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Coupled human-natural regeneration of indigenous coastal dry forest in Kenya

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ABSTRACT

Remaining fragments of East African coastal dry forests contain very high levels of endemic species and are in critical need of conservation and restoration. Little is known about natural regeneration dynamics of these forests, or the potential for human action to aid recovery of lost structures and functions after deforestation/degradation. Here, data and analyses are presented from long-term monitoring plots in a 20 year-old forest restoration project in Gede, Kenya, in a fragment of Zanzibar-Inhambane (ZI) regional forest mosaic. Study results provided previously unavailable indigenous tree species growth rates and human-assisted forest regeneration rates for ZI forests and highlighted issues relevant to conserving and regenerating remnants of coastal dry forest throughout East Africa. Enrichment plantings accelerated recovery of indigenous tree species diversity and increased species density above natural levels. A strategy of inter-planting within existing natural regeneration, including leaving large relic trees, accelerated regrowth of the forest, but the main beneficiary of the strategy was exotic *Azadirachta indica*, which came to dominate significant areas. Analyses indicated that *A. indica*, which produces insecticidal compounds, was significantly altering the structure of arthropod communities; flying to ground-dwelling arthropod ratios were higher where *A. indica* made up a higher proportion of above-ground woody biomass. Management strategies appear to be mostly restoring indigenous forest structures, despite continued casual illegal tree cutting and invasion by *A. indica*. Analysis of illegally harvested trees highlighted the important role of indigenous tree species as a source of ecosystems services to local people; an important consideration for forest conservation planning worldwide.

1. Introduction

Tropical dry forests are among the most degraded and threatened of tropical ecosystems and there is an urgent need to better understand how coupled human-natural processes can work to conserve and restore them (Vieira and Scariot, 2006). While there have been intensive studies of tropical dry forest dynamics, they have been concentrated in certain places (e.g., Costa Rica, Janzen, 1988) and there is comparatively little data on tropical dry forests in many regions of the world (Tarrasón et al., 2010). In particular, there is a relative scarcity of knowledge regarding regenerative capacity of indigenous tropical forest communities, in response to both natural and anthropogenic disturbances (Chazdon, 2003).

Some of the most vulnerable tropical dry forests may be the remaining fragments of East African coastal dry forests (Burgess and Clarke, 2000), which are part of the Zanzibar-Inhambane (ZI) regional forest mosaic ecoregion (White, 1983); this coastal forest belt once stretched from Somalia to Mozambique. This ecoregion is listed among the 200 most outstanding and representative areas of biodiversity globally (WWF, 2014), part of the Swahilian Regional Centre of Endemism (Burgess and Clarke, 2000). ZI forests include globally important areas for bird conservation and provide habitat for many species of invertebrates, butterflies, large and small mammals, including three globally threatened mammals (Burgess et al., 1998). Many of these forests also have high social value; e.g., a significant number are sacred Kaya forests of the Mijikenda (Kibet and Nyamweru, 2008). Though they contain high levels of endemic species and have been identified as key areas for conservation, little is known about the natural growth rates and regeneration dynamics of ZI forests, or about how to restore and sustain them after degradation.

Recent reviews suggest a need to evaluate forest restoration efforts with respect to both the human and natural components

