Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Non-native fruit trees facilitate colonization of native forest on abandoned farmland

Aerin L. Jacob[1,4,2,3], Martin J. Lechowicz[1,4], Colin A. Chapman[4,5,6]

Ecological restoration of abandoned, formerly forested farmland can improve the delivery of ecosystem services and benefit biodiversity conservation. Restoration programs can involve removing isolated, non-native trees planted by farmers for fruit or wood. As such "legacy" trees can attract seed dispersers and create microclimates that help native seedlings to establish, removing them may actually slow forest recovery. Working on abandoned farmland in Kibale National Park, Uganda, we evaluated the effect of legacy trees on forest recovery by measuring the number, diversity, and biomass of native seedlings and saplings regenerating in plots centered on avocado (*Persea americana*), mango (*Mangifera indica*), and *Eucalyptus* legacy trees compared with adjacent plots without legacy trees. The assemblages of native, forest-dependent tree species in plots around avocado and mango trees were distinct from each other and from those around eucalyptus and all the near-legacy plots. In particular, avocado plots had higher stem density and species richness of forest-dependent species than near-avocado plots, particularly large-seeded, shade-tolerant, and animal-dispersed species—key targets of many restoration plans. Furthermore, many of the species found in high numbers were among those failing to establish in ongoing large-scale forest restoration in Kibale. Taken together, our results demonstrate that the legacy trees facilitate the dispersal and establishment of native tree species. Retaining the existing legacy trees for a number of years could usefully complement existing management strategies to restore more biodiverse native forest in degraded lands. However, careful monitoring is needed to ensure that the legacy trees do not themselves establish.

Key words: abandoned agriculture, invasive species, Kibale National Park, nucleation, recruitment foci, seed dispersal

Implications for Practice

- Seeking to efficiently establish native forests on degraded, formerly forested land, many tree-planting programs focus on fast-growing native species. Fearing invasion, non-native trees planted between deforestation and reforestation are often removed.
- Some native tree species with low survival in planting programs (e.g. shade-tolerant species planted in open areas) recruit well under isolated non-native trees.
- Considering the multiple costs and benefits of different restoration strategies, it may be that removing isolated, non-native, and non-invasive trees is counterproductive to the efficient recovery of native forest.
- Leveraging the restoration potential of isolated non-native trees, or mimicking it by planting native species with similar characteristics, may accelerate forest recovery and free scarce reforesting resources to focus on more challenging locations.

Introduction

Between 1980 and 2000, more than half of new tropical farmland came from intact forests; another quarter came from disturbed forests (Gibbs et al. 2010). Socioeconomic, political, and/or ecological factors can cause people to abandon cultivated lands (Rey Benayas et al. 2007). Restoring forest on abandoned, formerly forested farmland has been advocated as a strategy to conserve biodiversity and enhance ecosystem services (Lamb et al. 2005; Chazdon 2008). Given the tradeoffs between reforestation cost, time, and goals (e.g. timber, carbon storage, and biodiversity), research is needed to help maximize efficiency and identify complementary restoration strategies (Lamb et al. 2005).

Accelerating natural forest recovery requires removing factors that inhibit dispersal and/or establishment of tree species, such as harsh microclimates, high seed predation, and competition with aggressive shrubs or grasses (Lamb et al. 2005). A promising, practical strategy is to protect existing isolated

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Author contributions: ALJ, CAC conceived and designed the research and collected the data; ALJ, MJL analyzed the data; ALJ, MJL, CAC wrote the manuscript.

[1] Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada
[2] Present address: School of Environmental Studies, University of Victoria, Victoria, BC V8W 2Y2, Canada
[3] Address correspondence to A. L. Jacob, email aljacob@uvic.ca
[4] Québec Centre for Biodiversity Science, McGill University, Montreal, QC H3A 1B1, Canada
[5] Department of Anthropology and McGill School of Environment, McGill University, Montreal, QC H3A 2T7, Canada
[6] Wildlife Conservation Society, Bronx, NY 10460, U.S.A.

doi: 10.1111/rec.12414
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12414/suppinfo

landscape features that attract seed dispersers and facilitate tree recruitment. Such features include native trees left standing when the forest was cleared ("remnant" trees) or non-native trees planted by farmers for fruit or wood ("legacy" trees). These trees can provide attractive perches, shade, and/or food for seed-dispersing animals, leading to elevated levels of seed rain (Galindo-González et al. 2000). Although the arrival of seeds does not necessarily lead to the germination and establishment of trees, the microclimate under isolated trees is often more favorable than the surrounding matrix; thus, they can become foci or nuclei of forest regeneration (Corbin & Holl 2012). Most nucleation studies have been done in the Neotropics; the comparatively few African studies tend to focus on remnant trees in abandoned farmland (Carrière et al. 2002; Eshiamwata et al. 2006), planted non-native trees in active farmland (Berens et al. 2008), or planted native trees in logged areas (Piiroinen et al. 2015). Furthermore, they often do not evaluate nucleation compared with conventional afforestation methods like planting trees.

