Nigeria, Barnes and Chapman (2014) found that seed rain in the grassland area 20–30 m from the forest edge was only 11% of that from the nearby forest while in Kibale forest in Uganda Duncan and Chapman (1999) found that the area dominated by *Pennisetum purpureum* Schumach. received roughly 1% of the seed rain about 100 m from the forest. This indicates dispersal limitation—a situation likely exacerbated by few effective dispersal agents such as frugivorous birds and bats using these areas

TABLE 3 List of the most common woody species with seedlings in bracken showing their mean seedling density (stems/ha), seed rain density (seeds m^{-2} $year^{-1}$), soil seed bank (viable seeds/m^2) and rate of seed persistence (% per 3-day interval).

Species	Seedlings	Seed rain	Soil seed bank	Seed persistence
(a) Forest				
Faurea saligna Harv.	58.4 ± 33.2	699.4 ± 271.2	0	70.8 ± 3.2
Psychotria mahonii C.H.Wright	68.0 ± 29.8	13.7 ± 6.1	4.9 ± 4.9	61.3 ± 6.1
Rytigynia ruwenzoriensis (De Wild.) Robyns	95.7 ± 31.8	15.2 ± 8.1	2.4 ± 2.4	NA
Clutia abyssinica Jaub. & Spach	5.7 ± 3.3	0	0	59.5 ± 6.0
Nuxia congesta R.Br. ex Fresen.	0	274.6 ± 137.9	14.7 ± 9.8	NA
Croton macrostachyus Hochst. ex Delile	0	18.1 ± 13.3	6.1 ± 6.1	NA
Macaranga capensis (Baill.) Sim	5.3 ± 2.0	3.2 ± 2.6	15.3 ± 12.2	57.3 ± 6.8
Allophylus abyssinicus (Hochst.) Radlk.	31.6 ± 9.3	88.6 ± 70.2	12.2 ± 12.2	55.3 ± 5.3
Maesa lanceolata Forssk.	0	0.9 ± 0.9	215.4 ± 84.6	NA
Ekebergia capensis Sparrm.	4.2 ± 1.7	1.8 ± 1.2	0	NA
Strombosia scheffleri Engl.	3.4 ± 1.6	0	0	33.0 ± 6.5
Chrysophyllum pruniforme Pierre ex Engl.	11.3 ± 6.7	9.4 ± 6.2	0	53.0 ± 6.4
Neoboutonia macrocalyx Pax	0.6 ± 0.6	21.1 ± 18.6	0	88.0 ± 1.8
Olinia rochetiana Juss.	0	3.8 ± 1.7	24.5 ± 24.5	83.8 ± 4.4
Polyscias fulva (Hiern) Harms	0	46.5 ± 45.8	0	32.3 ± 5.3
% All species in the forest	345.2 ± 60.7	1604.7 ± 334.6	264.4 ± 99.3	59.4 ± 2.4
(b) Bracken				
Faurea saligna Harv.	63.2 ± 52.5	130.7 ± 48.2	0	49.8 ± 3.5
Psychotria mahonii C.H.Wright	27.7 ± 16.5	71.6 ± 69.7	0	30.0 ± 7.0
Rytigynia ruwenzoriensis (De Wild.) Robyns	6.6 ± 3.8	9.6 ± 9.6	0	NA
Clutia abyssinica Jaub. & Spach	6.6 ± 2.6	0	3.1 ± 3.1	16.8 ± 3.9
Nuxia congesta R.Br. ex Fresen.	4.2 ± 2.8	686.0 ± 523.1	0	NA
Croton macrostachyus Hochst. ex Delile	2.4 ± 1.5	0.3 ± 0.3	0	NA
Macaranga capensis (Baill.) Sim	0.8 ± 0.6	1.5 ± 1.5	6.1 ± 4.0	20.3 ± 3.7
Allophylus abyssinicus (Hochst.) Radlk.	0.7 ± 0.5	0.6 ± 0.4	0	19.0 ± 4.9
Maesa lanceolata Forssk.	0.7 ± 0.7	16.7 ± 15.7	252.1 ± 233.3	NA
Ekebergia capensis Sparrm.	0.2 ± 0.2	0	0	NA
Strombosia scheffleri Engl.	0.1 ± 0.1	0.6 ± 0.6	0	16.5 ± 5.5
Chrysophyllum pruniforme Pierre ex Engl.	0	0.6 ± 0.6	0	17.5 ± 5.7
Neoboutonia macrocalyx Pax	0	0	0	65.5 ± 4.1
Olinia rochetiana Juss.	0	0	0	55.3 ± 4.9
Polyscias fulva (Hiern) Harms	0	0	0	8.0 ± 2.9
All species in bracken	115.6 ± 54.8	948.5 ± 581.8	303.5 ± 236.1	29.9 ± 2.4

and the low availability of perches for them (*sensu* Saavedra et al., 2015). We note that *Clutia abyssinica*, the only species whose seedlings showed a clear tendency to favor bracken, was not detected in the seed rain. This could have resulted from our seed traps being too high above the ground or too far from any plants to receive the ballistic-dispersed seeds from this short (occasionally to 5 m) multi-stemmed woody plant. Although its seeds are relatively small (seed size = 2.7 mm), we expected to find them in the seed rain as smaller seeds like those of *Allophylus abyssinicus* (seed size = 2.6 mm) and *Nuxia congesta* (seed size = 1.5 mm) were detected.

The density of viable seeds in the soil was generally low and had little discernible relationship with regeneration differences between forest and bracken. Our overall seed bank density of about 300 seeds/m^2 is about half the 500–600 seeds/m^2 found in later successional stages and less than a third of the 1,000–2,700 seeds/m^2 found previously in the early stages of succession following cultivation in three montane forests of Bwindi, Mgahinga, and Echuya (Karlowski, 2006). This may be due to the difference in methods (we likely lost many seeds smaller than 2 mm during washing and Karlowski (2006) did not target areas in or next to bracken). The limited seed bank may indicate that few species possess long-term seed dormancy. Previous studies in East and Southern Africa have found that many trees including *Croton macrostachuys*, *Prunus africana*, and *Symphonia globulifera* have recalcitrant seeds (Mng'omba, du Toit, & Akinnifesi, 2007; Muhanguzi, Obua, & Oryem-Origa, 2002; Negash, 2003, 2004; Shehaghilo, 1989; Wakjira & Negash, 2013). In addition, the low abundance of tree seeds in deforested areas has been reported to limit forest recovery elsewhere in the African tropics (Hall & Swaine, 1980; Mukhongo, Kinyamario, Chira, & Musila, 2011; Teketay & Granstrom, 1995). As such, the relative numbers provided by our data suggest that the soil seed bank has little apparent role or contribution to forest recovery in bracken-dominated clearings, although *Clutia abyssinica* as the only species whose seedlings favor bracken is an exception. The large number and diversity of seeds from nonwoody plants in the seed bank under bracken was unexpected (5,905 of 6,953 = 85% and 20 species). The implications of this are unclear, but it may be that when opportunities for germination arise, the ensuing competition is intense and contributes further to impeding woody regrowth. Further study would be required to evaluate this mechanism.

We also found that tree seed removal in bracken over a 3-day interval was about 173% of that in the nearby forest. Compounding this removal over a longer period shows that this differential process is adequate to explain marked differences between the forest and bracken. For example, even if forest and bracken started with the same seed number, maintaining the same 3-day rate of seed removal over a 30-day interval would result in more than 800 times more seeds in the forest. Other studies have also reported a significantly higher rate of seed removal in treeless areas than in nearby forest (in Indonesia, Blackham & Corlett, 2015; in Netherlands, den Ouden, 2000; and in Madagascar, Razafindratsima, 2017) although such patterns are not universal, for example, grassland versus forest in Kibale Forest in Uganda (Ssekuubwa, Loe, Sheil, Tweheyo, & Moe, in press).

The rapid removal of the grain crops compared to the native trees shows that selective factors are involved. A recent study in Lake Mburo National Park in Uganda also found that conspicuous and palatable seeds, including crop species, are more liable to removal than native trees (Acanakwo, Sheil, & Moe, 2017). In our study, we found that the conspicuous and less well-protected tree species *Strombosia scheffleri* (seed size = 23.7 mm) and *Chrysophyllum pruniforme* (seed size = 19.0 mm) had higher seed removal rates per 3 days in bracken and the forest than *Faurea saligna* (seed size = 1.1 mm), *Neoboutonia macrocalyx* (seed size = 7.6 mm), and *Olinia rochetiana* (seed size = 10.0 mm) which are protected by hard seed coats. When ranked *Strombosia scheffleri* had the highest removal rates in both bracken and forest and was consistently followed by *Chrysophyllum pruniforme*, *Faurea saligna*, *Olinia rochetiana*, and *Neoboutonia macrocalyx* (see Figure 3).

Our rodent capture rate was five times higher in bracken than in the forest. Dense cover in bracken provides good cover for rodents. A comparable study in Netherlands estimated that rodent density was four times higher in bracken than in the neighboring forest (den Ouden, 2000), and many previous studies in tropical African forests have reported significantly higher rodent densities in forest clearings than in the continuous forest (in Uganda, Isabirye-Basuta & Kasenene, 1987; in Ghana, Jeffrey, 1977; in Madagascar, Razafindratsima, 2017) although some studies have failed to find significant differences (e.g., in Tanzania, Cordeiro et al., 2009). Capture rates in our study, that is, 26 rodents per 100 trapping sessions, are similar to those found by one previous study in Bwindi and relatively high compared to various other tropical African forests. For example, in Bwindi, Kasangaki et al. (2003) found 36 rodents per 100 trap nights although Mawanda (2014) who worked on the forest edge caught only five rodents per 100 trap nights. In the East Usambara Mountains of Tanzania, Cordeiro et al. (2009) found about four rodents per 100 trap nights in the fragmented area and about five rodents per 100 trap nights in the continuous forest. We note, however, that there can be considerable local variation, for example, in Kibale Forest Isabirye-Basuta and Kasenene (1987) who do not quote trapping numbers directly, report 0.7–26 rodents/ha in a deforested area and 0.7–21.3/ha in mature forest. In addition, densities may vary considerably over time as seen in other regions, although there has been little attention to such variation in the wet tropics (Adler, 1994; Korpimäki, Brown, Jacob, & Pech, 2004; Krebs, 1996).

The most common rodents in bracken and at the forest edge (i.e., *Lophuromys* spp and *Hybomys univittatus*) are large and omnivorous implying that they opportunistically consume a range of food items including leaves, seeds, roots, insects, and small vertebrates (Kingdon, 1997). Despite some limitations with the camera traps, we still detected several larger rodents, too big for our traps, known for scatter-hoarding including the Forest giant pouched rat *Cricetomys emini* Wroughton and Carruther's mountain squirrel *Funisciurus carruthersi* Thomas (Appendix S5). While we expect that most seeds are consumed, the presence of species known for seed caching also raises the question of seed fate and whether these rodents move these seeds toward or away from the adjacent forest. In suitable contexts, rodents can aid (rather than impede) seed arrival (as found for *Carapa* spp. seeds in Nyungwe by Nyiramana, Mendoza, Kaplin, & Forget, 2011). Nonetheless, our data suggest that bracken may impact neighboring vegetation, at least up to 25 meters, through the influence on rodents and related seed removal.

This is the first study in the African tropics that simultaneously examines establishment limitation and key recruitment determinants (seed rain, soil seed bank, seed survival, and rodent densities) in both forest and bracken-dominated areas. We provide evidence of low seed rain and high rates of seed removal in bracken. Our previous observations have suggested that various additional factors, including shade, litter, and fire, may also contribute to the poor regeneration of woody plants in bracken clearings in Bwindi (Ssali et al., 2017). However, if seed arrival and removal are the primary limits to tree regeneration, we would predict that adding seeds and excluding rodents would bolster forest recovery in these bracken-dominated clearings.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

FS, SRM, and DS designed the study. FS carried out fieldwork and data analysis in collaboration with SRM and DS. FS led the writing with input from DS and SRM.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Paper III

The differential effects of bracken (*Pteridium aquilinum* (L.) Kuhn) on germination and seedling performance of tree species in the African tropics

Keywords: Afro-tropical forest; allelopathy; competition; ecological filter; interference; invasive species; *Pteridium aquilinum*; stalled succession; understorey

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Abstract: Bracken fern *Pteridium aquilinum* (L.) Kuhn stands act as an ecological filter that influences regeneration of other plants. Woody species are often slow to re-colonise bracken-dominated areas within forest landscapes likely reflecting, at least in part, effects on tree seeds and seedlings. We experimentally examined tree seed germination, seedling survival, and seedling growth under field conditions in the Bwindi Impenetrable National Park, Uganda. The six treatments were: 1) undisturbed ferns control (‘‘Bracken’’), 2) fern fronds cut and removed but litter left intact (‘‘Cut’’), 3) ferns and coarse litter removed “Cut and litter removed”, 4) fern fronds pinned down ‘‘Bent’’, 5) bracken and soil removed and replaced with forest soil “Forest soil” and 6) bracken and rhizomes removed but soil returned “Bracken soil”. We implemented the experiment in five locations with a total of 120 1 x 1-m plots, 28,800 seeds of 14 woody species and 1,920 seedlings of eight woody species.

The highest germination for all species combined occurred in the ‘Bracken’ treatment (39.7 ± 4.1%) followed by the ‘Cut’ treatment (29.3 ± 4.2%) and the ‘Bent’ treatment (27.3 ± 3.1%) while the ‘Forest soil’ treatment (6.3 ± 1.4%), ‘Bracken soil’ treatment (5.7 ± 1.2%) and the ‘Cut and litter removed’ treatment (5.4 ± 1.6%) had the lowest germination. When comparing germination percentage, we found that all late-successional species germinated better in full bracken while six of nine pioneers germinated better in the bracken-free plots. Seedling survival was greatest overall in the ‘Forest soil’ treatment (50.3 ± 4.9%) followed by the ‘Bracken’ treatment (48.1 ± 2.1%) while the ‘Cut’ treatment had the lowest survival (27.5 ± 2.8%). Three of four pioneer species survived best in bracken-free plots while two of four late-successional species survived best in full bracken. Cumulative growth in seedling height (cm ± 1 SE) for all test species combined was highest in the ‘Bracken soil’ treatment (7.5 ± 1.3) followed by the ‘Forest soil’ treatment (7.0 ± 0.8) while the ‘Cut’ treatment had the lowest height increment (1.9 ± 0.7). All test species grew better in bracken-free plots than in full bracken though none of the main effects were significant ($p<0.05$). Taken together, these

results imply that bracken hinders establishment of pioneer species but favours germination of late-successional species. This ecological filter is determined by shade and by soil mediated processes and contributes to stalled succession as most seed inputs are from pioneers.

1 INTRODUCTION

Bracken ferns (*Pteridium*: Dennstaedtiaceae) are long-lived clonal plants and form monodominant stands with dense canopies that may affect tree seedling establishment (Marrs & Watt, 2006; Suazo-Ortuño *et al.*, 2015). They are common over vast areas of deforested habitat worldwide (Holm *et al.*, 1997; Masozera, 2004; Verdcourt, 1999). Slow recovery of forest in these areas has often been attributed to the presence of bracken, and these ferns' dense cover, large and deep rhizomes, deep litter and allelopathic chemicals (den Ouden, 2000; Marrs & Watt, 2006; Priewasser, 2013). Bracken ferns are also thought to be toxic to most animals and can fuel wild fires (Adie *et al*., 2011; Roos *et al*., 2010). Bracken already forms stands over large areas of Africa's equatorial highlands where it is widely believed to impede forest recovery and reduces local conservation values (Masozera, 2004; Plumptre *et al*., 2002; Ssali *et al*., 2017). Given increasing human disturbance and that droughts and fire are predicted to escalate (IPCC, 2014) bracken patches are likely to expand.

Studies suggest that herbaceous plants can impose significant ecological filters on tree regeneration (George & Bazzaz 1999a; 1999b; Meiners, 2014). For example, pioneer tree species cannot establish beneath dense thicket canopies leading to slowed or stalled succession (Marques & Burslem, 2015). This may reflect low light conditions that can occur under a thicket where many strict heliophile pioneers will be unable to establish or persist (Sheil & Burslem, 2003). It may also reflect other forms of interference.

The understorey filter represents one of the primary determinants of tree regeneration mainly because it tends to favour strong competitors (George & Bazzaz, 1999a; 1999b). In the case of bracken, a single plant can produce hundreds of fronds which can grow up to 4 m tall (Marrs & Watt, 2006; Roos *et al*., 2010). The bracken canopy can reduce physical space, nutrients and light available for the establishment of other plants (Gaudio *et al*., 2011; Suazo-Ortuño *et al.*, 2015). Under this scenario, regeneration may be limited to species that can withstand low levels of resource availability. In addition, bracken fronds can smother seedlings when they collapse (Dolling, 1996; Marrs & Watt, 2006). A deep layer of litter can block incoming light at ground level and possibly obstruct the development of young emerging seedlings (Facelli & Picket, 1991; Ghorbani *et al*., 2006; Torti *et al*., 2001). If such impacts are selective, trees regenerating in deforested habitats might follow a modified or stalled successional pathway.

Temperate and neotropical studies have indicated that the germination, growth or viability of plants may be reduced by allelopathy (De Jesus Jatoba, 2017; Dolling, 1996). Here we define allelopathy as the direct plant-plant interference mediated by allelochemicals produced by bracken. However, the role of allelopathic interference has sparked controversy mainly because of the difficulty to separate chemical interference from other competitive processes (Cipollini *et al*., 2012; Ghazoul & Sheil, 2010; Inderjit *et al*., 2011). For instance, the inhibition of plant growth due to high concentrations of soluble aluminium may not be formally considered allelopathic interference even though it may play a similar role (see Ghazoul & Sheil, 2010).