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of specific forest ecosystem types (Lamb et al., 2005; Chazdon, 2008) and caution against measure of success that attempt to restore forests to a "putative natural state" (Stanturf et al., 2014). This raises important questions for forest managers regarding the relative role of natural regeneration in a global "Anthropocene" (Paquette and Messier, 2009), where anthropogenic process are becoming increasingly dominant. Remnants of ZI forest in Kenya have been estimated to hold more than 50% of Kenya's rare tree species, but are generally small and isolated from each other, embedded in a matrix of farmland, savannah-woodland and thicket (summing to only about 660 km^2 nationwide, Burgess et al., 1998). Though these remnants have some capacity to regenerate themselves, human assistance may be necessary to allow them to retain their indigenous tree species, in the face of exotic and invasive species that have been widely introduced into the landscape, and a continued dependence by local people on wood for lighting and domestic energy production (especially charcoal, WRI, 2007) and poles and timber for home building (Dahdouh-Guebas et al., 2000). Though Kenya's Vision 2030 plan for national development sets a target of increasing forest cover to 10% of the land area (Ogweno et al., 2009), most restoration efforts have been comprised of planting exotic plantations on deforested lands (e.g., Pellikka et al., 2009), with some more limited efforts to plant indigenous species (e.g., Farwig et al., 2008). So, there is a critical need to quantify the regenerative capacity of remaining remnants of indigenous forest and understand the potential for human action to help sustain them over time.

Here, we present the results of a study of coupled human-natural regeneration processes in a fragment of ZI forest in Kenya, where a forest restoration project was established two decades ago. Our broad objectives were to quantify productivity and community dynamic processes resulting from natural regeneration and indigenous species enrichment plantings that employed multi-species mixtures and varied the level of existing vegetation. The latter included retention of an exotic, invasive tree species, *Azadirachta indica*, which we hypothesized could alter community dynamics. We also wanted to quantify human-assisted regeneration rates for ZI forests and establish baseline growth metrics for the large number of tree species, indigenous to East African dry forests, which were planted as part of the restoration effort. Specifically, we examined: (1) the survival and growth of the enrichment plantings and their relative contribution to restoring forest structure and biodiversity, (2) the impact and implications of illegal harvesting on the restoration effort, (3) the relative contribution of natural regeneration to restoring forest structure and biodiversity, and (4) the influence of invasive *A. indica* on forest structure, biodiversity and productivity and on the composition of forest arthropod communities. The latter were chosen because arthropod (especially insect) diversity and abundance are increasingly being used as bio-indicators for environmental change and degradation (Thomas, 2005; Nichols et al., 2007).

2. Methods and materials

2.1. Study area

A restoration project was established in 1992 in an isolated 44 ha fragment of ZI forest at the Gede National Monument (GNM), in Kenya, located at Latitude −3.31° and Longitude 40.01°, at about 20 m altitude above sea level. The climate consists of two rainy seasons annually, which are highly variable in length and intensity from year to year, but the long rains most typically last from March to June and the short rains come in October and November (Roberston et al., 2002). The extended dry periods between the rains and close proximity to the equator create natural conditions for tropical dry forest (Burgess and Clarke, 2000). The GNM itself contains the ruins of a thirteenth-century stone city, a historic site for endemic Swahili culture, which is surrounded by the forest. The perimeter of the GNM was fenced in 1991 to limit casual cultivation, cutting of trees and firewood collection by people from surrounding villages, which contributed to forest clearing and degradation.

The objectives of the original restoration project are explained in Robertson et al. (2002) whom initiated indigenous species enrichment plantings in 1992 to restore a deforested/degraded portion of the forest. Species were selected as being indigenous to Gede or found at other collection sites, but thought likely to be indigenous to Gede. About 45% of materials were wild seedlings collected from the remaining GNM Forest and the other 55% were grown in the nursery from propagated cuttings or seed sources (84% were sourced from Gede NM). Ease of propagation and attractiveness to frugivores were also considered as species selection criteria. Trees were planted from 1992 through 1995, during the long rainy season, in holes about 25 cm depth and at least 1 m apart. Compost was placed in the bottoms of holes and trees were staked. Initial plot maintenance was carried out to keep newly planted trees clear of weeds and vines. Plantings were given water during dry periods up to a year after planting (about 7 l once or twice a week). The average initial height of planted trees was 1 m.