Efficient forest restoration is critically important in Central Africa's Albertine Rift, where some of the continent's highest species richness and endemism coincide with very dense, fast-growing, and poor rural human populations whose livelihoods depend on forests (Cordeiro et al. 2007; Plumptre et al. 2007). A recent global meta-analysis of tropical protected area downgrading, downsizing, or degazettement found the highest impact in Uganda, where 55% of protected areas had been affected, often from local land pressures such as subsistence farming (Mascia et al. 2014).

Uganda's Kibale National Park contains large areas recovering from subsistence farming, in addition to primary and secondary tropical forest, and grassland (Jacob et al. 2014). Management policy directs "restor(ing) natural forest cover" on abandoned farmland inside the park, mainly by preventing fire, planting native trees, and removing non-native species, including legacy trees ("all exotic species left from the encroachment"; UWA 2003). In some areas, fire prevention alone is enough to facilitate natural forest regeneration in areas dominated by grass (Lwanga 2003); in others, active restoration (e.g. cutting grass and planting trees) is deemed necessary as trees and shrubs are slow to establish (UWA-Face Project 2009). However, local people reported native trees regenerating under legacy trees, and earlier studies have demonstrated the roles of isolated native trees acting as nuclei of tree recruitment (Duncan & Chapman 1999; Majid et al. 2011; Piiroinen et al. 2015).

We investigated whether the legacy trees could be a potential complement to ongoing afforestation efforts in Kibale and elsewhere. We evaluated how the presence and species of legacy trees affected the regeneration of forest-dependent, forest-nondependent, and open habitat tree species on abandoned farmland inside Kibale. Understanding how legacy trees affect the composition and recruitment of native trees can inform the effectiveness of nucleation as a strategy to accelerate forest recovery and create more diversified, efficient restoration.

Methods

Study Area

Kibale National Park (795 km^2) is a mid-altitude moist tropical rainforest in western Uganda (0°13′–0°41′N, 30°19′–30°32′E). The park lies on a plateau with elevation ranging from 1,590 m in the northwest to 900 m in the southwest with drainage south into Lake George through the Mpanga and Dura Rivers. This gradient in elevation corresponds to a north-to-south gradient from low-to-high temperature and high-to-low rainfall, and is reflected in the change from evergreen and semi-deciduous forest in the north and center, to grasslands and woodlands in the southwest (Struhsaker 1997). In 1926, the British Protectorate Government designated the southwestern part of Kibale as a Game Corridor managed for controlled hunting; in 1993 it was merged with the adjacent Kibale Forest Reserve and upgraded to national park status.

Agricultural and population pressures on Kibale are among the highest of all Ugandan protected areas (Hartley et al. 2010). Starting during civil unrest in the 1970s, thousands of people encroached into Kibale, subsistence farming and/or degrading over 145 km^2 of grassland and forest until they were evicted in 1992 (Jacob 2014). Over the last 30 years, planting trees and preventing fire has decreased grassland and increased native forest cover inside the park: today, land cover is 74% unlogged and regenerating forest, 15% bare ground and short grasses, 6% tall grasses, 4% wetland, and 1% shrubs (Jacob et al. 2014).

We worked in a 5 km^2 area of abandoned farmland on grassy hilltops and hillsides in west-central Kibale (Fig. 1), adjacent to the park boundary and near degraded riverine forest and afforested areas. Average elevation is 1,450 m and slope angles are generally less than six degrees. Soils tend to be well-drained, black or reddish brown clay or loamy clay (UWA-Face Project 2009). Extensive cultivation of this area was reported during the period of encroachment (i.e. near Kyemboga village by the early 1980s; Van Orsdol 1983): crops included maize, matooke (cooking bananas), sorghum, and millet, and goats were kept at 93% of farms in the grassland area. Today, dominant grasses include *Pennisetum purpureum*, *Imperata cylindrica*, and *Cymbopogon afronardus*. The most common grassland native trees are *Acacia sieberana* and *Erythrina abyssinica*. The legacy trees avocado (*Persea americana*) and mango (*Mangifera indica*) planted for fruit, and *Eucalyptus* species planted for fuelwood and timber, are scattered throughout the study area (Fig. 1).