In the Bwindi Impenetrable National Park, bracken-dominated clearings are persistent in some cases for four decades and often have near negligible tree regeneration. Initial exploration has indicated that the limited regrowth in bracken at least partly reflects both dispersal limitation and establishment limitation with high rates of seed removal that likely relates to a markedly higher density of rodents than in neighbouring forests (Ssali *et al*., 2017; 2018). We carried out a field experiment to examine seed germination, seedling survival, and growth of forest trees in five bracken-dominated clearings. We examined both early and late successional species. Early successional species (often termed “pioneer”) are the species that are associated with disturbed areas and young regrowth, they are generally relatively shade intolerant, short-lived, fast growing species and typically produce small seeds and have low wood density. Late-successional species (often termed “non-pioneer”) in contrast tend to dominate in undisturbed old-growth forests and tend to be more shade tolerant, longer-lived, slow growing species and are more likely to have large seeds and high wood density (Ghazoul & Sheil, 2010; Turner, 2001). This is the first study in the African tropics that examines tree seed germination, seedling survival, and growth of forest trees in bracken-dominated clearings.

The field experiment was implemented in six treatments: 1) undisturbed ferns control (‘‘Bracken’’), 2) fern fronds cut and removed but litter left intact (‘‘Cut’’), 3) ferns and coarse litter removed “Cut and litter removed”, 4) fern fronds pinned down ‘‘Bent’’, 5) bracken and soil removed and replaced with forest soil “Forest soil” and 6) bracken and rhizomes removed but soil returned “Bracken soil”. The reason for this combination of treatments is its practicality and its potential ability to distinguish (infer) the effects of bracken canopy (e.g., 4 versus 1), bracken litter (3 versus 2), bracken rhizomes (6 versus 3) and soil conditions (6 versus 5). Our hypothesis was that bracken affects seed germination and survival and growth of seedlings through a range of interference processes. We asked: 1) How does the presence of bracken influence the establishment of woody species? 2) Is this dependent on the bracken canopy, litter, rhizome or soil mediated processes? Identifying the dominant interactions would be an important advance in understanding how bracken hinders tree regrowth and may guide the restoration and management of bracken-dominated forest clearings.

2 MATERIALS AND METHODS

2.1 Study area

Bwindi Impenetrable National Park (henceforth “Bwindi”) is a UNESCO World Heritage site located at 0°53'–1°08' S, 29°35'–29°50' E near the equator in South-West Uganda. The park spans a wide elevational gradient ranging from 1,160 to 2,607 m asl and has been classified as a moist lower montane forest (Hamilton, 1982; Howard, 1991). Bwindi’s climate is tropical with annual mean temperature ranging between 7°C and 29°C and annual rainfall averaging between 1,130 to 2,390 mm (Howard, 1991). Bwindi's soils are humic ferralsols derived from the underlying Precambrian geology and have moderate to high acidity and are deficient in bases (Butynski, 1984; Howard, 1991; Twongyirwe *et al*., 2013).

Bwindi is rugged with steep-sided hills and narrow valleys and has extensive clearings in some areas of the forest which were created by past fires, logging, mining and human settlements (Babaasa *et al*., 2004; Olupot *et al*., 2009; Ssali *et al*., 2017). In many areas, these clearings are dominated by bracken fern *Pteridium aquilinum* ssp *centrali-africanum* or ssp *capense* (Marrs & Watt, 2006; Ssali *et al*., 2017; Thomson *et al*., 2005). The African mountain bamboo *Yushania alpina* (K. Schum.) Lin. and various Acanthaceae including the thicket-forming *Mimulopsis solmsii* Schweinf. and *Mimulopsis arborescens* C.B. Clarke also dominate other areas both in the continuous forest and in the open clearings (Sheil, 2012). Bracken has little, if any, conservation value unlike many of the other understorey species which are, for example, key food plants for mountain gorillas *Gorilla beringei beringei* Matschie (Rothman *et al*., 2014).

2.2 Experimental set-up

Our experiment was implemented under field conditions in 120 1 x 1-m plots spread across five sites. The inter-site distance ranged from roughly 260 m to about 1800 m. Each site had four sets of six treatments: 1) ferns left undisturbed as a control (''Bracken''), 2) ferns removed by cutting fronds and leaving the litter intact (''Cut''), 3) ferns and all the coarse litter removed by cutting fronds and raking the litter "Cut and litter removed", 4) fern fronds bent toward the edges of plots to reduce bracken shade ''Bent'', 5) bracken removed with the surrounding soil and replaced with soil from non-bracken areas "Forest soil" and 6) bracken removed by cutting fronds and digging and incorporating rhizomes into the soil "Bracken soil" (see Fig. 1). The ‘Bracken’ treatment plots were fenced with strong wooden sticks to prevent fronds from collapsing and covering seeds and seedlings used in the experiment. All plots were visited every two weeks to reinforce the manipulations and weed out herbaceous plants.

2.3 Seed germination

Seeds of 14 woody species were placed in all experimental plots. The 14 species were the pioneers *Allophylus abyssinicus* (Hochst.) Radlk., *Dombeya torrida* (J.F.Gmel.) Bamps, *Faurea saligna* Harv., *Galiniera saxifraga* (Hochst.) Bridson, *Macaranga capensis* (Baill.) Sim, *Maesa lanceolata* Forssk., *Polyscias fulva* (Hiern) Harms, *Psychotria mahonii* C.H.Wright and *Rapanea melanophloeos* (L.) Mez and also the non-pioneers *Mystroxylon aethiopicum* (Thunb.) Loes., *Myrianthus holstii* Engl., *Olea capensis* L., *Strombosia scheffleri* Engl. and *Syzygium guineense* (Willd.) DC. Nomenclature follows Global Plants (http://plants.jstor.org/). We selected these species because they are common and the seeds were available (ITFC unpublished data). Ripe fruits of *Myrianthus holstii* were collected from the nearby village, as they were not readily available in the forest, and the seeds manually separated from the fleshy aril. Healthy and mature seeds of all other species were collected from trees located near the ITFC research station. All seeds (n = 28,800) were air dried on paper prior to use.

We placed 28 plastic containers open at both ends and covered on top with a 5 x 5-mm wire-mesh to keep out rodents in two 50 x 50-cm stations within each plot and used a funnel to deposit 10 seeds (for 10 small-seeded species) or 5 seeds (for four large-seeded species) in each open container to avoid crowding. An additional open container was placed at each station to control for any seed rain. We then covered each seed station with a wire-mesh tied to wooden sticks with flexible wire. Each site was checked every two weeks between June 2015 and December 2015 and the number of germinated seeds recorded. We occasionally recovered and replaced seeds that were washed out due to heavy rains. We removed any seedlings of non-experimental species that emerged in the study plots and left those from the experiment to grow beyond the end of the study.

2.4 Seedling survival and growth

We transplanted seedlings (≤ 30 cm tall, n = 1920) of eight forest species into the experimental plots. The selected species were four pioneers *Allophylus abyssinicus* (Hochst.) Radlk., *Ficalhoa laurifolia* Hiern, *Macaranga capensis* (Baill.) Sim and *Psychotria mahonii* C.H.Wright and also four non-pioneers *Chrysophyllum pruniforme* Pierre ex Engl., *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb., *Syzygium guineense* (Willd.) DC. and *Vepris nobilis* (Delile) Mziray. We collected batches of healthy seedlings (≤ 30 cm tall, n = 240) of similar height and vigour per species and from the same location inside the park. During transplantation, we dug out each seedling with the surrounding soil and planted each batch on the day of collection. The seedlings were then grouped into tall and relatively shorter seedlings and one from each group planted in each plot. Prior to planting, we carefully removed soil from the seedlings avoiding damage to the roots. The seedlings were spaced 20 cm apart and their planting depth varied depending on each individual's root length. To avoid desiccation, we planted the sites on consecutive days and watered all the seedlings on the day of planting, two days after planting and two weeks after planting. We recorded seedling growth, damage and mortality every month for a period of one year. The height of each seedling was measured with a ruler from the base of the stem to the apical meristem. Height measurements made within three days after planting were used as initial height.

2.5 Data analysis

We examined the effect of bracken on seed germination and seedling survival by testing for differences in the proportion of germinated seeds (as a fraction of remaining plus germinated seeds) and seedling survival between the six treatments over a period of 28 weeks and 54 weeks respectively. For these two response variables, we fitted binomial generalised linear mixed-effects models (GLMM) with treatment and species identity as fixed effects and included species, site and plot identity as random factors with plot identity nested within site. We used the function *glmer* from package lme4 (Bates *et al*., 2015) to fit the GLMMs and selected the best models by first fitting saturated models with fixed effects and two-way interactions and sequentially removing the least significant terms starting with the interactions using the update function (Crawley, 2013; Zuur *et al*., 2013). Successional guild was not included as an explanatory variable as it would mask a number of important ecological responses to the experimental treatments given that the designation of species as pioneers or non-pioneers is based on various characteristics (Ghazoul & Sheil, 2010; Turner, 2001).

To examine whether seedling performance was affected by bracken, we tested for differences in relative seedling growth rates between the treatments over a period of 54 weeks. We used relative seedling growth rates as a response variable to account for differences that arise from initial height differences. Relative seedling growth rates (RGR) were calculated following Hunt (1982): RGR = ln(final plant height) – ln(initial plant height) / time in weeks. We fitted a linear mixed effects model (LME) with treatment and species identity as fixed effects and included species, site and plot identity as random factors with plot identity nested within site. The LME model was fitted using the function *lme* and the R package lme4 following Crawley (2013). We checked the adequacy of the LME model by plotting residuals versus fitted values to verify homogeneity and residuals versus each explanatory variable to check independence following Zuur *et al*. (2013).

3 RESULTS

3.1 Seed germination

A total of 1,466 seeds had germinated after 28 weeks and 7,399 seeds were still visible. Germination differed among treatments with the highest germination occurring in intact bracken (Table 1; Fig. 2). All 14 species germinated in the 'Bracken' and 'Bent' treatments while 13 species germinated in the 'Cut' treatment, nine species in the 'Cut and Litter removed' treatment, 11 species in the 'Bracken soil' treatment and 11 species in the 'Forest soil' treatment (Fig. 3). The mean probability of germination was higher in bracken for eight species, although only three species i.e. *Mystroxylon aethiopicum*, *Syzygium guineense* and *Psychotria mahonii* reached significance (Fig. 3; Appendix 1). Two species i.e. *Rapanea melanophloeos* and *Maesa lanceolata* germinated better in the 'Bent' treatment than in the five other treatments although when compared to the 'Bracken' treatment and the 'Cut' treatment, the differences were not significant. *Macaranga capensis* and *Allophylus abyssinicus* germinated better in the 'Cut' treatment than in the five other treatments although the germination of *Allophylus abyssinicus* in the 'Cut' treatment was not significantly better than that in the 'Bracken' and the 'Bent' treatments. *Faurea saligna* germinated better in the 'Forest soil' treatment than in the five other treatments but the difference was not significant when compared to the germination of *Faurea saligna* in the 'Cut' treatment. *Polyscias fulva* germinated better in the 'Forest soil' and 'Bracken' soil treatments than in the four other treatments (see Fig. 3 and Appendix 1).

Seeds of 11 out of 14 test species germinated better in the 'Bracken' treatment than in the 'Bent' treatment with five species reaching significance (Fig. 3; Appendix 1). *Macaranga capensis*, *Maesa lanceolata* and *Rapanea melanophloeos* were the exceptions but the differences were not significant. Strikingly, seeds of 13 out of 14 test species germinated better in the 'Cut' treatment than in the 'Cut and Litter removed' treatment with 11 species reaching significance. Further, five out of 14 test species germinated better in the ‘Bracken soil’ treatment than in the ‘Forest soil’ treatment with two species reaching significance. Conversely, six out of 14 test species germinated better in the ‘Forest soil’ treatment than in the ‘Bracken soil’ treatment with three species reaching significance (see Fig. 3 and Appendix 1).

3.2 Seedling survival

Out of 1,920 seedlings planted across treatments, 754 survived to the end of the experiment. Survival outcomes differed significantly among treatments and species with the highest survival occurring in the ‘Forest soil’ treatment (Table 1; Fig. 4). Four of the eight test species survived best in the ‘Forest soil’ treatment across all treatments with *Macaranga capensis* and *Ficalhoa laurifolia* surviving significantly better in the ‘Forest soil’ treatment than in the ‘Bracken’ treatment (Fig. 5; Appendix 2). In contrast, three species survived best in the ‘Bracken’ treatment across all treatments with *Psychotria mahonii* and *Vepris nobilis* reaching significance. *Podocarpus latifolius* survived best in the ‘Cut and Litter removed’ treatment compared to all other treatments though the difference was only significant when compared to the ‘Cut’ treatment (Fig. 5; Appendix 2).

Seedling survival was better in the ‘Bracken’ treatment than in the ‘Bent’ treatment for six out of eight test species with the GLMM analysis showing significant differences for *Psychotria mahonii* and *Vepris nobilis* (Fig. 5; Appendix 2). Survival was lower in the ‘Cut’ treatment than in the ‘Cut and Litter removed’ treatment for six species with significant differences shown by *Macaranga capensis* and *Podocarpus latifolius*. The ‘Bracken soil’ treatment had lower seedling survival than the ‘Forest soil’ treatment for all test species with significant differences shown by *Allophylus absyssinicus* and *Vepris nobilis* (Fig. 5; Appendix 2).

3.3 Seedling growth

The highest cumulative growth in seedling height (cm ± 1 SE) occurred on 'Bracken soil' (7.5 ± 1.3) and was closely followed by the growth on 'Forest soil' (7.0 ± 0.8; Fig. 6). Relative seedling growth differed significantly among treatments but this effect varied by species (Table 1). Whereas relative seedling growth in the 'Bracken' treatment was significantly higher than relative growth in the 'Cut' treatment for *Psychotria mahonii*, it was significantly lower than that in the 'Forest soil' treatment for *Macaranga capensis* (Fig. 7). However, there was no significant difference between relative seedling growth in the 'Bracken' treatment versus the 'Bent' treatment, between the 'Cut' treatment versus the 'Cut and litter removed' treatment and between the 'Bracken soil' treatment versus the 'Forest soil' treatment for any of the eight species (Fig. 7). Most species generally suffered high levels of damage with the greatest damage occurring in the 'Bracken soil' and 'Cut and litter removed' treatments (see Appendix 4). We found no significant difference in relative growth across treatments when seedlings with top damage were excluded (Appendix 5).

We also examined whether initial seedling size partly explains the variation in relative growth rates and found that it had a significant effect (Appendix 7). We further examined whether the performance of test species across treatments would be different when absolute growth is used instead of relative growth rate. We found a similar pattern except for *Syzygium guineense* which grew significantly better in the 'Bracken soil' treatment than in intact bracken (Appendix 8).

4 DISCUSSION

The effects of bracken on seed germination, seedling survival and growth of forest trees are both facilitative and inhibitory. In our field experiments that lasted seven months (germination) and one year (seedlings), we found that seed germination and seedling survival of late-successional species such as *Syzygium guineense* and *Vepris nobilis* were higher in full bracken than in bracken-removal plots. This implies that bracken and litter play an important role in moderating the conditions for germination and seedling establishment. In contrast most pioneer species such as *Macaranga capensis* and *Ficalhoa laurifolia* consistently germinated, survived and grew better in bracken-removal plots than in full bracken. Thus, it seems clear that effects of bracken hamper establishment and progression of pioneer species to later life-cycle stages. Taken together, and acknowledging that most seeds arriving in bracken are likely to be pioneers (see Ssali *et al*., 2017), these results imply that the filtering imposed by bracken will hinder succession.

4.1 Germination

Seed germination was generally higher in full bracken than in the five bracken-removal treatments. Most of the species with higher germination (percentage) in intact bracken including *Syzygium guineense* and *Mystroxylon aethiopicum* were late-successional species that are usually characterised by large and desiccation-sensitive seeds (Muhanguzi *et al*., 2002; Shehaghilo, 1989; Teketay & Granström, 1997). Bracken likely provided more favourable microclimatic conditions. In contrast, the germination of pioneer species including *Macaranga capensis* and *Maesa lanceolata* – which usually produce seeds with environmental sensors that delay germination until light or temperature conditions become suitable (Ghazoul & Sheil, 2010) – increased (though non-significantly) where fronds were bent. We also found that two pioneer species *Macaranga capensis* and *Allophylus abyssinicus* germinated better in plots where bracken was cut without removing litter (although the germination of *Allophylus abyssinicus* in the ‘Cut’ treatment was not significantly better than that in the ‘Bracken’ and the ‘Bent’ treatments). Overall, these results suggest that while bracken facilitates the germination of shade-tolerant species it appears to hinder the germination of light-demanding species.

When comparing plots with and without litter, we found that 13 of 14 test species germinated best in the presence of litter with 11 species reaching significance. This finding is in contrast with the generalised expectation that litter inhibits germination because it reduces the quantity and quality of light (see Facelli & Picket, 1991; Ghorbani *et al*., 2006). Litter removal can create a hotter and drier environment as observed by Gallegos *et al*., (2015) in the neotropics. In any case, our results highlight the importance of litter in influencing germination. They also suggest that below-ground competition, mechanical inhibition or allelopathic interference by bracken are weak or absent. These field experiments thus contrast with previous temperate and neotropical studies which found that leaf-extracts and fresh bracken litter can inhibit germination (Dolling *et al*., 1994; Facelli & Picket, 1991).