Data Collection

From July 2010 to December 2011, and in April 2013, we thoroughly searched the study area for mature avocado ($n = 11$), mango ($n = 9$), and eucalyptus ($n = 15$) legacy trees at least 30 m from the forest edge. We measured the diameters at breast and ground height (DBH and DGH, with DBH measured at 1.2 m above the ground). We excluded legacy trees <15 cm DGH based on local reports that this was the minimum size capable of producing fruit (A. Jacob unpublished data). Seedling recruitment was determined in a 10 m radius circular plot around each individual legacy tree ("legacy plots," each 314 m^2). Although

Figure 1. Grassland and recolonizing forest on abandoned farmland in Kibale National Park, Uganda, with eucalyptus legacy trees on the right and ridgeline. Photograph by A. L. Jacob.

most plots contained a single legacy tree, we included plots with multiple legacy trees of the same species and centered the plot on the largest legacy tree; we excluded plots with more than one species of legacy tree ≥15 cm DGH to separately evaluate the effect of the three species of legacy trees. All seedlings, saplings, and mature trees ("regenerating stems") within each legacy plot were identified to species level where possible, and their height, DGH, and DBH if ≥1.2 m tall measured. We compared legacy plots to equal-sized paired "near-legacy plots" located at a random compass bearing and distance (20–50 m) from each legacy tree. We excluded near-legacy plots if they contained, or if the center of the plot was within 20 m of, an avocado, mango, or eucalyptus legacy tree ≥15 cm DGH.

Data Analysis

Focusing on sources from Kibale and Uganda, we searched the literature and unpublished records to determine ecological attributes (dispersal mechanism, guild, and seed weight) for all native tree species recorded (Table S1, Supporting Information). Following Lwanga (1996), we categorized each species in one of three ecological subtypes to indicate its broad habitat requirements: open habitat (occurring in woodland, grassland, rocky places, bush/thickets, dry scrub, swamp, and/or moorland), forest-dependent (occurring in forest interior, forest edge, dry forest, and/or riverine/lakeshore forest), or forest non-dependent (occurring in at least one of the open habitats and at least one of the forested habitats). To better evaluate nuances relevant to forest regeneration, we conducted analyses on forest-dependent species separate from forest-nondependent and open habitat species. All data were analyzed using the software R (R Core Team 2015).

Regeneration Assemblages. We used the multivariate Canonical Discriminant Analysis (CDA) in the R package candisc (Friendly & Fox 2009) to compare the assemblages of tree species regenerating around avocado, mango, and eucalyptus legacy trees and in their respective near-legacy plots. Nine tree species represented in the data (Table S1) by only one or two stems were omitted from the two CDA analyses, which evaluated differences in the stems frequencies of (1) 33 forest-dependent species and (2) 21 forest non-dependent and one open habitat species characterizing the six types of legacy or near-legacy plots. The CDA analyses identify the tree assemblages characterizing the six types of legacy or near-legacy plots, minimizing the differences within each pre-defined type of plot while maximizing differences among them. Represented graphically, the outcome of the CDA illustrates both the differences among the six assemblages and the influence of individual tree species in each plot type. Using the canonical graphs as a template, we also coded animal- and non-animal- dispersed tree species, and used a *t*-test to compare the seed weights (average weight of 1,000 seeds; Table S1) of the tree species characterizing different types of study plots. We compared these assemblages to information on the native tree species used in the UWA-Face tree planting programs in

Kibale and Mt. Elgon National Parks (Table S1), Uganda's largest forest restoration project.

Restoration Metrics. We assessed three univariate metrics (response variables) commonly used to evaluate forest restoration projects: density, species richness, and biomass of regenerating stems in each of the six types of plots (Appendix S1). We estimated fresh aboveground biomass of each regenerating stem using an Uganda-specific equation for individual trees in tropical moist deciduous forest: $Y = \exp(-0.89 + 2.053 \times \log10(\mathrm{DBH}))$ (equation 562 in Henry et al. 2011), and summed the total for each plot (hereafter "biomass"). We used paired *t*-tests to evaluate if presence and species of legacy tree affected density (square-root transformed), species richness, and biomass of regenerating stems of forest-dependent, and forest-dependent and open habitat tree species, in each plot. We used the effect size Cohen's d to assess the standardized difference between the means for each variable and plot type; effect size emphasizes the size of the difference rather than simply statistical significance (Sullivan & Feinn 2012). As a guideline, $d = 0.2$, 0.5, and 0.8 are considered small, medium, and large effects; if $d > 1$ or 2, the difference is larger than one or two standard deviations.