When we compared bracken soil and forest soil, we found contrasting outcomes of seed germination of small-seeded pioneer and large-seeded non-pioneer species. Three small-seeded pioneer species i.e., *Allophylus abyssinicus* (seed size = 2.6 mm), *Faurea saligna* (seed size = 1.1 mm) and *Maesa lanceolata* (0.5 mm) germinated significantly better in forest soil while two large-seeded non-pioneer species, i.e, *Myrianthus holstii* (seed size = 15.3 mm) and *Olea capensis* (seed size = 11.3 mm), germinated significantly better in bracken soil. This indicates that small-seeded pioneers are somehow more sensitive to bracken soil than large-seeded non-pioneers which favour it. We hesitate to ascribe this combined negative and positive influence to allelopathy. These contrasting effects may reflect chemical or microbial differences but these would need to be clarified by further study.

4.2 Seedling survival

Pioneer species generally survived better on forest soil than under full bracken but non-pioneers had a reverse pattern suggesting that bracken hampers survival by shading out seedlings of light-demanding species. This was particularly evident for *Macaranga capensis* and *Ficalhoa laurifolia* which survived significantly better on forest soil than under full bracken and had improved survival (though non-significant) when bracken was bent (see Fig. 4). In contrast, late-successional species survived better under full bracken indicating that unlike pioneers seedlings of late-successional species can benefit from a bracken canopy (see also Gallegos *et al*., 2015). Moreover most species were negatively affected by litter removal (see Fig. 4). These results likely reflect the improved infiltration and moisture retention with litter.

We also found that bracken hampers seedling survival via soil. This was inferred from seedlings surviving better on forest soil than on bracken soil for all test species with significant differences attained by *Allophylus absyssinicus* and *Vepris nobilis*. Previous studies in temperate and neotropical regions have also concluded that allelochemical compounds produced by bracken inhibit seedling establishment (De Jesus Jatoba, 2017; Dolling, 1996). As with the germination data, further work would be needed in order to clarify which factors were involved.

4.3 Growth

The best seedling growth for most species occurred either on forest soil or on bracken soil suggesting that bracken interferes with seedling growth. In addition, five out of eight species grew better where fern fronds were bent which reduced light competition. *Podocarpus latifolius*, one of the three species that grew better in full bracken than in the bent treatment, is late-successional and has deep roots and retains leaves throughout the year. Like *Podocarpus latifolius*, the two other species *Psychotria mahonii* and *Ficalhoa laurifolia* grow slowly while two of the species that performed poorly in bracken i.e., *Macaranga capensis* and *Allophylus abyssinicus* are fast-growing deciduous species (see Katende *et al*., 1995; Kattge *et al*., 2011). Generally, this finding implies that fast-growing pioneer species are likely outcompeted by bracken.

When we compared seedling growth in bracken soil versus that in forest soil, we found that six of eight species grew faster in forest soil though none of the differences reached significance. We also compared the growth of seedlings in plots with litter versus plots where litter was removed and found that five of eight species grew faster in litter-free plots though again the differences were non-significant. These results suggest that microbes, nutrients or toxins in bracken soil and litter may have hampered seedling growth. As reported by previous studies in temperate and neotropical regions (see e.g., De Jesus Jatoba, 2017; Dolling, 1996; Silva Matos & Belinato, 2010), allelochemical compounds produced by bracken can inhibit root and stem growth of tree seedlings.

4.4 Role of browsing

Our study was not designed to examine herbivory but we found it necessary as a consequence of our observations. The low level of seedling damage in plots with intact bracken compared to plots where bracken was bent or removed may be attributed to avoidance of bracken by herbivores. A comparable study in Netherlands found that seedlings growing under bracken are less liable to damage by herbivores such as roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) (den Ouden, 2000). In our study, we found that the tree species with shorter, and thus perhaps less apparent, seedlings (*Allophylus abyssinicus*, *Vepris nobilis* and *Psychotria mahonii*) suffered less damage in intact bracken than in bracken-free plots (see Appendices 4 and 6). These species also ranked among the best four survivors in intact bracken with survival of 55% or greater after 54 weeks of the experiment. Thus bracken may facilitate seedling survival partly due to reduced browsing.

4.5 Future directions

Our results are intriguing but raise questions. The role of shade remains uncertain. If the study were to be repeated, we would favour the treatments (particularly the more exposed bracken soil and forest soil treatments) being replicated with varying degrees of artificial shade so that we can better separate shade from other influences. We would also recommend a wider buffer-zone on the intact bracken control plots to reduce the influence of side light. Fencing to exclude or control access to larger and smaller herbivores may also clarify mechanisms.

The soil and litter mediated interactions warrant further investigation. We are unable to distinguish strict allelopathy from other processes that might lead to interference such as aluminium toxicity, nutrient depletion and microbial associations (see Ghazoul & Sheil, 2010, Cippolini *et al*., 2012; Mariotte *et al*., 2018). Furthermore, the apparently positive impacts of bracken soil on germination of some species (*Myrianthus holstii* and *Olea capensis*) are inconsistent with allelopathy.

Bracken's negative impact on the germination and survival of early successional species, versus the positive influence on late successional species is striking. Others have noted that allelopathy appears to play a greater role in the ecological relationships of pioneer versus shade tolerant species (Meiners, 2014). In the study of bracken elsewhere both negative (interference) and positive (facilitating) responses have been observed (Dolling, 1996; Günter *et al*., 2009; Gallegos *et al*., 2015; Marrs *et al*., 2000), but we believe that ours is the first to record both within a common community. This may reflect growth potential or more complex interactions via the soil (Mariotte *et al*., 2018; Meiners, 2014). The ecological, evolutionary, and practical implications of these differences warrant further evaluation.

5 CONCLUSIONS

This study provides evidence of both inhibition and facilitation by bracken. While pioneer species performed better in bracken-free plots, late-successional species germinated better and had better seedling survival in full bracken. Bracken acts as an ecological filter that removes early successional species from the seedling community by hampering their germination, survival and growth through shading and soil mediated processes.

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Tables, Figures and Appendices

Table 1: Effect of treatment and species identity on seed germination, seedling survival and seedling growth based on final models after a stepwise backwards selection process. Details of the final models are provided in Appendices 1–3.

	χ^2	df	P	Type of model
a) Seed germination				Binomial GLMM
Treatment	425.9	5	< 0.001	
Species	795.1	13	< 0.001	
Treatment × Species	219.0	65	< 0.001	
b) Seedling survival				Binomial GLMM
Treatment	61.8	5	< 0.001	
Species	208.6	7	< 0.001	
Treatment × Species	49.3	35	0.056	
c) Seedling growth				LME model
Treatment	43.6	5	< 0.001	
Species	4.7	7	0.692	
Treatment × Species	60.6	35	0.005	

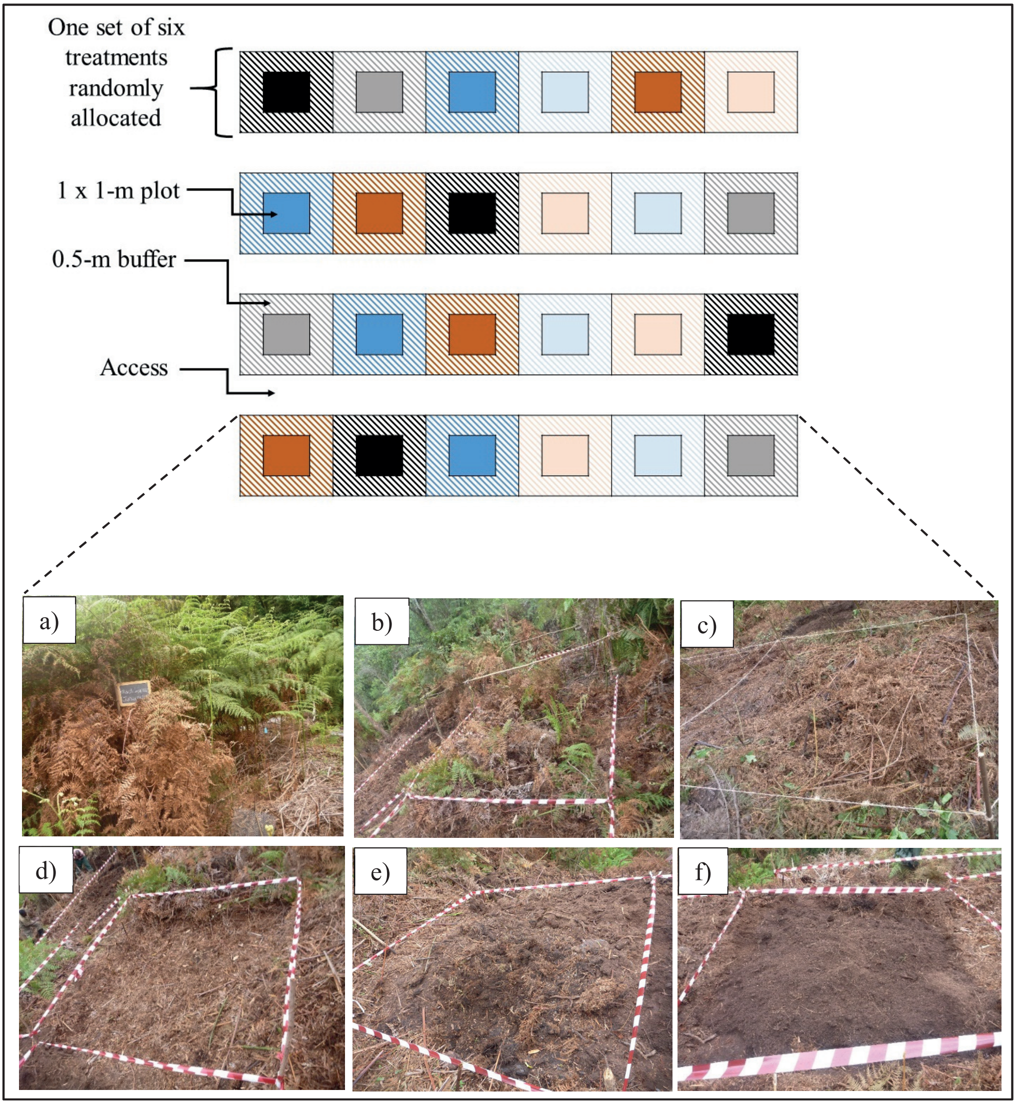


Fig. 1: Layout of bracken-removal treatments replicated in five study sites: a) Bracken, b) Bent, c) Cut, d) Cut and litter removed, e) Bracken soil and f) Forest soil.

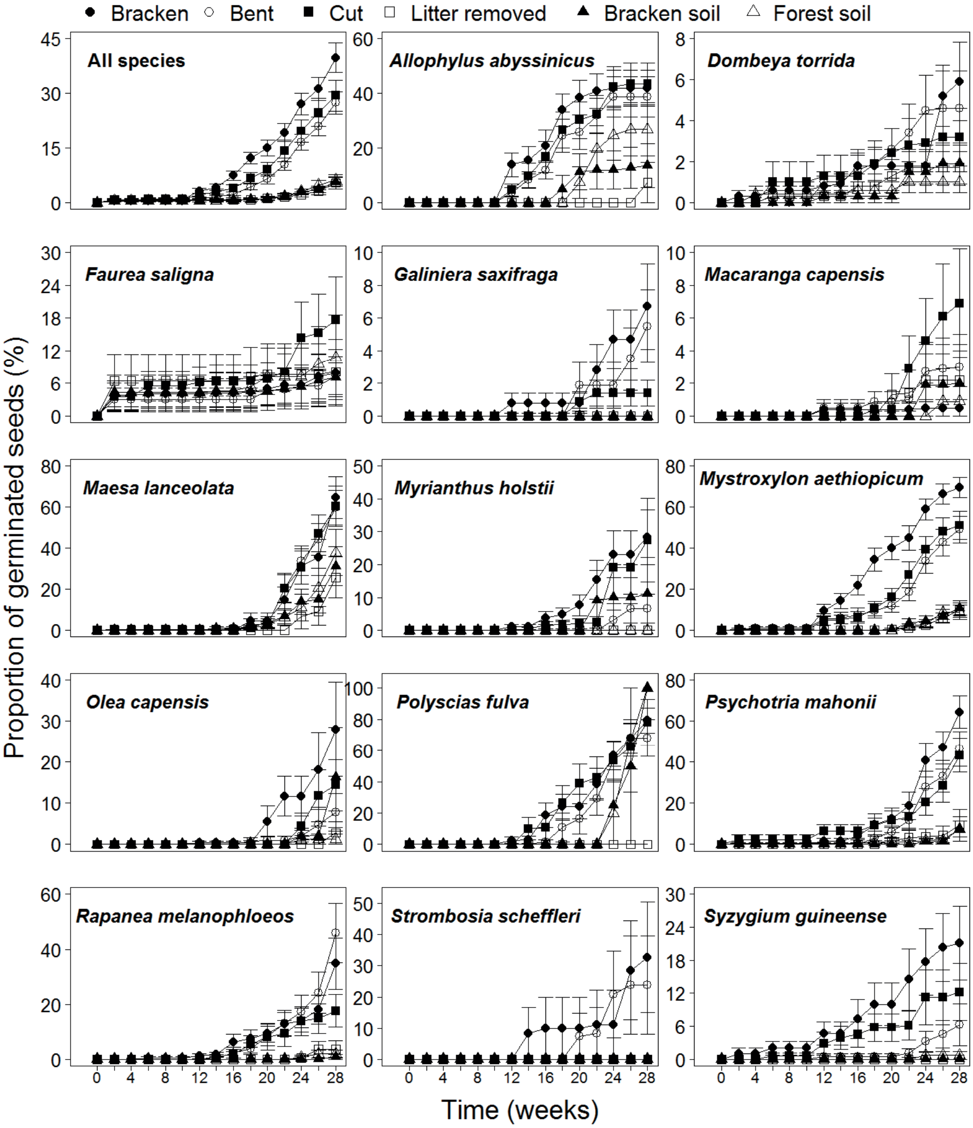


Fig. 2: Proportion of germinated seeds (cumulative total germinated divided by the sum of germinated plus remaining seeds) of woody species placed in six treatments for 28 weeks. The values represent plot means (± 1 SE) for all census intervals.

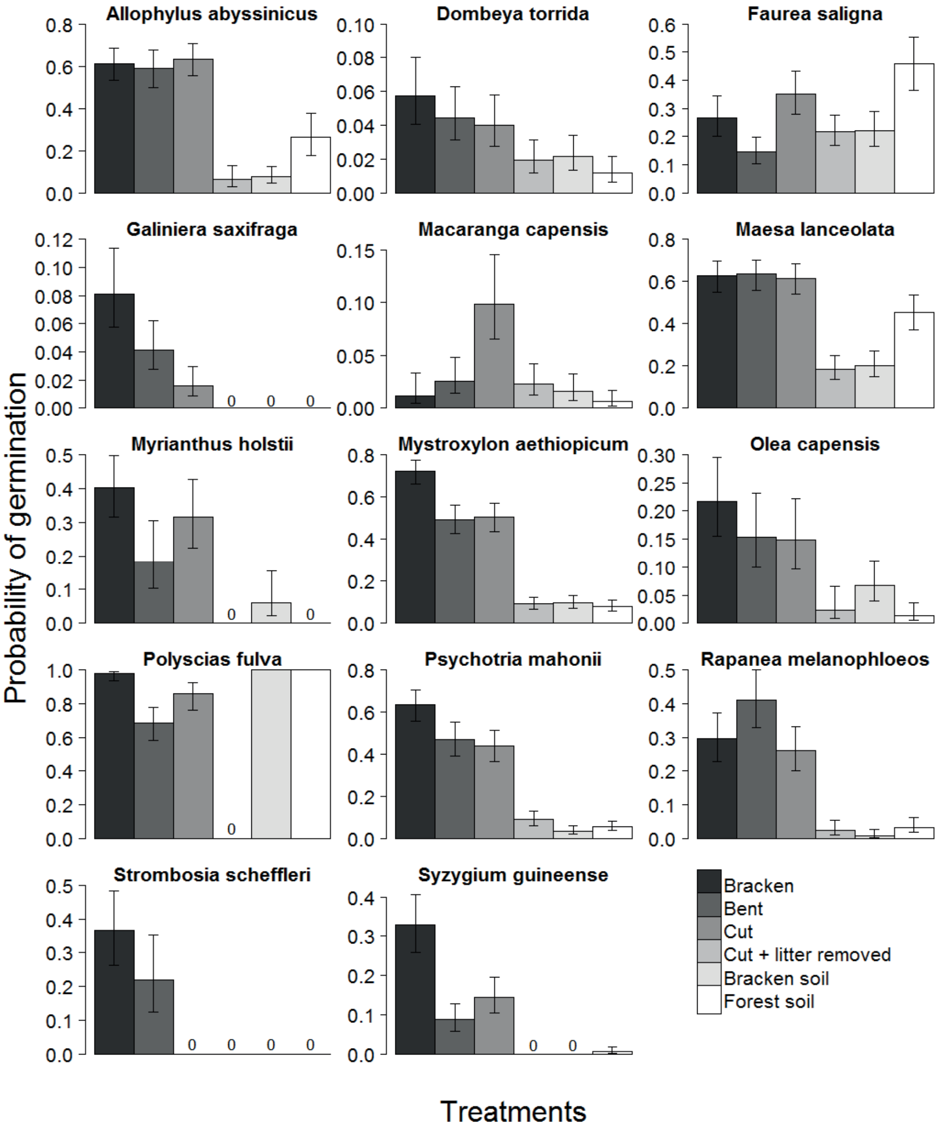


Fig. 3: Probability of seed germination of woody species placed in six treatments for 28 weeks (cumulative total germinated divided by the sum of germinated plus remaining seeds after the full period). Bars represent predicted treatment means (± 1 SE) based on coefficients of the best binomial GLMM.