Results

We counted a total of 8,250 regenerating stems of 78 tree species in the 35 pairs of study plots ($n = 11$ avocado, 9 mango, and 15 eucalyptus legacy trees; Table S1). Median distance from closed-canopy native forest to the center of a plot was 761 m (range 34–1,348 m). Six non-native species (775 stems, or 9.4% of total stems, including of the three legacy species) were analyzed separately. The 72 native species (7,475 stems) we recorded represent one-third (34%) of the total number of tree species recorded in Kibale (Howard 1991); we categorized 48 species as forest dependent (2,575 stems), 23 species as forest non-dependent (4,842 stems), and one species as restricted to open habitat (58 stems; Table S1). The three most common species were found in every plot type and made up more than half of the total regenerating stems: *Bridelia micrantha* (29%), *Maesa lanceolata* (15%), and *Shirakiopsis elliptica* (11%). Fifteen species occurred only in fruit plots (nine in avocado, three in mango, and three shared; Table S1); many of these individuals were well-established (i.e. up to 7 cm DBH). Two species occurred only in eucalyptus plots (Table S1).

Regeneration Assemblages

There were distinct assemblages of forest-dependent tree species regenerating in avocado and mango legacy plots (Fig. 2). The species most characteristic of regeneration under avocado were *Celtis gomphophylla*, *C. africana*, *Cola gigantea*, *Chrysophyllum* spp., *Dracaena* spp., and *Oxyceros longiflorus*, and under mango were *Macaranga schweinfurthii*, *Pterygota mildbraedii*, and *Funtumia africana*. Many of the species characterizing avocado legacy plots were shade-tolerant species with heavy, animal-dispersed seeds; only one was non-animal dispersed (*Markhamia lutea*; Fig. 2; Table S1). There was no difference between the average seed weights of the regenerating tree species characterizing avocado and mango legacy trees ($t_{16} = 1.01$, $p = 0.33$), but fewer in the mango assemblage were shade tolerant or animal dispersed. The seed weights of species characterizing avocado and mango legacy plots were heavier than those characterizing the other four plot types ($t_{11} = 2.41$, $p = 0.03$; $t_8 = 2.54$, $p = 0.03$; Table S1).

There were few differences in the assemblages characterizing regeneration by forest-nondependent and open habitat species in the legacy and near-legacy plots (Fig. 3). The most characteristic species establishing in avocado and mango legacy plots were *Ficus asperifolia* (separating avocado from eucalyptus, near-avocado, and near-eucalyptus, but not mango or near-mango plots) and *Dovyalis* spp. (separating avocado from eucalyptus and the three types of near-legacy plots, but not mango).

Legacy Tree Effects on Regeneration of Native and Non-native Tree Species

The strongest facilitative effects of legacy trees on regeneration were in avocado plots, expressed by an increased number of stems and species of forest-dependent tree species (Table 1; Appendix S1; Fig. S1A & 1D). Mango legacy trees had a similar, positive effect on regeneration (cf stem density and species richness) of forest-dependent tree species, though given the smaller sample size for mango these differences only approached significance (Table 1; Appendix S1; Fig. S1C & 1D). Eucalyptus legacy trees had a facilitative effect on regeneration of forest-nondependent and open-habitat tree species that was expressed in increased stem density (Table 1; Appendix S1; Fig. S2B).

We also found 775 regenerating stems of non-native species in the legacy plots; the majority were seedlings too small to measure for DBH. Most regenerating stems of legacy species were found in conspecific legacy plots (likely the parent tree). Of the 688 avocado stems recorded, 83% were found in avocado, 7% in mango, and 1% in eucalyptus plots, and 4% in near-avocado, 4% in near-mango, and 1% in near-eucalyptus plots. Nearly three-quarters of these were seedlings too small for us to measure DBH (i.e. <1.2 m tall); of the established stems, 11 were ≥15 cm DBH (i.e. planted legacy trees, but smaller than the focal avocado legacy tree in that plot; mean DBH = 3.2 ± 2.5 cm). Of the 36 mango stems recorded, 78% were found in mango, 19% in avocado, and 3% in near-avocado plots. Half were seedlings too small to measure; seven stems were ≥15 cm DBH (mean DBH = 2.9 ± 2.7 cm). All of the 40 eucalyptus stems were found in eucalyptus plots (likely planted as a woodlot) and none were seedlings (mean DBH = 15.2 ± 14.0 cm). In addition to the three legacy species, we recorded seven guava (*Psidium guajava*) stems (six seedlings too small to measure for DBH, one 1.0 cm DBH stem), three *Senna spectabilis* stems (two seedlings, one 9.4 cm DBH planted stem), and one lemon (*Citrus limon*) stem (a seedling).