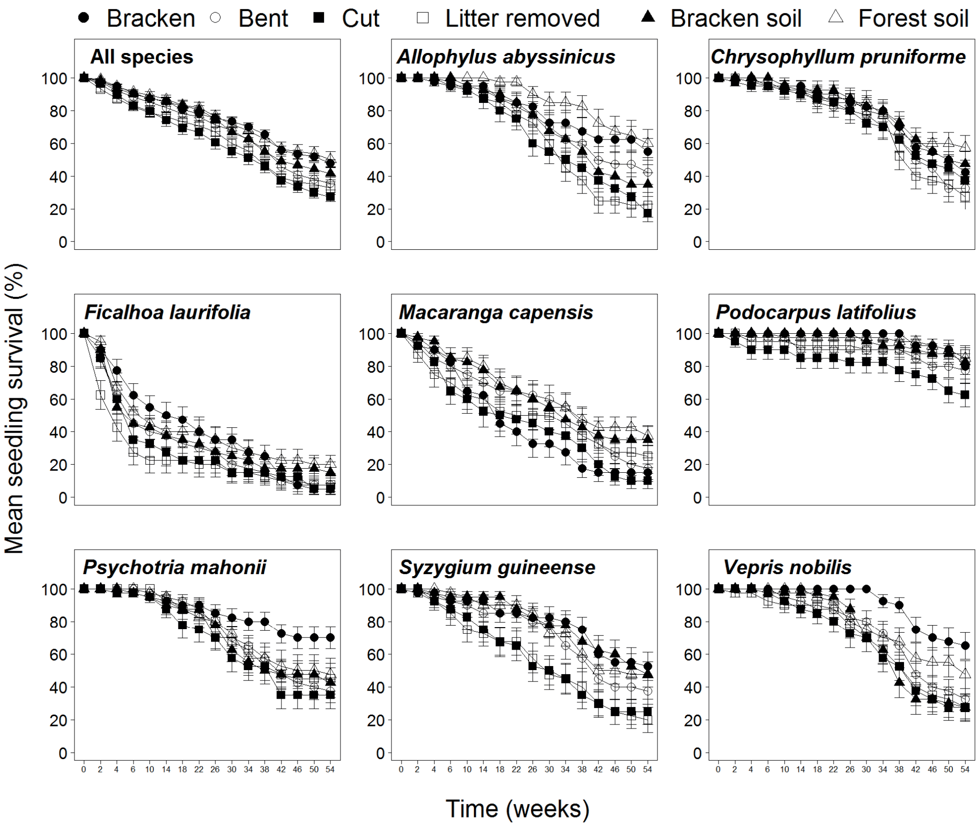


Fig. 4: Mean percentage survival of seedlings of woody species transplanted into six treatments for 54 weeks (surviving total divided by original total). The data are plot means (± 1 SE) for all census intervals.

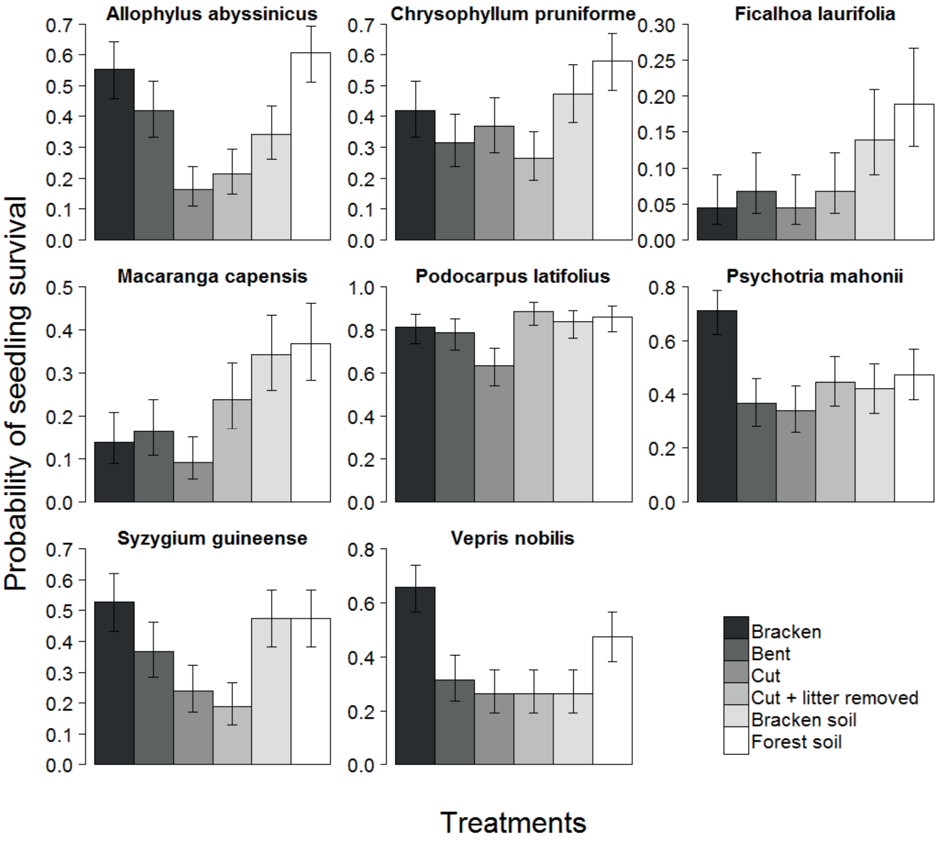


Fig. 5: Probability of seedling survival of woody species transplanted into six treatments for 54 weeks (surviving total divided by original total). Bars represent predicted treatment means (± 1 SE) based on coefficients of the best binomial GLMM.

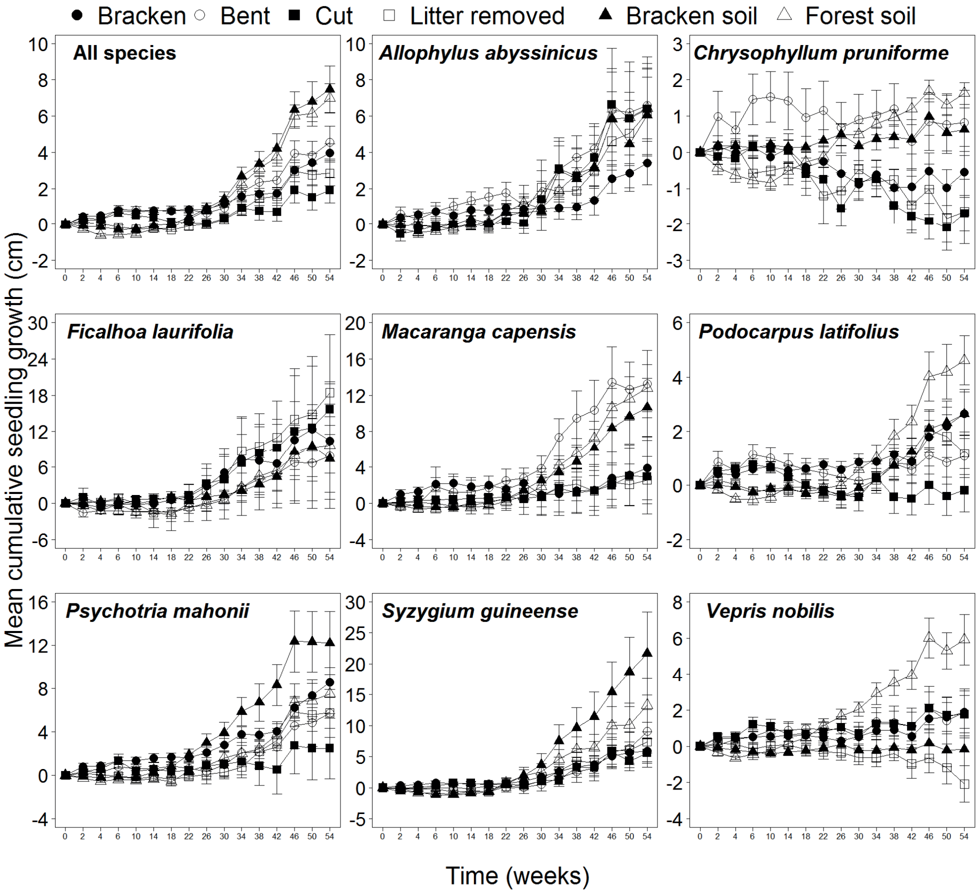


Fig. 6: Cumulative growth (cm) in seedling height of woody species transplanted into six treatments for 54 weeks. The values represent mean seedling growth (± 1 SE) per stem for all census intervals.

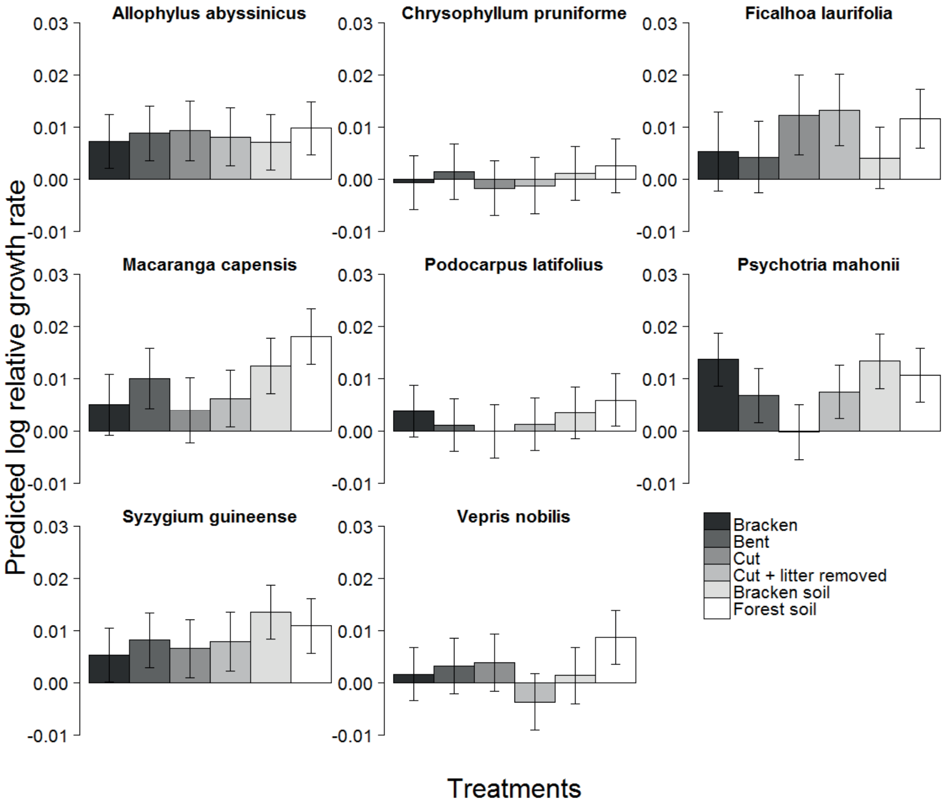


Fig. 7: Predicted log relative seedling height growth ("units" in $\log_e$(cm cm^{-1} week^{-1})) per treatment for each species. Only the seedlings that survived until the last measurement were considered. Bars represent treatment means (± 1 SE) predicted from coefficients of the LME model.

Appendix 1: Effect of bracken on seed germination based on the final binomial GLMM with treatment and species as fixed effects (species, site and plot identity were included as random factors).

	Estimate	SE	P
Intercept (Bracken / *Mystroxylon aethiopicum*)	0.95	0.28	0.001
Bent	-0.98	0.22	< 0.001
Cut	-0.94	0.22	< 0.001
Litter removed	-3.24	0.30	< 0.001
Bracken soil	-3.18	0.29	< 0.001
Forest soil	-3.40	0.31	< 0.001
Allophylus abyssinicus	-0.50	0.28	0.078
Dombeya torrida	-3.76	0.32	< 0.001
Faurea saligna	-1.97	0.34	< 0.001
Galiniera saxifraga	-3.38	0.34	< 0.001
Macaranga capensis	-5.36	1.03	< 0.001
Maesa lanceolata	-0.44	0.27	0.107
Myrianthus holstii	-1.35	0.34	< 0.001
Olea capense	-2.24	0.38	< 0.001
Polyscias fulva	2.73	1.04	0.009
Psychotria mahonii	-0.41	0.28	0.136
Rapanea melanophloeos	-1.82	0.31	< 0.001
Strombosia scheffleri	-1.51	0.46	0.001
Syzygium guineense	-1.67	0.30	< 0.001
Bent × *Allophylus abyssinicus*	0.89	0.43	0.039
Cut × *Allophylus abyssinicus*	1.04	0.40	0.010
Litter removed × *Allophylus abyssinicus*	0.08	0.83	0.924
Bracken soil × *Allophylus abyssinicus*	0.24	0.60	0.691
Forest soil × *Allophylus abyssinicus*	1.92	0.60	0.001
Bent × *Dombeya torrida*	0.71	0.46	0.121
Cut × *Dombeya torrida*	0.57	0.47	0.231
Litter removed × *Dombeya torrida*	2.10	0.61	0.001
Bracken soil × *Dombeya torrida*	2.15	0.58	< 0.001
Forest soil × *Dombeya torrida*	1.76	0.72	0.014
Bent × *Faurea saligna*	0.22	0.47	0.642
Cut × *Faurea saligna*	1.35	0.45	0.002
Litter removed × *Faurea saligna*	2.98	0.47	< 0.001
Bracken soil × *Faurea saligna*	2.93	0.49	< 0.001
Forest soil × *Faurea saligna*	4.24	0.52	< 0.001
Bent × *Galiniera saxifraga*	0.27	0.52	0.607
Cut × *Galiniera saxifraga*	-0.74	0.69	0.283
Litter removed × *Galiniera saxifraga*	-14.79	1571	0.992
Bracken soil × *Galiniera saxifraga*	-14.79	1555	0.992
Forest soil × *Galiniera saxifraga*	-14.57	1556	0.993

Bent × *Macaranga capensis*	1.76	1.19	0.140
Cut × *Macaranga capensis*	3.14	1.10	0.004
Litter removed × *Macaranga capensis*	3.90	1.21	0.001
Bracken soil × *Macaranga capensis*	3.43	1.27	0.007
Forest soil × *Macaranga capensis*	2.72	1.46	0.063
Bent × *Maesa lanceolata*	1.02	0.38	0.007
Cut × *Maesa lanceolata*	0.89	0.37	0.016
Litter removed × *Maesa lanceolata*	1.24	0.47	0.009
Bracken soil × *Maesa lanceolata*	1.29	0.46	0.005
Forest soil × *Maesa lanceolata*	2.69	0.45	< 0.001
Bent × *Myrianthus holstii*	-0.12	0.73	0.870
Cut × *Myrianthus holstii*	0.57	0.56	0.309
Litter removed × *Myrianthus holstii*	-15.48	2655	0.995
Bracken soil × *Myrianthus holstii*	0.83	1.11	0.456
Forest soil × *Myrianthus holstii*	-15.26	3342	0.996
Bent × *Olea capense*	0.56	0.60	0.351
Cut × *Olea capense*	0.48	0.60	0.422
Litter removed × *Olea capense*	0.81	1.12	0.470
Bracken soil × *Olea capense*	1.82	0.68	0.008
Forest soil × *Olea capense*	0.37	1.11	0.742
Bent × *Polyscias fulva*	-1.92	1.12	0.087
Cut × *Polyscias fulva*	-0.92	1.22	0.448
Litter removed × *Polyscias fulva*	-19.14	5594	0.997
Bracken soil × *Polyscias fulva*	17.29	10800	0.999
Forest soil × *Polyscias fulva*	18.86	5664	0.997
Bent × *Psychotria mahonii*	0.32	0.39	0.414
Cut × *Psychotria mahonii*	0.15	0.37	0.684
Litter removed × *Psychotria mahonii*	0.38	0.52	0.464
Bracken soil × *Psychotria mahonii*	-0.68	0.63	0.280
Forest soil × *Psychotria mahonii*	0.02	0.51	0.969
Bent × *Rapanea melanophloeos*	1.49	0.44	0.001
Cut × *Rapanea melanophloeos*	0.76	0.43	0.072
Litter removed × *Rapanea melanophloeos*	0.47	0.82	0.567
Bracken soil × *Rapanea melanophloeos*	-0.62	1.08	0.566
Forest soil × *Rapanea melanophloeos*	0.90	0.72	0.211
Bent × *Strombosia scheffleri*	0.26	0.79	0.745
Cut × *Strombosia scheffleri*	-17.12	3885	0.996
Litter removed × *Strombosia scheffleri*	-14.95	3553	0.997
Bracken soil × *Strombosia scheffleri*	-14.89	3893	0.997
Forest soil × *Strombosia scheffleri*	-14.79	3368	0.996
Bent × *Syzygium guineense*	-0.65	0.49	0.184
Cut × *Syzygium guineense*	-0.12	0.44	0.792
Litter removed × *Syzygium guineense*	-15.85	1795	0.993
Bracken soil × *Syzygium guineense*	-15.93	1741	0.993
Forest soil × *Syzygium guineense*	-0.89	1.08	0.413

Appendix 2: Effect of bracken on seedling survival based on the final binomial GLMM with treatment and species as fixed effects (species, site and plot identity were included as random factors).