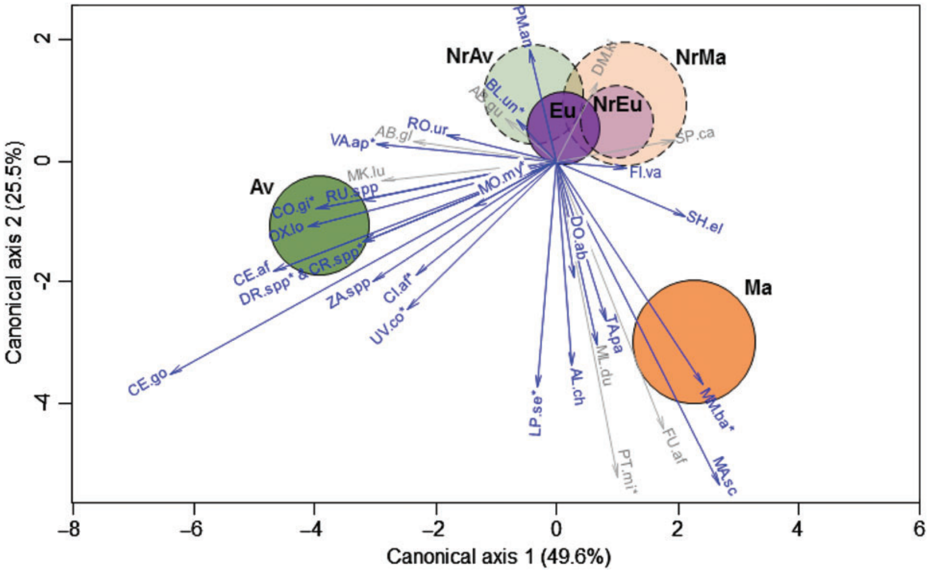

Figure 2. Canonical discriminant analysis based on the frequency of regenerating stems for 33 forest-dependent tree species with 99% confidence ellipses around the replicates for the six plot types: Av = avocado plot (green, solid line), NrAv = near-avocado plot (light green, dashed line), Eu = eucalyptus plot (purple, solid line), NrEu = near-eucalyptus plot (light purple, dashed line), Ma = mango plot (orange, solid line), NrMa = near-mango plot (light orange, dashed line). The closer are any two plots, the more similar are the frequencies of trees regenerating in those plots. The direction of the vector associated with a tree species illustrates its influence in differentiating the plot types; longer vectors indicate greater influence. The more acute the angle between two vectors, the more similar is their influence; conversely, vectors pointing in opposite directions indicate tree species with contrary influence. Very small vectors for *Croton* spp. and *Chaetachme aristata* were removed from the biplot for clarity. Codes for regenerating tree species are given in Table S1. Vectors and species codes in blue and gray indicate animal- and wind-dispersed species, respectively; species codes with an asterisk indicate one of the top 20 heaviest-seeded species.

Discussion

By demonstrating that legacy trees can facilitate native forest recovery, particularly late successional and heavy-seeded tree species that failed to establish in the Kibale replanting program, our study provides compelling reason to reassess the relative restoration costs and benefits of removing legacy trees at early stages of forest restoration. Many protected forests across East and Central Africa have a similar encroachment and reforestation challenges, including Mt. Elgon (UWA-Face Project 2007) and Mgahinga Gorilla National Parks, Uganda (Lejju et al. 2001); Mau Forest Reserve, Kenya (Mullah et al. 2012); southern Mt. Kilimanjaro, Tanzania (William 2003); and Nyungwe and Gishwati-Mukura National Parks, Rwanda (Ordway 2015), among others (Mascia et al. 2014). Developing cost-effective and efficient ways to restore degraded forest inside protected areas, and creating corridors to link small, isolated forest patches, is closely tied to conserving tropical forest biodiversity. Furthermore, many of these forests are surrounded by high-density and fast-growing rural human populations. As people depend directly or indirectly on forest ecosystem services (e.g. water, timber, and non-timber forest products), restoration also is important for human livelihoods and well-being (Chazdon 2008).