	Estimate	SE	P
Intercept (Bracken / *Allophylus abyssinicus*)	0.21	0.38	0.572
Bent	-0.53	0.46	0.251
Cut	-1.84	0.54	0.001
Litter removed	-1.52	0.51	0.003
Bracken soil	-0.87	0.47	0.066
Forest soil	0.22	0.47	0.642
Chrysophyllum pruniforme	-0.53	0.46	0.250
Ficalhoa laurifolia	-3.27	0.80	< 0.001
Macaranga capensis	-2.03	0.56	< 0.001
Podocarpus latifolius	1.25	0.52	0.016
Psychotria mahonii	0.68	0.48	0.156
Syzygium guineense	-0.11	0.46	0.817
Vepris nobilis	0.44	0.47	0.349
Bent × *Chrysophyllum pruniforme*	0.08	0.67	0.904
Cut × *Chrysophyllum pruniforme*	1.62	0.71	0.023
Litter removed × *Chrysophyllum pruniforme*	0.81	0.70	0.248
Bracken soil × *Chrysophyllum pruniforme*	1.08	0.66	0.102
Forest soil × *Chrysophyllum pruniforme*	0.42	0.66	0.520
Bent × *Ficalhoa laurifolia*	0.97	1.06	0.357
Cut × *Ficalhoa laurifolia*	1.84	1.16	0.113
Litter removed × *Ficalhoa laurifolia*	1.96	1.07	0.069
Bracken soil × *Ficalhoa laurifolia*	2.10	0.98	0.032
Forest soil × *Ficalhoa laurifolia*	1.38	0.95	0.149
Bent × *Macaranga capensis*	0.72	0.77	0.349
Cut × *Macaranga capensis*	1.37	0.88	0.120
Litter removed × *Macaranga capensis*	2.18	0.77	0.005
Bracken soil × *Macaranga capensis*	2.03	0.74	0.006
Forest soil × *Macaranga capensis*	1.06	0.73	0.145
Bent × *Podocarpus latifolius*	0.38	0.73	0.603
Cut × *Podocarpus latifolius*	0.93	0.75	0.217
Litter removed × *Podocarpus latifolius*	2.10	0.81	0.010
Bracken soil × *Podocarpus latifolius*	1.04	0.75	0.167
Forest soil × *Podocarpus latifolius*	0.14	0.76	0.851
Bent × *Psychotria mahonii*	-0.90	0.67	0.179
Cut × *Psychotria mahonii*	0.29	0.73	0.688
Litter removed × *Psychotria mahonii*	0.41	0.70	0.560
Bracken soil × *Psychotria mahonii*	-0.35	0.68	0.606
Forest soil × *Psychotria mahonii*	-1.22	0.67	0.069
Bent × *Syzygium guineense*	-0.11	0.66	0.863
Cut × *Syzygium guineense*	0.58	0.73	0.429
Litter removed × *Syzygium guineense*	-0.05	0.72	0.946

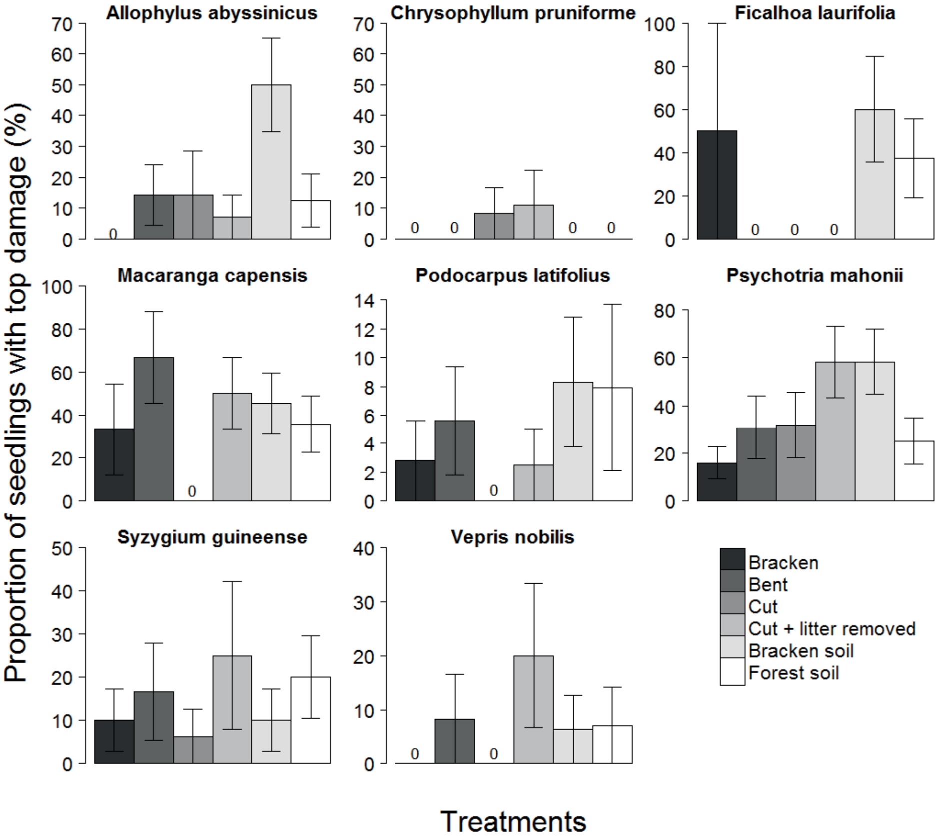
Bracken soil × *Syzygium guineense*	0.66	0.66	0.320
Forest soil × *Syzygium guineense*	-0.43	0.66	0.513
Bent × *Vepris nobilis*	-0.90	0.67	0.183
Cut × *Vepris nobilis*	0.16	0.73	0.823
Litter removed × *Vepris nobilis*	-0.16	0.71	0.818
Bracken soil × *Vepris nobilis*	-0.81	0.69	0.237
Forest soil × *Vepris nobilis*	-0.98	0.66	0.140

Appendix 3: Effect of bracken on relative seedling growth based on the final LME model with treatment and species as fixed effects (species, site and plot identity were included as random factors).

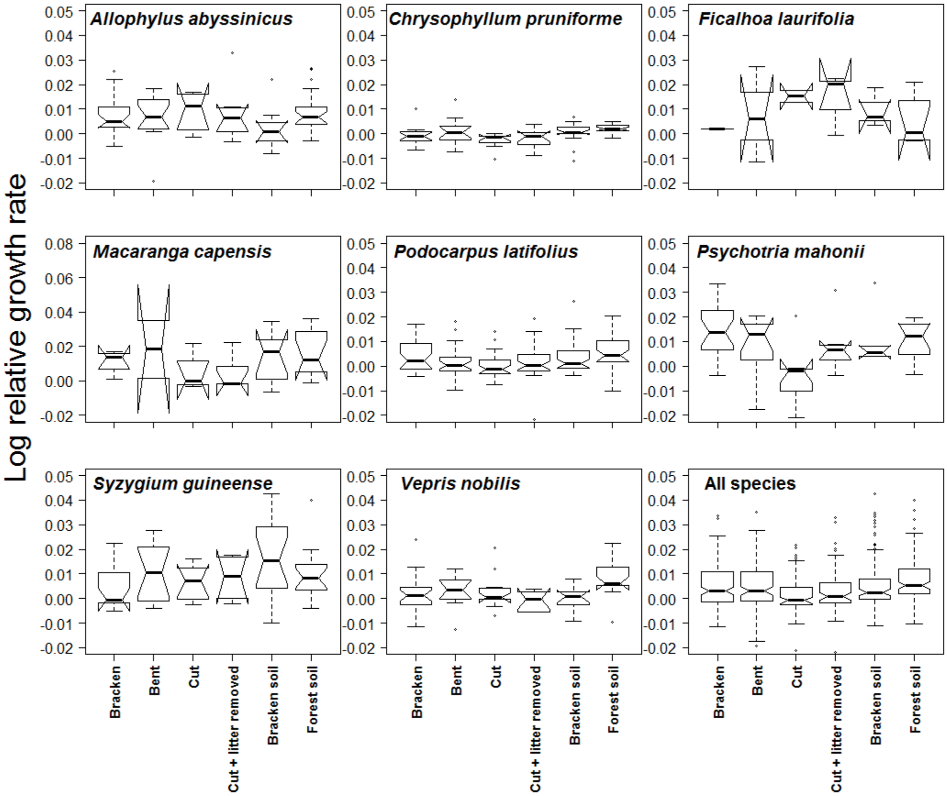
	Estimate	SE	P
Intercept (Bracken / *Allophylus abyssinicus*)	0.007	0.005	0.156
Bent	0.002	0.003	0.556
Cut	0.002	0.004	0.566
Litter removed	0.001	0.003	0.794
Bracken soil	< 0.001	0.003	0.940
Forest soil	0.003	0.002	0.307
Chrysophyllum pruniforme	-0.008	0.007	0.253
Ficalhoa laurifolia	-0.002	0.009	0.831
Macaranga capensis	-0.002	0.007	0.769
Podocarpus latifolius	-0.003	0.007	0.608
Psychotria mahonii	0.006	0.007	0.344
Syzygium guineense	-0.002	0.007	0.785
Vepris nobilis	-0.006	0.007	0.412
Bent × *Chrysophyllum pruniforme*	0.001	0.004	0.901
Cut × *Chrysophyllum pruniforme*	-0.003	0.005	0.564
Litter removed × *Chrysophyllum pruniforme*	-0.001	0.005	0.752
Bracken soil × *Chrysophyllum pruniforme*	0.002	0.004	0.612
Forest soil × *Chrysophyllum pruniforme*	0.001	0.004	0.842
Bent × *Ficalhoa laurifolia*	-0.003	0.008	0.741
Cut × *Ficalhoa laurifolia*	0.005	0.009	0.589
Litter removed × *Ficalhoa laurifolia*	0.007	0.008	0.394
Bracken soil × *Ficalhoa laurifolia*	-0.001	0.007	0.884
Forest soil × *Ficalhoa laurifolia*	0.004	0.007	0.595
Bent × *Macaranga capensis*	0.003	0.005	0.522
Cut × *Macaranga capensis*	-0.003	0.006	0.623
Litter removed × *Macaranga capensis*	< 0.001	0.005	0.955
Bracken soil × *Macaranga capensis*	0.008	0.005	0.122
Forest soil × *Macaranga capensis*	0.011	0.005	**0.025**
Bent × *Podocarpus latifolius*	-0.004	0.003	0.210
Cut × *Podocarpus latifolius*	-0.006	0.004	0.161
Litter removed × *Podocarpus latifolius*	-0.003	0.004	0.386
Bracken soil × *Podocarpus latifolius*	< 0.001	0.004	0.972
Forest soil × *Podocarpus latifolius*	< 0.001	0.003	0.920
Bent × *Psychotria mahonii*	-0.008	0.004	0.024
Cut × *Psychotria mahonii*	-0.016	0.004	**< 0.001**
Litter removed × *Psychotria mahonii*	-0.007	0.004	0.085
Bracken soil × *Psychotria mahonii*	< 0.001	0.004	0.977
Forest soil × *Psychotria mahonii*	-0.005	0.003	0.113
Bent × *Syzygium guineense*	0.001	0.004	0.748
Cut × *Syzygium guineense*	-0.001	0.005	0.853
Litter removed × *Syzygium guineense*	0.002	0.005	0.722

Bracken soil × *Syzygium guineense*	0.008	0.004	0.030
Forest soil × *Syzygium guineense*	0.003	0.004	0.400
Bent × *Vepris nobilis*	< 0.001	0.004	0.991
Cut × *Vepris nobilis*	< 0.001	0.005	0.969
Litter removed × *Vepris nobilis*	-0.006	0.004	0.167
Bracken soil × *Vepris nobilis*	< 0.001	0.004	0.997
Forest soil × *Vepris nobilis*	0.005	0.004	0.189

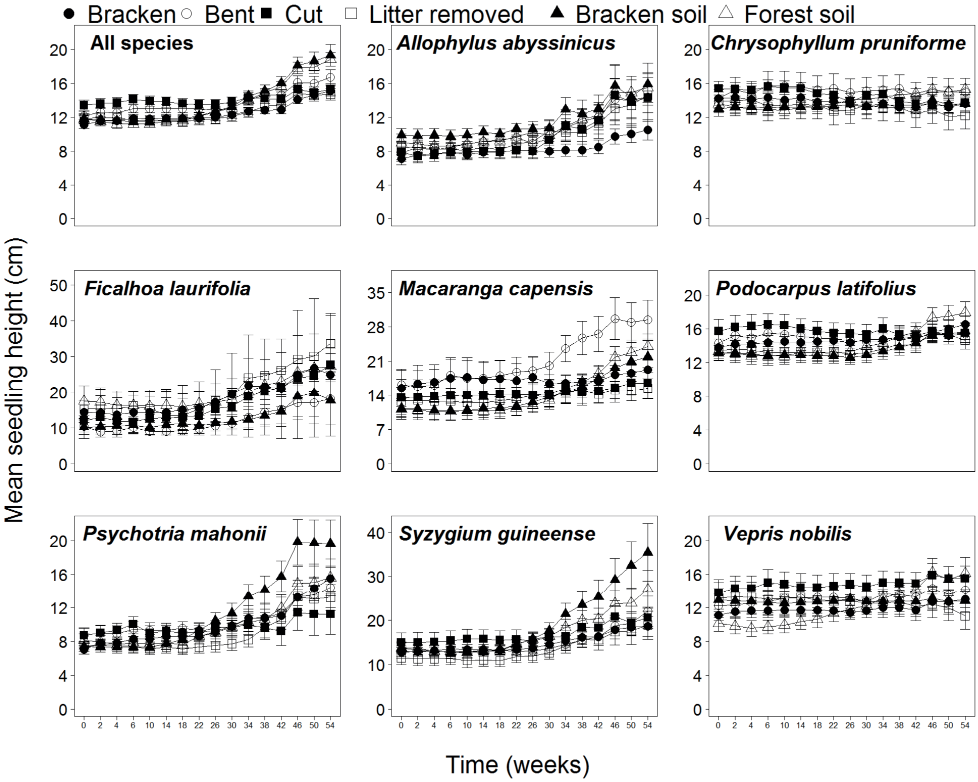
Appendix 4: Proportion of seedlings with top damage per treatment for plants that survived to the end of the experiment. Bars represent plot means (± 1 SE) for the final census.



Appendix 5: Log relative seedling height growth ("units" in $\log_e(\text{cm cm}^{-1}\text{ week}^{-1})$) for plants without top damage plotted for each species across all treatments. The values represent mean log relative seedling growth (± 1 SE) per stem in each treatment.



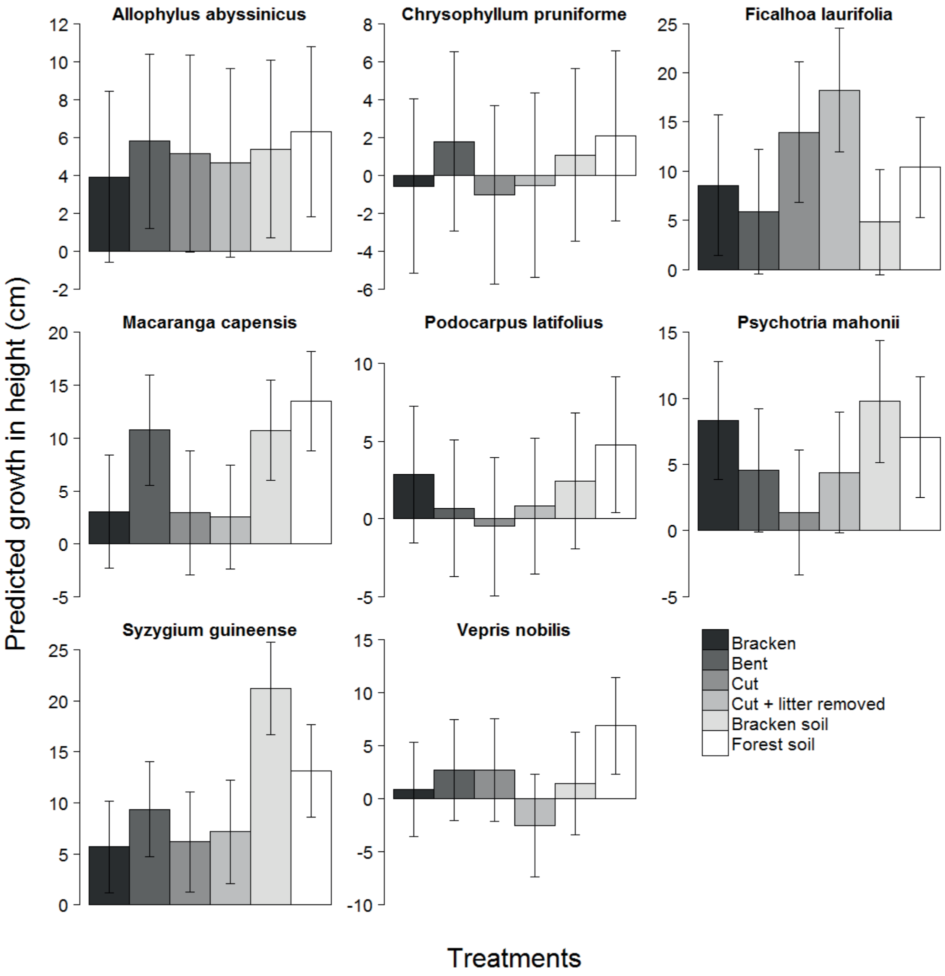
Appendix 6: Mean seedling height (± 1 SE) of woody species transplanted into six bracken-removal treatments for a period of 54 weeks.



Appendix 7: Influence of initial seedling height on relative seedling growth rate based on the final LME model after a stepwise backwards selection process.