Complementarity With Tree Planting Program

The UWA-Face restoration program is the largest tree planting effort in Uganda, aiming to restore native forest cover (i.e. "climax" forest) across 100 km^2 of abandoned farmland in Kibale (34.2 km^2 planted as of 2008; UWA-Face Project 2009) and 250 km^2 in Mt Elgon (81.2 km^2 planted as of 2007; UWA-Face Project 2007). Three approaches are, or were previously, used to increase forest cover, biomass, woody species richness and/or timber supply in Kibale: (1) preventing fire by clearing large swaths of vegetation in grasslands to create fire-breaks, and planting fast-growing (2) native and (3) non-native tree species (*Pinus* and *Cupressus* spp. for timber; Jacob 2014). When Kibale was upgraded to national park status in 1993, management specified planting only native tree species and removing non-native trees, including "all exotic species left from the encroachment" (i.e. the legacy trees, UWA 2003).

Since 1994, 30 species of native trees have been planted in Kibale and 14 species in Mt. Elgon restoration areas; 30 of those species were also recorded during this study. Because many planted species had high mortality, current tree planting in Kibale focuses on six species that recruited well (Omeja et al. 2011; survival data unavailable for Mt. Elgon). We found eight forest-dependent species that failed to grow in the tree planting program characterizing the legacy plots: four in avocado plots (the shade-bearing, animal-dispersed species *Chrysophyllum* spp., *Monodora myrstica*, and *Uvariopsis congensis*, and the pioneer, wind-dispersed species *Markhamia lutea*), four in mango plots (the shade-bearing, animal-dispersed species *Diospyros abyssinica*, *Mimusops bagshawei*, and *Lepisanthes senegalensis*, and the non-pioneer

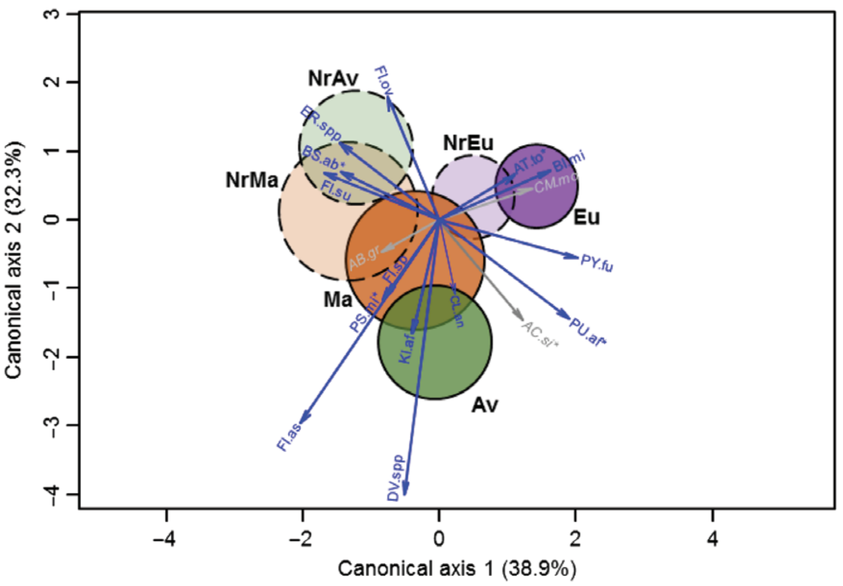

Figure 3. Canonical discriminants analysis based on the frequency of regenerating stems of 21 forest-nondependent and one open habitat tree species with 99% confidence intervals around the replicates of the six plot types: Av = avocado plot (green, solid line), NrAv = near-avocado plot (light green, dashed line), Eu = eucalyptus plot (purple, solid line), NrEu = near-eucalyptus plot (light purple, dashed line), Ma = mango plot (orange, solid line), NrMa = near-mango plot (light orange, dashed line). The closer are any two plots, the more similar are the frequencies of trees regenerating in those plots. The direction of the vector associated with a tree species illustrates its influence in differentiating the plot types; longer vectors indicate greater influence. The more acute the angle between two vectors, the more similar is their influence; conversely, vectors pointing in opposite directions indicate tree species with contrary influence. Codes for regenerating tree species are given in Table S1. Vectors and species codes in blue and gray indicate animal- and wind-dispersed species, respectively; species codes with an asterisk indicate one of the top 20 heaviest-seeded species.

Table 1. Mean forest structure and diversity measures (and standard deviations) of native, forest-dependent (FF), or forest-nondependent (Fn) and open habitat (O) tree species regenerating overall and in the six types of study plots.

	Stem Density (stems/ha)		*Number of Species (per plot)*		*Biomass (kg/ha)*	
	FF	*Fn + O*	*FF*	*Fn + O*	*FF*	*Fn + O*
Total	1,172 (935)	2,229 (2,195)	6.94 (3.89)	5.5 (2.23)	423 (513)	845 (755)
Avocado	1,633 (1,132)	2,389 (1,461)	10.82 (3.37)	7.45 (1.29)	545 (404)	1,099 (711)
Near-avocado	935 (445)	1,818 (1,247)	7.36 (3.44)	6.27 (2.2)	593 (644)	948 (591)
Eucalyptus	1,172 (760)	3,040 (3,410)	6.27 (2.55)	4.93 (1.87)	215 (270)	787 (750)
Near-eucalyptus	800 (846)	1,879 (2,476)	5.33 (4.15)	4.40 (2.23)	367 (645)	715 (719)
Mango	1,589 (1,320)	2,243 (1,483)	7.22 (4.74)	5.33 (3.00)	477 (391)	1,031 (1,106)
Near-mango	1,097 (927)	1,755 (1,295)	5.22 (2.77)	5.11 (1.36)	453 (6,250)	533 (666)

light-demander wind-dispersed *Funtumia africana*), as well as 14 other forest-dependent species not used in the tree planting program. Researchers and managers have also recorded the number of native tree species found naturally regenerating in the restoration areas: in our study, we found 34 of the 36 species naturally regenerating in Kibale, and 24 of the 43 naturally regenerating in Mt Elgon. Many of these are forest dependent, shade-bearing species growing in highest frequency in our avocado or mango legacy plots.

Particularly when viewed in concert with previous Kibale research on the roles of isolated native trees acting as nuclei of tree recruitment (Duncan & Chapman 1999; Majid et al. 2011; Piiroinen et al. 2015), there is growing support for other approaches that complement the current restoration focus of planting a small number of native tree species and preventing fire. Tree species biodiversity and biomass are also increasing in unplanted areas: woody biomass was twice as high in grassland protected from fire for 32 years (cost is approximately US\$500/km^2/yr) than in abandoned farmland planted with native trees 10–15 years prior (approximately US\$120,000/km^2/yr; Omeja et al. 2011; Omeja et al. 2012). As the legacy trees recruited diverse tree assemblages, including many failed planted species, these two approaches appear complementary.

Role of Animal Dispersers

Fruit legacy trees, particularly avocado, helped to recruit heavy-seeded and/or shade-tolerant tree species dispersed by animals. These types of species are frequently absent from secondary forests and are of particular interest in restoration programs (Lamb et al. 2005). The high fat content of avocado fruits make them attractive to frugivores (Gautier-Hion et al. 1985). However, forest-dwelling animals differ in the distance they will venture away from contiguous forest. In Kibale, elephants (*Loxodonta africana*) travel unimpeded throughout the area both day and night; large, fairly terrestrial primates like chimpanzees (*Pan troglodytes*) and baboons (*Papio anubis*) range widely during the day, but return to the forest at night to sleep. Dung and tracks from these three species are frequently seen in the study area (A. Jacob, personal observation). Furthermore, we found regenerating stems of heavy-seeded tree species dispersed by large mammals. For instance, *Balanites wilsoniana* and *Cola gigantea*, both very heavy-seeded, late successional species wholly dependent on large mammals for dispersal, were found in mango and avocado plots, respectively. In addition to attracting large mammal seed dispersers (e.g. elephants and chimpanzees), the dense shade under avocado and mango trees may facilitate the growth of such species.

Smaller but highly mobile frugivores likely play important roles in dispersing forest seeds to the legacy trees. For instance, black-and-white-casqued hornbills (*Bycanistes subcylindricus*), which are frequently observed in the study area, are extremely effective seed dispersal agents (Kalina 1988). In Tanzania's Eastern Usambara Mountains, the silvery-cheeked hornbill (*B. brevis*) dispersed 26 times more seeds than small frugivorous monkeys (Cordeiro et al. 2004). Local fruit bats (i.e. *Hypsignathus monstrosus* and *Epomops franqueti*; Struhsaker 1997) are attracted to tall, isolated trees in disturbed areas of Kibale but tend to disperse small seeds (Duncan & Chapman 1999). The seeds of many tree species dispersed by hornbills and bats were found in legacy plots; we assume they visit the legacy trees to feed and/or roost.