	χ^2	df	P	Type of model
				LME model
Treatment	49.1	5	< 0.001	
Species	6.5	7	0.488	
Initial height	145.4	1	**< 0.001**	
Treatment × Species	62.8	35	0.003	
Treatment × Initial height	3.2	5	0.663	
Species × Initial height	77.5	7	**< 0.001**	

Appendix 8: Predicted absolute seedling growth (cm) per treatment for each species. Only the seedlings that survived until the last measurement were considered. Bars represent treatment means (± 1 SE) predicted from coefficients of the LME model.



Paper IV

Damage to artificial seedlings across a disturbed Afromontane forest landscape

Running Head: Seedling damage across an Afromontane landscape

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ABSTRACT

Damage can influence and impede forest regeneration. The intensity and pattern of damage to seedlings in the African highland forests has not previously been examined in detail. We used artificial seedlings to determine how (non-species specific) damage varies across a fragmented forest landscape in the Bwindi Impenetrable National Park, Uganda. A total of 848 artificial seedlings were 'planted' in 106 plots across 18 transects and monitored monthly, and replaced as necessary, for 20 months. We divided damage into that due to vertebrates, plant debris and unknown agents. Our particular interest was to determine how damage frequency varies with location and site conditions. From our 16,960 monthly stem assessments, 1,289 damage events were recorded. The mean 'seedling' damage per transect per year (± 1 SE) was 59.5 ± 2.3%. Damage was significantly more frequent in sites dominated by short herbs (66.1 ± 3.0) than in sites dominated by shrubs (60.1 ± 2.6) and ferns (47.9 ± 2.7). The mean proportion of artificial seedlings damaged by each class of agents was 45.8 ± 2.1% for vertebrates, 21.4 ± 2.1% for plant debris and 3.8 ± 0.6% for unknown agents. These rates surpass those reported in other montane forests, likely reflecting the density of large vertebrates in our site. While most damage was attributable to animals, most of the variation among sites was due to plant debris.

Key words: Bwindi, forest regeneration, herbivores, plant debris, seedling damage, thick understorey, topographic variation

THE DYNAMIC BALANCE BETWEEN FOREST AND NON-FOREST VEGETATION remains incompletely understood (Hoffmann *et al*. 2012, Murphy & Bowman 2012, Nackley *et al*. 2017). Considerable areas with stalled forest recovery occur worldwide and likely reflect various factors including recurrent damage to regrowth (Clark & Clark 1991, Holm *et al*. 1997, Boyes *et al*. 2011). Non-species specific seedling damage results from natural processes including trampling, branch falls, tree falls, landslides, fire and wind and human activities such as timber cutting and extraction (Clark & Clark 1989, Plumptre 1993, Pickett *et al*. 1999, Ghazoul & Sheil 2010). Slow growing seedlings and saplings exposed to frequent damage may die or spend much of their lifetime in the understorey where they may intermittently lose much or all of the height they gain in growth (Clark & Clark 1989, Turner 2001, Ghazoul & Sheil 2010). Frequent damage can potentially slow or prevent tree establishment thus interfering with forest recovery and impacting conservation values and carbon storage.

We assessed the frequency and spatial pattern of damage to artificial seedlings in an area of rugged partially forested terrain in the Bwindi Impenetrable National Park, Uganda. Such artificial seedlings have become a standard approach for assessing non-species specific damage rates (Clark & Clark 1989, Alvarez-Clare & Kitajima 2009, Rosin *et al*. 2017). Though there have been suggestions that animals may sometimes respond in an atypical way to artificial seedlings (Gillman *et al*. 2002), the method is easy to replicate and provides an estimate of background rates of non-species specific damage (Clark & Clark 1989, Drake & Pratt 2001, Gillman *et al*. 2002).

In the Bwindi Impenetrable National Park (“Bwindi”) in Uganda, forest cover is locally patchy and fragmented and includes large long-lived clearings where seedlings are rare and dense and persistent understorey plants such as *Pteridium aquilinum* (L.) Kuhn, *Mimulopsis* *arborescens* C.B. Clarke and *Acanthus polystachyus* Delile are prevalent (Babaasa *et al*. 2004, Sheil, 2012, Ssali *et al*. 2017). One plausible explanation for the limited forest recovery is that seedlings may be damaged and killed, or repeatedly broken, and thus seldom recruit into larger less vulnerable trees. Studies elsewhere, particularly from temperate and neotropical regions, have shown that frequent damage to seedlings and saplings influences regeneration (Clark& Clark 1991, Koestel & Rankin-de Mérona 1998, Paciorek *et al*. 2000). Apart from a localised study of trampling in the Virunga Volcanoes (see Plumptre 1993), assessments are lacking for montane forests in equatorial Africa.

Following the approach developed by Clark and Clark (1989), we sought to determine how much damage occurs and how it varies with location. We hypothesised that the frequency of damage is influenced by multiple factors including (1) canopy cover, (2) human activities and (3) landscape position. Our expectation was that damage to artificial seedlings would be more frequent in open areas where ground feeding animals tend to be more abundant than in the more closed forest (Laws *et al*. 1975, Ssali *et al*. 2012). We also expected more frequent damage farther from roads and from the park edge since larger animals often tend to avoid these features (Olupot & Sheil 2010, Mugerwa *et al*. 2013). Furthermore, we expected less damage where slopes impede ready access to large mammals (Ssali *et al*. 2012).

METHODS

STUDY AREA.—The Bwindi Impenetrable National Park (henceforth “Bwindi”) is a montane forest located near the equator in South-West Uganda (0°53'–1°08' S, 29°35'–29°50' E). The 321 km^2 forest spans 1,160 to 2,607 m asl and has been managed as a National Park since 1991 and as a UNESCO World Heritage site since 1994 (Howard 1991, IUCN 1994). The climate is equatorial with two rainfall peaks from March to May and September to November. Annual rainfall ranges from 1,130 to 2,390 mm and the mean temperature ranges between 7°C and

29°C determined primarily by elevation. The driest months are December-January and July-August. Bwindi has a steep and rugged topography and is a source for the Rivers Ishasha, Nshongi and Ndeego flowing to Lakes Bunyonyi, Mutanda and Edward. Mubwindi—an open swamp of about 1 km^2—is the only sizeable flat area in the park (Butynski 1984, Marchant & Taylor 1997). The park is traversed by a public road that runs from Ruhija through the Bamboo zone and connects to the nearby town of Kabale. About 36 vehicles travel this road each day (Barr *et al*. 2015, Uganda Wildlife Authority: BINP General Management Plan 2014 -2024).

Our study area was located near the Institute of Tropical Forest Conservation (ITFC)—a research station at Ruhija (2,355 m asl). Common canopy trees in this area include *Neoboutonia macrocalyx* Pax, *Dombeya torrida* (J.F.Gmel.) Bamps and *Croton macrostachyus* Hochst. ex Delile in lower-slope sites, *Pittosporum viridiflorum* Sims, *Olea capensis* L. and *Strombosia scheffleri* Engl. in mid-slope sites and *Agauria salicifolia* (Comm. ex Lam.) Hook.f. ex Oliv., *Erica benguelensis* (Welw. ex Engl.) E.G.H.Oliv. and *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb. in hilltop areas (FS pers. obs.). In the understorey *Pteridium aquilinum* (L.) Kuhn, *Triumfetta* spp, *Mimulopsis arborescens* C.B. Clarke, *Mimulopsis solmsii* Schweinf. and *Impatiens* spp tend to dominate (Nkurunungi *et al*. 2004, Sheil 2012).

Bwindi's large herbivores include elephant *Loxodonta africana* Blumenbach, mountain gorilla *Gorilla beringei beringei* Matschie, bush pig *Potamochoerus larvatus* F. Cuvier, black-fronted duiker *Cephalophus nigrifrons* Thomas and yellow-backed duiker *Cephalophus silvicultor* Afzelius (Olupot & Sheil 2010, Ssali *et al*. 2012, Mugerwa *et al*. 2013).

STUDY SET-UP.—We established 18 transects spread across a range of vegetation types i.e. forest with bamboo, forest with heather, open areas (with poor regeneration) and forest with rich and medium tree cover encompassing areas accessible from the ITFC research station and known to be visited by large vertebrates such as elephants, gorillas, bush pigs and duikers. The transects were chosen based on accessibility to both lower, mid and upper slope positions in a relatively compact area. Each transect had six plots spread over the full range of topographic positions, except for one over gentler terrain that had eight plots and one in the heather forest that had just two. In all but one case the transect began in a relatively level lower slope position, and ran upslope traversing the full range of topographic positions toward the hilltop, following a compass bearing. In each location we avoided local bias in site selection by adding a random distance (five paces) to left or right. Each plot was established by choosing a nearby tree (dbh > 5 cm) which was marked to aid relocation, in positions that corresponded to our main topographic features. Transects did not follow established tracks.

In each plot, we recorded slope position (lower slope, mid-slope and hilltop), GPS coordinates and dominant understorey plants e.g. *Pteridium aquilinum*, *Oplismenus hirtellus* (L.) P.Beauv. and *Mimulopsis solmsii* (categorised as ferns, short herbs and shrubs). We measured or estimated: 1) canopy openness (%, using a densiometer), 2) basal area (m^2 ha^{-1}, using a 'relascope'), 3) slope angle (°, using a clinometer), 4) elevation (m, using a GPS), 5) number of trees supporting large masses of climbers (%, visually determined in each plot, see below), and 6) distance from the nearest bracken clearing (m, determined by counting paces from each plot to the nearest bracken clearing). For our measure of climber abundance we recorded the number of trees with and without climbers following Alder and Synnott (1992). We used these counts to calculate the percentage of trees supporting climbers. We also determined the shortest horizontal distance between each plot and the park boundary, motorable road and water source (i.e. rivers, streams and wetlands) from the Bwindi GIS database using ArcGIS 10.5 (ESRI 2011).

We constructed each of our initial 848 artificial seedlings and 1246 replacements from two plastic drinking straws (19.5 cm length × 0.7 cm diameter) stapled into a cross and attached to a 13 cm long, 3 mm diameter wire "root" (following Clark and Clark, 1989). We located artificial seedlings in 106 slope-based plots. In each plot, eight 'seedlings' were placed 3 m apart and replicated along 18 transects running from valleys to hilltops. We tagged each seedling with a 2-m yellow string, which lay on the ground tied to the base of the metal root, for easy location of artificial seedlings since the understorey vegetation in many of our plots was thick. The artificial seedlings were relocated and examined every month from July 2011 to February 2013. For comparison with previous studies, three categories of damage were recorded. An artificial seedling was classified as “damaged by vertebrates” if it was trampled, uprooted, gnawed upon, or missing, with evidence of vertebrate activity including animal trails, diggings and tooth marks. If an artificial seedling was bent or flattened, with evidence of fallen debris on or very close to it, it was considered “damaged by plant debris”. If an artificial seedling was damaged or lost but there was no clear evidence of the cause, it was classified as “unknown”. Each month uprooted, lost and damaged artificial seedlings were replanted or replaced as necessary.

We conducted a second smaller study to assess which large mammals might be impacting the artificial seedlings in and around bracken-dominated clearings. We did this by deploying camera traps (Reconyx model RM45 preset with a 1-s delay between subsequent images; http://www.reconyx.com) along eight additional transects comprising three points that span the edge: in the forest (-25 m), at the edge (0 m) and in bracken (25 m). Ten artificial seedlings were placed 1-m apart within view of each camera. Both the cameras and ‘seedlings’ were relocated in April 2015, after 30 days. Unlike in the previous study, we did not classify damage. We also counted camera “events” defined as sequences of observations of each animal or group of animals separated by less than one minute. Taxonomy follows Wilson and Reeder (2005).

DATA ANALYSIS.—Our 106 plots were located from 0.5 to 2.8 km of the nearest park edge with elevation ranging from 2,066 to 2,527 m asl and slope from 5 to 40°. We evaluated the factors associated with damage to artificial seedlings (i.e. a binary response: damaged or not damaged) by fitting generalized linear models (GLMs) with negative binomial errors. Our evaluations and analyses included eleven single factors and all their potential two-way interactions. We examined total damage along with vertebrate damage, plant-debris damage and damage by unknown agents as distinct response variables. Potential explanatory factors included canopy openness, basal area, dominant understorey species, proportion of trees with climbers, slope position, slope angle, elevation, distance from the nearest water source, distance from the nearest motorable road, distance from the nearest park edge and distance from the nearest bracken clearing. For canopy openness and basal area, we also incorporated the squared terms in order to assess potential nonlinear effects.

To fit the GLMs, we used the function *glm.nb* from the R "MASS" package (Venables & Ripley 2002). We selected the best models by first fitting saturated models with fixed effects and two-way interactions and sequentially removing the least significant terms starting with the interactions using the update function (Crawley 2013, Zuur *et al*. 2013). We excluded one variable from each of the variable pairs that were highly correlated ($r > 0.5$) i.e. canopy openness versus basal area and distance to the nearest water source versus distance to the nearest park edge (Fig. S1). For each response variable, we run two sets of initial models with all significant single factor explanatory variables (see Table 1) and their two-way interactions included (but left out one explanatory variable from the highly correlated variable pair). We then selected the initial model with the lowest AIC for the subsequent model simplification process. To permit comparisons, we also calculated annual rates using a modified formula from Sheil *et al*. (1995): $100\,(1-(1-(N_t/N_0)/100)^{12})$, where N_0 and N_t are the number of artificial seedlings at the start and the number of damaged artificial seedlings at the end of each monthly census, respectively.

RESULTS

‘SEEDLING’ DAMAGE.—From our 16,960 artificial seedling assessments over 20 months, a total of 1,289 were damaged; 875 by vertebrates, 357 by plant debris and 57 by unknown agents. Most of the variation among sites was due to plant debris (Fig. 1). On average (± 1 SE), overall damage across the 18 transects was 7.4 ± 0.4% per month and 59.5 ± 2.3% per year. Though we were not always able to distinguish which animals damaged the artificial seedlings, we observed 17 elephant trampling events in three transects (i.e., one transect had seven elephant visits while two transects had five visits each). Trampling by elephants resulted in the damage of all artificial seedlings in a single visit to two of our plots located along the transect in the Bamboo zone. We often saw damage by other animals including duikers, baboons, gorillas and bush pigs, but signs were often ambiguous and overlapping, so we did not attempt a summary. We detected no fires or landslides in the study area during our study.

When performing single factor analysis, the frequency of overall damage to artificial seedlings was significantly related with eight of our eleven explanatory variables (Table 1). Damage increased with canopy openness and was more frequent in sites dominated by short herbs than in those dominated by shrubs and ferns (Table 1 and Fig. 2). Our multivariate assessments indicated that overall patterns of damage were best explained as functions of slope position, basal area, distance from the nearest water source and distance from the nearest motorable road (Table 2). Damage frequency followed a U-shaped trend with basal area in all slope positions, declining with increasing tree cover until it begins to increase again from 46.3 m^2 ha^{-1} onwards (though there was considerable uncertainty at high basal area). Damage also decreased with distance from water, increased with distance from the nearest road in all slope positions, and was less frequent in hilltop locations than in mid-slope and lower-slope sites

(Table 2; Fig. 3). Keeping other factors constant, an artificial seedling was 30% more likely to be damaged in a lower-slope site than in a hilltop site (Table 2; Fig. 3).

The mean proportion of artificial seedlings damaged over 20 months by each class of agents (yr^{-1} ± 1 SE) was 45.8 ± 2.1% by vertebrates, 21.4 ± 2.1% by plant debris and 3.8 ± 0.6% by unknown agents. For vertebrates, damage frequency decreased with distance from the nearest water and increased with distance from the nearest road especially in mid-slopes (Table 2; Fig. 4). For plant debris, the frequency of damage increased with climber abundance and was significantly lower in hilltops than in other slope positions (Table 2; Fig. 5). Artificial seedlings on hilltops were 68% less likely to be damaged by falling woody debris than on lower-slopes and controlling for other factors, a 10% increase in climber abundance was associated with a 10% increase in debris damage.

The damage attributable to unknown agents was significantly related only with distance to the nearest bracken dominated clearing (Table 1). We found a significantly higher level of such damage within 100 m of bracken clearings (yr^{-1} ± 1 SE; 5.8 ± 1.4%) than in sites farther away (2.6 ± 0.6%).

VERTEBRATES AT FOREST EDGES.—From our second study, over 30 days, the total number of vertebrate camera-trap "events" was 179 in the forest, 183 at the edge and 57 in bracken (Table 3). The mean proportion of artificial seedlings damaged was 5.0 ± 0.5% in the forest, 11.3 ± 1.3% at the edge and 5.0 ± 1.0% in bracken. Though suggestive there was no significant correlation between vertebrate camera-trap "events" and the frequency of damage to artificial seedlings in forest ($\tau = -0.28$, $n = 8$, $P = 0.39$), at the edge ($\tau = 0.48$, $n = 8$, $P = 0.12$), in bracken ($\tau = 0.22$, $n = 8$, $P = 0.51$) and in all segments combined ($\tau = 0.23$, $n = 24$, $P = 0.17$; see Fig. 6).

DISCUSSION

The 61.3% rate of damage per stem per year was higher than that reported from other tropical montane forests but lower than in several lowland sites (Table 4). Most of the damage in our site was attributable to animals while most of the variation was due to plant debris. Artificial seedlings experienced a higher frequency of damage in more (versus less) open areas, farther (versus nearer) distance from roads and on relatively gentle (versus steeper) slopes. Generally, our results indicate a complex pattern of small-scale damage causing processes and relationships with implications for the regeneration of tree species vulnerable to damage—such vulnerable species are likely to include any that occur at low density and take several years to reach less vulnerable sizes.

The artificial seedlings were simple to construct, deploy and record. Our camera trap observations didn't indicate any atypical treatment of the artificial seedlings by animals though we found some that had been chewed and we suspect that baboons or monkeys may occasionally have damaged 'seedlings' out of curiosity. Using artificial seedlings to assess damage rates avoids the complexity of assessing damage to real seedlings and eases comparisons across sites, but it also limits the ecological realism. Real plants could certainly suffer much greater damage if they attract herbivores—and thus the damage rates we record are likely a minimum. We agree with previous studies that have highlighted both the benefits and limits of these approaches (Clark & Clark 1989, Gillman *et al*. 2002, Alvarez-Clare & Kitajima 2009).

The observed increase in damage frequency with canopy openness appears to reflect a higher abundance of falling plant debris and foraging animals in open versus closed forest. We found greater among-site variation in damage by falling plant debris (damage per year was 25.8 ± 3.0% in open sites vs 17.9 ± 1.8% in closed forest) than by foraging animals (damage was 45.1 ± 3.2% in open sites vs 43.1 ± 2.1% in closed forest). Treefalls and branchfalls appear to be more frequent in open and disturbed areas. Much of the falling debris likely results from the fast-growing and weak stemmed species that often predominate in relatively open areas (e.g., *Neoboutonia macrocalyx, Croton macrostachuys* and *Tabernaemontana pachysiphon* Stapf). The frequency of debris damage was also positively associated with climber abundance which may cause branch breakage and toppling of trees, and can also be a consequence and thus an indicator of disturbance (Schnitzer *et al*. 2004, Eilu & Obua 2005, Tobin *et al*. 2012).

The frequency of vertebrate damage increased with distance from the nearest road and this likely reflects the combined influence of traffic and sharp habitat edges. Damage frequency also decreased with distance from water possibly highlighting how animals use water—such effects are seen for example with elephants which are known to stay close to Mubwindi Swamp during droughts (Babaasa 2000, Ssali *et al*. 2012). Further, damage frequency declined with progression from lower-slope to mid-slope to hilltop sites, likely indicating that animals are more abundant in these lower slope habitats. We infer that localised concentration of animals likely results in high damage frequency especially if these areas are repeatedly used (Laws 1970, Plumptre 1993, Ssali *et al*. 2012). This is clearly true for elephants for which even a single visit in an area may result in the damage of many seedlings (FS and DS pers. obs.).

Damage was significantly more frequent in sites dominated by short herbs than those dominated by shrubs or ferns. Ground feeding herbivores are likely attracted to areas dominated by herbs such as *Oplismenus hirtellus*, *Droguetia iners* (Forssk.) Schweinf. and *Pilea holstii* Engl. For instance, the most common herbivores in our camera trap study—the Yellow-backed duiker and Black-fronted duiker (see Fig. S2)—tend to be attracted to sites with herbaceous vegetation where they may also trample tree seedlings (Plumptre 1991, Kingdon 1997, Terborgh *et al*. 2016). In general we observe abundant signs of animal activity in and around forest clearings especially trails of baboons, monkeys and duikers and diggings by bush pigs. Though artificial seedlings located in bracken received less damage compared to some other vegetation types, such as the short understorey herbs (damage per year was 47.0 ± 10.7% in bracken vs 60.1 ± 2.6% in the short understorey herbs), the damage appears sufficient to further impede the slow forest recovery seen in these areas. Indeed the herbivore activity seen at the forest edge in these areas seems likely to counteract much of the regrowth that might otherwise occur. There is a local belief—which we were unable to verify—that elephants like to aggregate and socialise in open clearings thus preferentially trampling these areas. Though it did not occur at our monitored locations, our informal observations in the wider landscape show that elephants feed in these clearings: they pull up bracken plants and cut the rhizomes from the ground with their toes, swinging their front feet from side-to-side, a process leaving bare soil that is soon recolonised by bracken but devoid of seedlings (FS and DS pers. obs.).

Our results have implications for tree regeneration. First, seedlings, particularly those of slower growing shade tolerant species, are vulnerable to high damage frequency since they remain vulnerable over many years. We thus predict that the seedlings that reach large size will be those that grow quicker and escape from vulnerable to less vulnerable (larger) sizes (see Sheil & Salim 2004). Second, frequently disturbed areas may take long to recover due in part to a high frequency of debris damage and a self-perpetuating cycle in which disturbed vegetation maintains and attracts further disturbance. Finally, as seen in our studies of bracken-dominated clearings, seedling densities in these open areas are low (Ssali *et al*. 2017), due in part to limited seed rain and low seed persistence (Ssali *et al*. 2017, Ssali *et al*. 2018), and thus an annual 61.3% damage rate is likely to further slow recovery. Exclosure studies would be required to assess this influence.

CONCLUDING REMARKS.—We found a high frequency of damage to artificial seedlings in a montane forest in equatorial Africa. The mean likelihood of damage was 61.3% per stem per year with considerable variation among sites and across the wider landscape and with particularly high frequencies in areas that have already been subjected to recurrent disturbance. Slow growing trees likely suffer recurrent damage from falling plant debris and trampling by large herbivores before they reach less vulnerable sizes. Such damage likely further reduces forest recovery in areas where seedling densities are already depleted by low seed arrival and poor seedling establishment and growth.

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DATA AVAILABILITY

Data will be made available via Dryad Digital Repository: https://datadryad.org/

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TABLE 1. Single-factor explanatory variables of overall ‘seedling’ damage, vertebrate damage, plant-debris damage and the damage by unknown agents based on negative binomial GLMs.

	χ^2	df	P	Form of relationship
Overall damage				
Canopy openness	5.6	1	**0.018**	Positive
Canopy openness + Canopy openness^2	4.1	1	**0.044**	Unimodal
Slope position	47.7	2	**< 0.001**	Lower > Mid > Hilltop
Dominant understorey plants	24.8	2	**< 0.001**	Ferns < Shrubs < Short herbs
Local basal area	9.5	1	**0.002**	Negative
Local basal area + Local basal area^2	0.6	1	0.434	U-shaped
Distance to nearest roads	9.9	1	**0.002**	Positive
Slope angle	5.6	1	**0.018**	Negative
Distance to nearest water source	5.2	1	**0.023**	Negative
Proportion of trees with climbers	3.9	1	**0.048**	Positive
Elevation	2.5	1	0.113	Negative
Distance from bracken clearing	2.1	1	0.151	Near < Far
Distance to nearest park boundary	1.6	1	0.207	Positive
Damage by vertebrates				
Canopy openness	0.9	1	0.342	Positive
Canopy openness + Canopy openness^2	0.8	1	0.367	Unimodal
Slope position	14.8	2	**< 0.001**	Mid > Lower > Hilltop
Dominant understorey plants	4.7	2	0.192	Ferns < Shrubs < Short herbs
Local basal area	1.7	1	0.194	Negative
Local basal area + Local basal area^2	0.2	1	0.636	Unimodal
Distance to nearest roads	4.5	1	**0.033**	Positive
Slope angle	2.6	1	0.105	Negative
Distance to nearest water source	6.6	1	**0.010**	Negative
Proportion of trees with climbers	0.3	1	0.556	Positive
Elevation	0.1	1	0.726	Negative
Distance from bracken clearing	2.1	1	0.151	Near < Far
Distance to nearest park boundary	4.4	1	**0.035**	Positive
Damage by plant debris				
Canopy openness	6.2	1	**0.013**	Positive
Canopy openness + Canopy openness^2	6.7	1	**0.001**	Unimodal
Slope position	55.5	2	**< 0.001**	Lower > Mid > Hilltop
Dominant understorey plants	55.3	2	**< 0.001**	Ferns < Shrubs < Short herbs
Local basal area	13.5	1	**< 0.001**	Negative
Local basal area + Local basal area^2	3.6	1	0.059	U-shaped
Distance to nearest roads	8.0	1	**0.005**	Positive
Slope angle	5.4	1	**0.020**	Negative
Distance to nearest water source	0.9	1	0.334	Negative
Proportion of trees with climbers	8.7	1	**0.003**	Positive
Elevation	8.0	1	**0.005**	Negative
Distance from bracken clearing	1.7	1	0.196	Near < Far
Distance to nearest park boundary	0.5	1	0.466	Negative

Damage by unknown agents				
Canopy openness	1.7	1	0.187	Positive
Canopy openness + Canopy openness^2	0.1	1	0.711	Positive
Slope position	3.6	2	0.163	Mid > Hilltop > Lower
Dominant understorey plants	3.1	2	0.373	Ferns > Shrubs > Short herbs
Local basal area	0.2	1	0.656	Negative
Local basal area + Local basal area^2	0.9	1	0.343	U-shaped
Distance to nearest roads	1.2	1	0.268	Negative
Slope angle	2.2	1	0.134	Positive
Distance to nearest water source	3.1	1	0.80	Negative
Proportion of trees with climbers	0.4	1	0.555	Negative
Elevation	215.3	1	0.331	Positive
Distance from bracken clearing	6.3	1	**0.012**	Near > Far
Distance to nearest park boundary	0.01	1	0.906	Negative

TABLE 2. Best predictors of overall damage, vertebrate damage and plant-debris damage based on final models after a stepwise backwards selection process. Initial models included the significant single factor variables and their two-way interactions.

	Estimate	Error	P
Overall damage			
Intercept	2.96	0.18	< **0.001**
Local basal area	-0.02	0.01	**0.013**
Local basal area^2	0.00	0.00	**0.034**
Distance from nearest water source	0.00	0.00	**0.008**
Distance from nearest road	0.00	0.00	**0.003**
Slope position (mid-slope)	0.04	0.10	0.666
Slope position (hilltop)	-0.35	0.12	**0.003**
Damage by vertebrates			
Intercept	2.11	0.16	< **0.001**
Distance from nearest water source	0.00	0.00	0.603
Distance from nearest road	0.00	0.00	0.604
Slope position (mid-slope)	0.10	0.26	0.689
Slope position (hilltop)	-0.21	0.22	0.339
Distance from nearest water source × Slope position (mid-slope)	-0.01	0.00	< **0.001**
Distance from nearest water source × Slope position (hilltop)	0.00	0.00	**0.040**
Distance from nearest road × Slope position (mid-slope)	0.00	0.00	**0.008**
Distance from nearest road × Slope position (hilltop)	0.00	0.00	0.124
Damage by plant debris			
Intercept	1.42	0.14	< **0.001**
Slope position (mid-slope)	-0.38	0.18	**0.037**
Slope position (hilltop)	-1.26	0.18	< **0.001**
Proportion of trees with climbers	0.01	0.00	**0.004**

TABLE 3. The number of vertebrate "events" over 30 days in the forest, edge and bracken (n = 8 sites)

Common name	Scientific name	Forest	Edge	Bracken
Yellow-backed duiker	*Cephalophus silvicultor* Afzelius	56	113	14
Black-fronted duiker	*Cephalophus nigrifrons* Gray	80	38	33
African Elephant	*Loxodonta africana* Blumenbach, 1797	0	0	1
Bushpig	*Potamochoerus larvatus* F. Cuvier	1	0	0
L'hoest's monkey	*Cercopithecus l'hoesti* P. Sclater	27	12	2
Chimpanzee	*Pan troglodytes* Blumenbach	0	3	0
Mountain gorilla	*Gorilla beringei beringei* Matschie	1	3	0
Side-striped jackal	*Canis adustus* Sundevall	1	0	0
Servaline genet	*Genetta servalina* Pucheran	1	3	1
African golden cat	*Profelis aurata* Temminck	1	4	2
Handsome francolin	*Francolinus nobilis* Reichenow	2	2	0
Rodents	NA	9	5	4
Total		179	183	57

TABLE 4. Proportion of artificial seedlings damaged per year (%) in this study and 15 tropical and temperate forest sites. The superscripts a and b denote open forest (canopy openness > 25%) and closed forest (canopy openness ≤ 25%), respectively.

Forest type	Location	Study duration	Census interval	*N*	Overall damage	Vertebrate damage	Plant debris damage	Unknown damage	Source
Moist tropical forest	La Selva, Costa Rica	1 yr	1 mo	500	82.4	21.0	19.2	42.2	Clark & Clark (1989)
Temperate deciduous forest	New Jersey, USA	10 mo	25-35 d	200	64.8	46.8	2.4	15.6	McCarthy & Facelli (1990)
Tropical wet forest	Simbu province, PNG	1 yr	26-49 d	418	31.8	7.0	13.8	11.0	Mack (1998)
Seasonal tropical forest	Manaus, Brazil	1 yr	4 wk	1100	41.5	4.9	27.5	9.1	Scariot (2000)
Moist montane tropical forest	(+Pigs) Hawaii Volcanoes National Park, USA	1 yr	5-6 wk	150	15.3	4.7	11.3	68.7	Drake & Pratt (2001)
	(–Pigs) Hawaii Volcanoes National Park, USA			150	20	0	20	0	
Tropical *terra firme* forest	Beni Biosphere Reserve, Bolivia	6 mo	1 mo	500	85	80	—	5	Roldán & Simonetti (2001)
Temperate evergreen forest	North Island, New Zealand	2 yr	4-6 wk	1200	5.1–18.8	0.5–6.5	1.8–16.3	—	Gillman *et al.* (2002)
Temperate evergreen forest	North Island, New Zealand	2 yr	1 mo	192	—	—	9.7	—	Gillman & Ogden (2005)
Seasonal tropical forest	Soberanía National Park, Panama	16 wk	2 wk	1260	133.3	—	13.0	120.3	Sánchez-Thorin *et al.*, (2006)
Seasonal tropical forest	Barro Colorado Island, Panama	1 yr	1-2 wk; 4 wk	200	47.5	15.5	9.5	22.5	Alvarez-Clare & Kitajima (2009)
Lower montane tropical forest	Atlantic Forest, São Paulo, Brazil	1 yr	3 mo	1200	31.8	1.1	11.2	19.5	Portela & Santos (2009)

Temperate evergreen coniferous forest	Wind River Experimental Forest, USA	1 yr	1 yr	1920	33.1	4.4	—	25.0	Larson (2013)
Moist tropical forest	Tambopata, Peru	1 yr	1 mo	278	91.4	77.0	14.4	0	Rosin *et al*. (2017)
Moist tropical forest	Ivindo, Gabon	1 yr	1 mo	297	79.2	59.3	4.7	15.2	Rosin *et al*. (2017)
Moist tropical forest	DVCA, Malaysian Borneo	1 yr	1 mo	143	99.3	66.4	21.7	11.2	Rosin *et al*. (2017)
Moist lower montane tropical forest	(All plots) Bwindi, Uganda	20 mo	1 mo	16960	61.3	47.0	22.5	4.0	This study
	(Open forest[a]) Bwindi, Uganda			5920	65.2	48.4	28.0	4.0	
	(Closed forest[b]) Bwindi, Uganda			11040	59.0	46.3	19.4	3.9	
	(Lower-slopes) Bwindi, Uganda			6400	69.8	52.3	33.3	2.4	
	(Mid-slopes) Bwindi, Uganda			3520	67.0	52.7	24.6	5.3	
	(Hilltops) Bwindi, Uganda			7040	47.7	38.4	10.2	4.7	

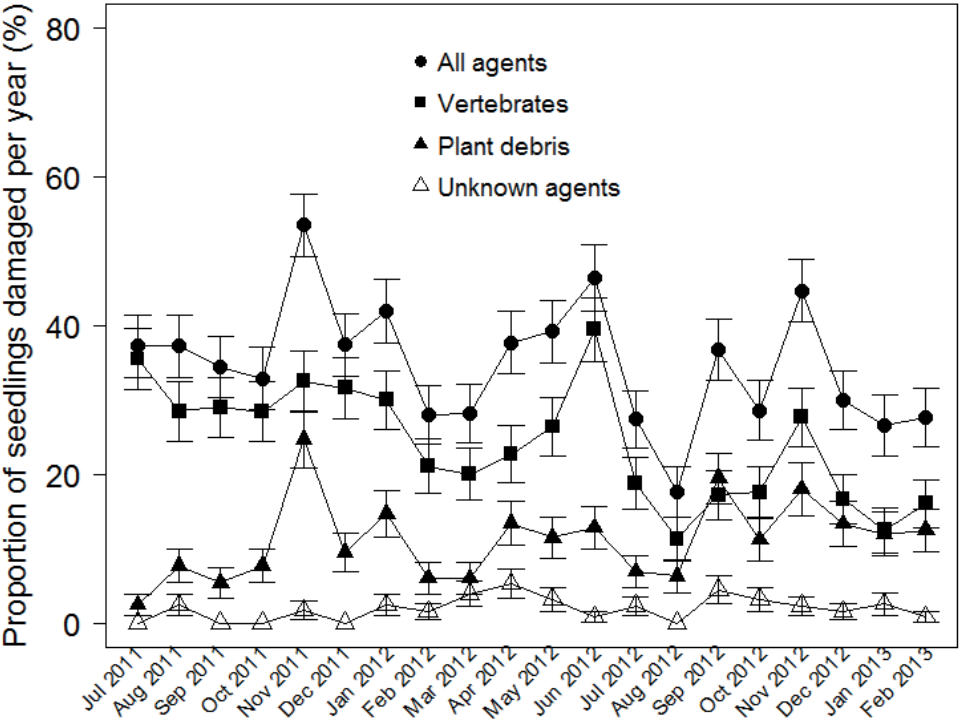


FIGURE 1. Damage to artificial seedlings per year plotted for each class of agents across the 20 monthly censuses.