Possible Negative Effects of Legacy Trees

As eliminating established populations of non-native species can be very difficult, it is understandable that many management plans require removing non-native species at the onset of restoration activities (SER 2004). Although legacy trees can facilitate recruitment, and possibly survival and growth, of native trees, managers may be concerned about allelopathic effects associated with some non-native trees (including in Kibale, e.g. non-native conifer plantation; Struhsaker et al. 1989) and/or the threat of invasion. We did not find any eucalyptus seedlings and very few mango seedlings; as mango is shade-intolerant (Thompson et al. 2007), seedlings might not survive well in the heavy shade of the parent tree. Although avocado seedlings were numerous under conspecifics, the seeds are not viable for long and lack of light under the dense canopy can hinder seedling growth and reproduction (Itow 2003). It is unclear if removing mature avocado and mango legacy trees would unintentionally increase conspecific seedling growth and survival, or if subsequent growth of aggressive grasses (e.g. *Pennisetum purpureum*) would out-compete both legacy and native seedlings. Local restoration experts report that avocado seedlings are not often seen outside the legacy tree area and are thought to pose little threat to native forest regeneration (W. Chemutai, UWA-Face Project, and P. Omeja, Makerere University Biological Field Station, 2014, personal communication).

Management Summary

We caution against removing legacy trees at the initial stages of a restoration program without evaluating their potential to complement existing restoration efforts. The long-term growth and survival of the regenerating stems could be repeatedly monitored with and without removing the legacy trees (e.g. as part of existing semi-annual monitoring; UWA-Face Project 2007, 2009). Logistics would likely not be prohibitive: in Kibale, 96% of non-native regenerating stems were found less than 10 m from a legacy tree (i.e. within the legacy plot). If legacy trees are to be retained for a period of time—for instance until the canopy of the regenerating trees begins to close—these areas could be prioritized in ongoing fire prevention and/or native tree corridors could be planted to connect legacy tree nuclei to each other, existing forest patches in the matrix, and/or contiguous closed-canopy forest. Weighing the ecological costs and benefits of immediate or delayed action versus inaction would inform management strategies to better conserve biodiversity (e.g. rare, large-seeded, and/or late successional tree species; trees that provide food for wildlife) and provide ecosystem services (e.g. storing carbon, preventing erosion, and locally used plants).

Even if managers decide to remove some or all of the legacy trees, our results suggest that nucleation could be added as a forest restoration strategy. Natural recruitment foci could include logs (Slocum 2000), rocks (Carlucci et al. 2011), termite mounds (Støen et al. 2013), and patches of shrubs (Sharam et al. 2009; Corbin & Holl 2012) or trees (Cole et al. 2010; especially tall ones with fleshy fruits). Leveraging natural successional processes that facilitate passive forest regeneration can free scarce financial and logistical resources, diversifying restoration strategies to actively focus on challenging locations.

Acknowledgments

Permission to conduct this research was granted by Office of the President, Uganda Wildlife Authority, and the Uganda National Council of Science and Technology. We are grateful to the Kibale Fish and Monkey Project field assistants, P. Omeja, and D. Twinomugisha for valuable expertise and field assistance, and to the Uganda Wildlife Authority and the Face the Future Foundation for logistical assistance. We thank B. Malombe and the National Museums of Kenya for tree trait information; M. Granados, F. Hamilton, M. Lesosky, E. Low-Decarie, and D. Matthews for advice; and E. Bennett, V. Gerard, A. Gonzalez, P. Parker, J. Rhemtulla, and anonymous reviewers for helpful comments which improved the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, the Fonds de recherche du Québec—Nature et technologies, and the Québec Centre for Biodiversity Science.

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Coordinating Editor: John Parrotta

Supporting Information

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

Figure S1. Key restoration metrics for forest dependent species found regenerating during this study.
Figure S2. Key restoration metrics for forest non-dependent and open habitat species found regenerating during this study.
Table S1. Ecological attributes of 72 indigenous tree species found regenerating during this study.
Appendix S1. Restoration metrics.

Received: 16 May, 2016; First decision: 21 June, 2016; Accepted: 21 June, 2016