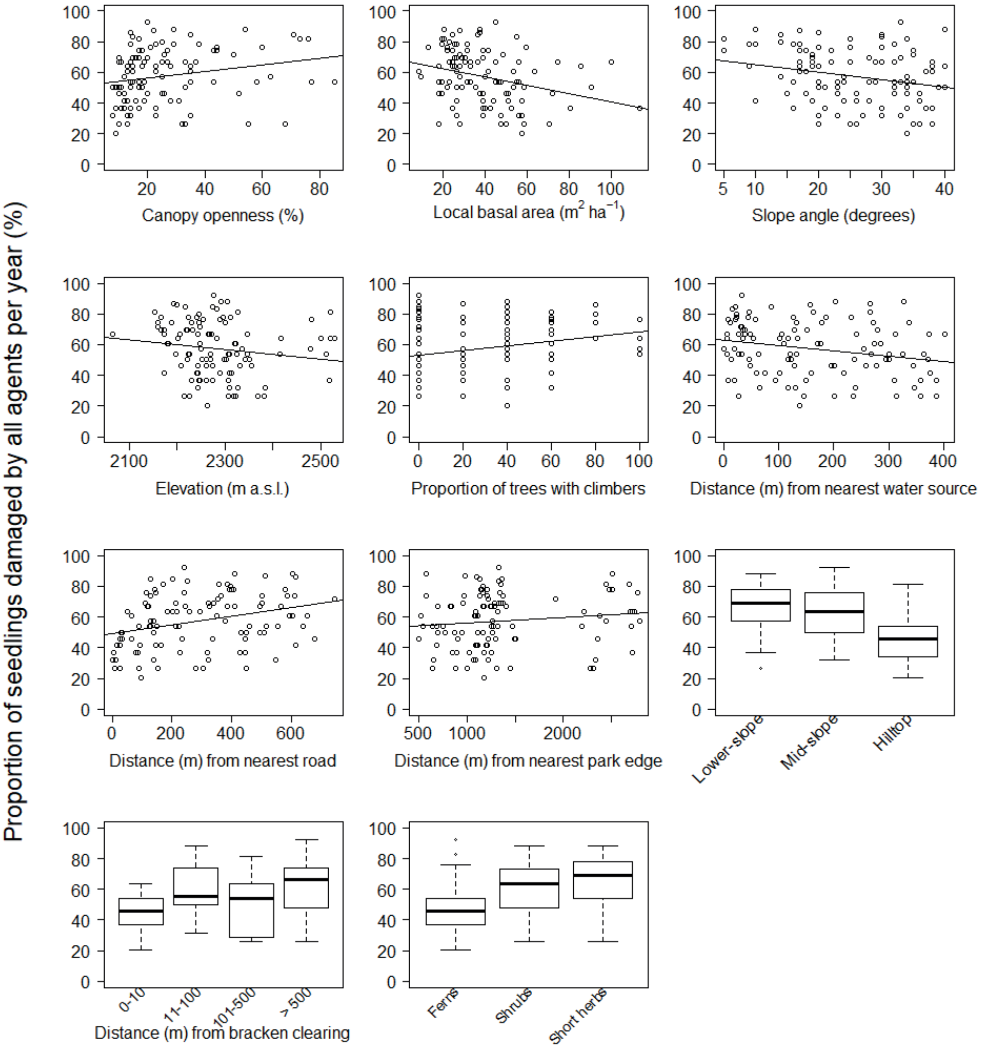


FIGURE 2. Proportion of artificial seedlings damaged by all agents per year versus each of the eleven explanatory variables. The data points represent plot values (n = 106) for all damage assessments over 20 months. Eight of these explanatory variables were significantly related with the frequency of damage by all agents (see Table 1).

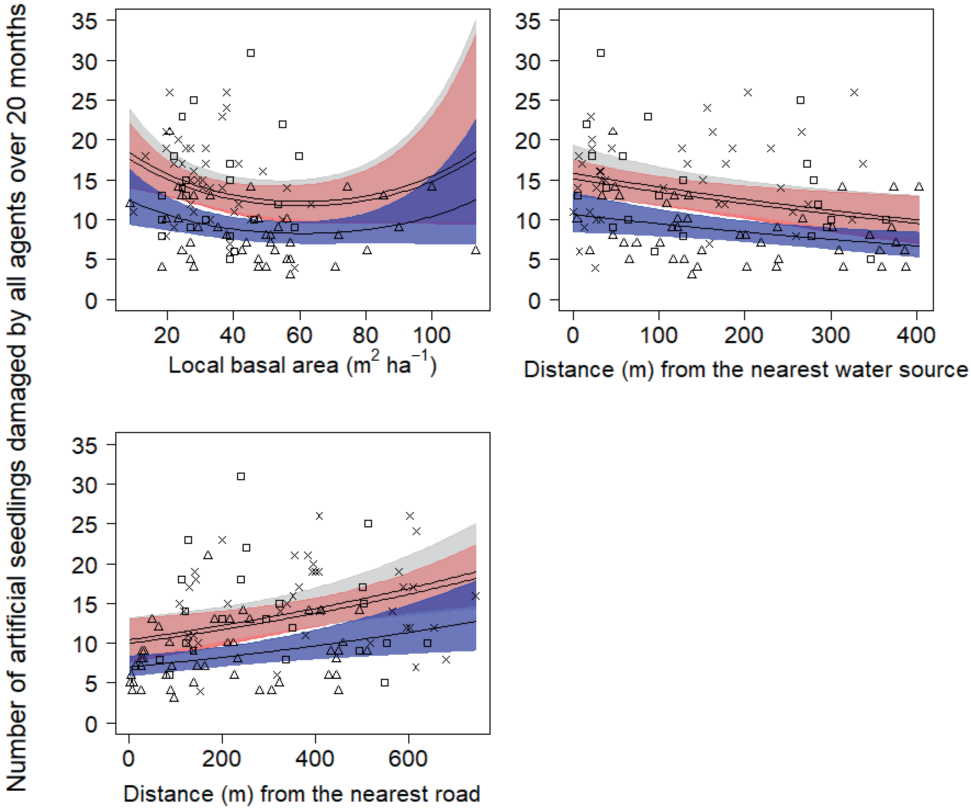


FIGURE 3. Observed number of artificial seedlings damaged by all agents versus basal area, distance from the nearest water source and distance from the nearest road for each slope position. Data points represent plot values for all damage assessments over 20 months (maximum potential damage = 160 artificial seedlings per plot). Lower-slopes are denoted by crosses (and red shading), mid-slopes by open boxes (and grey shading) and hilltops by open triangles (and blue shading). Prediction lines and 95% confidence intervals are based on coefficients of the best negative binomial GLM (see Table 1).

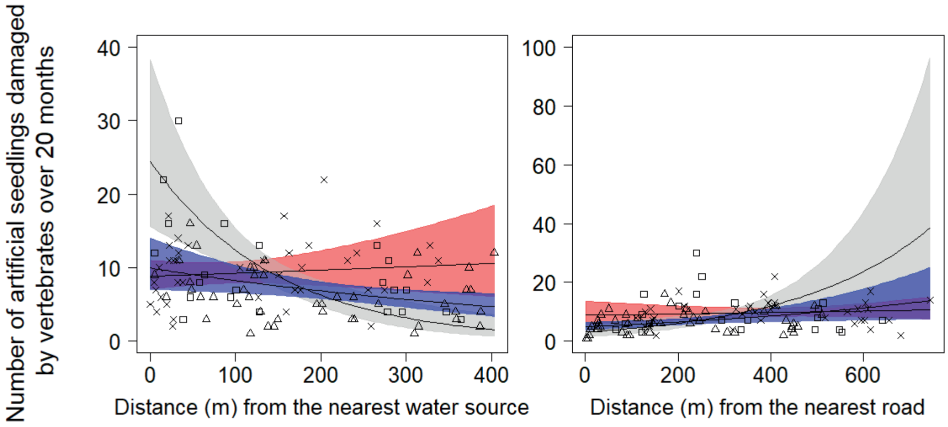


FIGURE 4. Observed number of artificial seedlings damaged by vertebrates versus distance from the nearest water source and distance from the nearest road for each slope position. Data points represent plot values for all damage assessments over 20 months (maximum potential damage = 160 artificial seedlings per plot). Lower-slopes are denoted by crosses (and red shading), mid-slopes by open boxes (and grey shading) and hilltops by open triangles (and blue shading). Prediction lines and 95% confidence intervals are based on coefficients of the best negative binomial GLM (see Table 1).

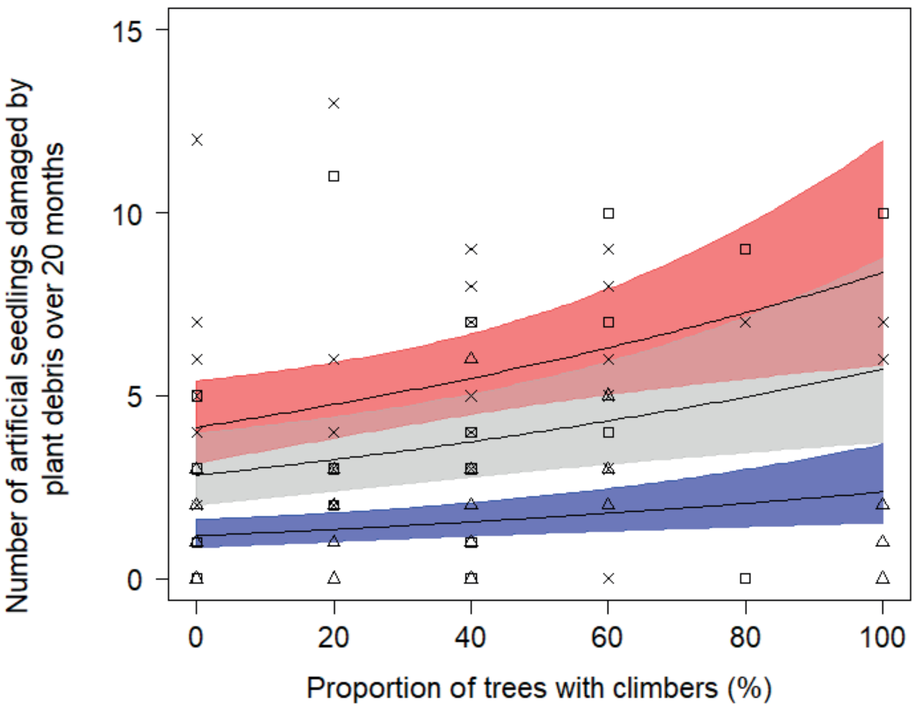


FIGURE 5. Observed number of artificial seedlings damaged by plant debris versus proportion of trees with climbers for each slope position, with prediction lines and 95% confidence intervals based on coefficients of the best negative binomial GLM (see Table 1). Data points represent plot values for all damage assessments over 20 months (maximum potential damage = 160 artificial seedlings per plot). Lower-slopes are denoted by crosses (and red shading), mid-slopes by open boxes (and grey shading) and hilltops by open triangles (and blue shading).

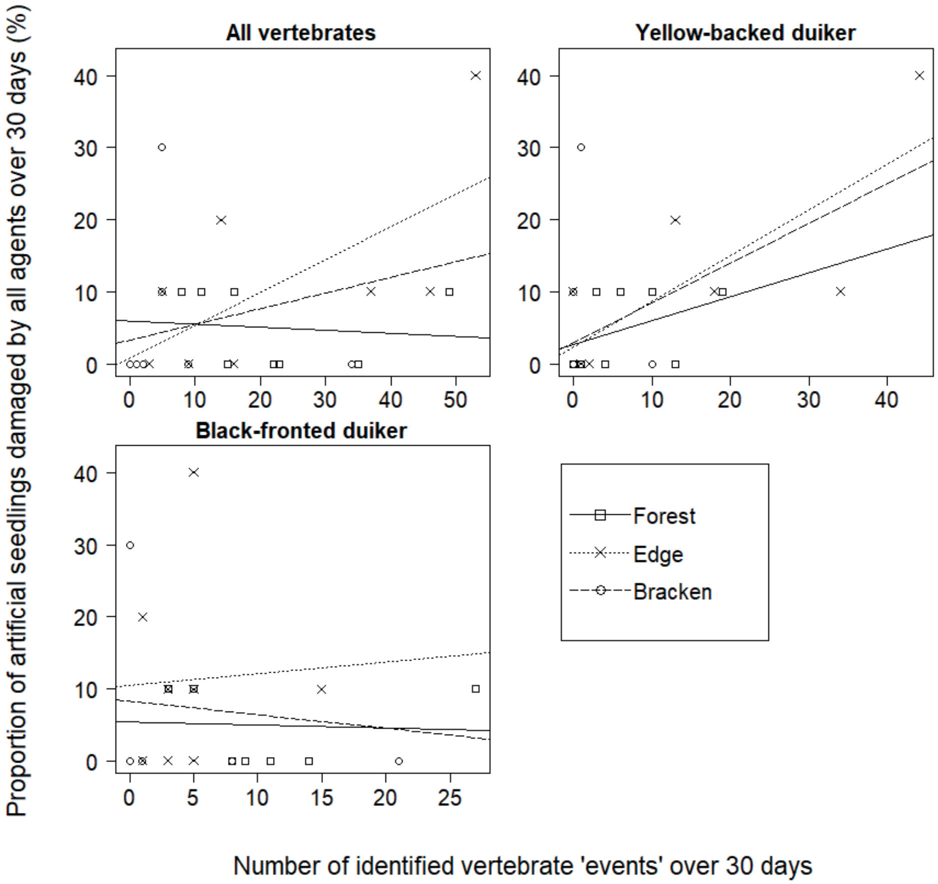


FIGURE 6. Proportion of artificial seedlings damaged by all agents plotted against number of identified vertebrate ‘events’ over a period of 30 days.

FIGURE S1. Pairwise correlation coefficients and p-values of explanatory variables recorded in each plot (n = 106) across eight study sites. The explanatory variables are EDGEDIST = distance from the nearest park edge, WATERDIST = distance from the nearest water source, ROADDIST = distance from the nearest road, COPENNESS = canopy openness, SLOPEANGLE = slope angle, BASALAREA = local basal area, PROPCLIMBERS = proportion of tree trees with climbers and ELEVATION = elevation.

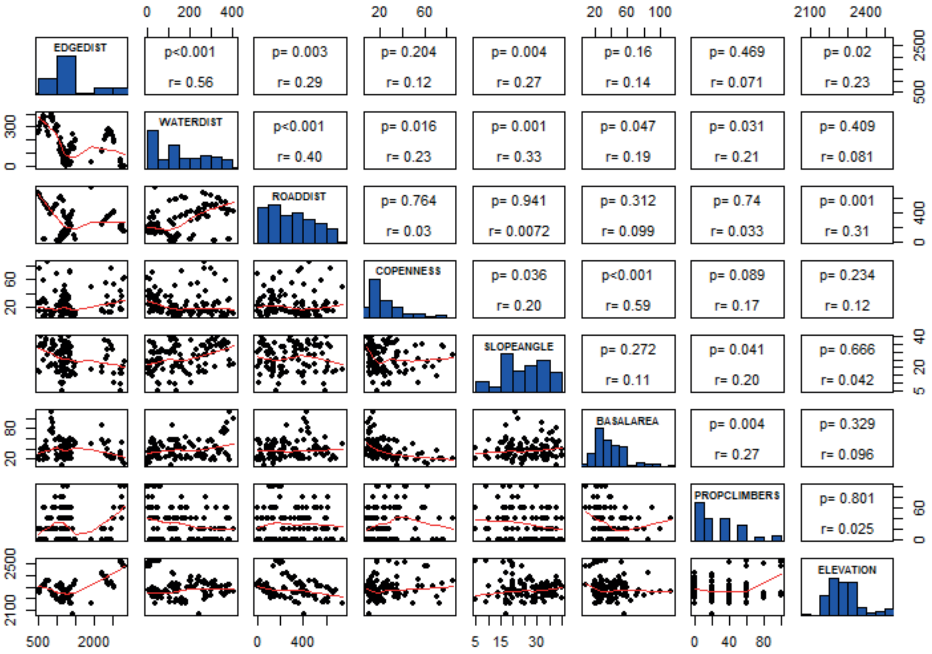
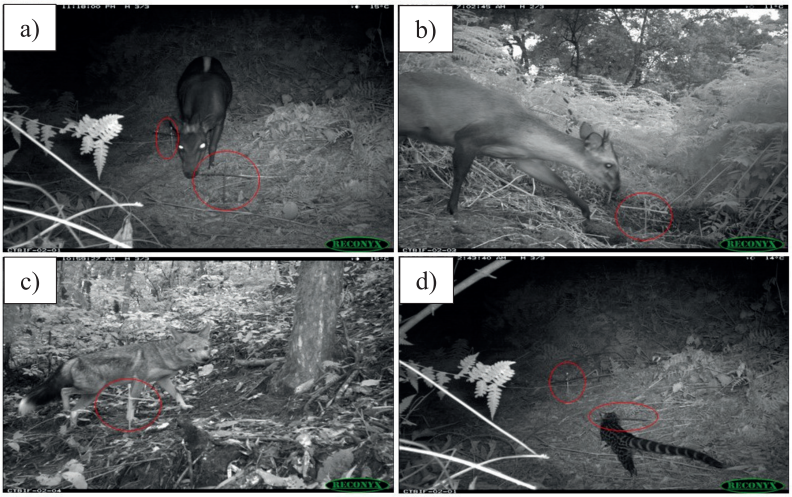


FIGURE S2. Camera trap images of vertebrates walking close to artificial seedlings (in red circles). The vertebrate species are a) Yellow-backed duiker *Cephalophus silvicultor* Afzelius, b) Black-fronted duiker *Cephalophus nigrifrons* Gray, c) Side-striped jackal *Canis adustus* Sundevall and d) Servaline genet *Genetta servalina* Pucheran.



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