The site was divided into a grid of 400 m^2 monitoring plots, with 1 m buffer paths around them. About half of the plots were in open areas without woody regeneration, with the rest set in areas with some significant woody vegetation already established (small trees and shrubs that seeded into cleared areas); a few plots had a few larger relic trees at the time of planting. In plots with patches of existing woody vegetation, planting was carried out around naturally regenerating seedlings and saplings and trees were planted around relic trees. Roberston et al. (2002) called this planting strategy "copse" planting and hypothesized that it may have some benefits in terms of providing initial ground cover for planted trees. Initial vegetation was not measured, but it was noted that larger remnant trees were mainly *Xylopia parviflora*, *Trichilia emetica*, *Dalbergia melanoxylon* and the exotic *A. indica*. Seedlings and saplings of *A. indica* and the exotic shrub, *Lantana camara* were considered to be weedy invaders at the site.

2.2. Vegetation data collection

In 2012, twenty-nine of the original thirty-two monitoring plots were selected for re-measurement; three of the original plots were cleared for an apiary. A complete census of remaining planted trees on each monitoring plot was conducted, using a stem map describing the location of each planted tree on each plot. A census of non-planted woody plants with any stem with a diameter at breast height (DBH) $\geqslant$ 2.5 cm, measured 1.3 m above ground, was also conducted. If multi-stemmed, the diameters of all stems were recorded.

For each planted tree, the following data were recorded: (1) species, (2) DBH, to nearest 0.1 cm, (3) total tree height (nearest 0.1 m), meaning the height above ground to the highest living point on the tree (live leaf or bud), and (4) a tree status was recorded as live, dead, missing or illegally harvested, the latter meaning the main stem had been cut; in this case stem diameter was recorded at stump height. Trees were also assigned to one of five canopy classes (CC):

1. Suppressed (S) – All parts of the tree's crown are below that of surrounding trees.
2. Mostly Suppressed (M) – Most of tree's crown is below crowns of surrounding trees, but the highest parts extend into gaps in the canopy of taller competitor's.

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3. Co-dominant (C) – The tree's crown is actively competing with neighboring crown's and is only partially shaded by them.
4. Dominant (D) – Most of the tree's crown is above its immediate neighbors.
5. Emergent (E) – Tree's crown extends well above the surrounding canopy.

The data described above were also recorded for non-planted, naturally-regenerated individuals, except that heights were only measured on a subset of non-planted trees within each canopy class.

2.3. Vegetation data analysis

Since the exact age of the planted species were known, tree growth rates for each indigenous species could be estimated over a 17–20 year period. Forest productivity was estimated in terms of biomass growth rates for both planted and naturalized vegetation. Tree measurement data were used to compute aboveground biomass (AGB, dry weight basis). Since species-specific equations were not available, a tree biomass equation developed by Brown (1997) for tropical dry forests, covering a similar DBH range, was used: $\text{AGB} = \exp\{-1.996 + 2.32\ln(\text{DBH})\}$ to estimate standing stocks and AGB change over time. Since some of the plots had significant existing woody vegetation at the time of planting, average AGB accumulation was computed separately for plots with and without significant pre-existing vegetation to determine the contribution of existing vegetation to forest biomass accumulation.

Counts of individual stems by species were used to compute overall species richness and the Shannon Index (SI) of biodiversity (Magurran, 1988): $\text{SI} = -\sum p_i \log(p_i)$, where p_i is proportion of all individuals made up by the ith species. These biodiversity metrics were related to productivity metrics to examine relationships between forest change and change in species composition. Forest structural complexity was gauged by an index suggested for tropical dry forests by Murphy and Lugo (1986), which is the product of basal area (m^2/0.1 ha), maximum tree height (m), stem density (stems/0.1 ha) and species richness on a 0.1 ha plot, times a constant of $(0.1/.04) * 10^{-3}$ when extrapolated from the study plot size to 0.1 ha.

Logistic regression analysis was used to compute the survival odds ratio (number of live to dead) for planted trees in response to initial conditions. The number of illegally harvested trees recorded on plots was used to determine the impact of "poachers" on forest regeneration. To determine a relative preference for species by poachers, a harvest ratio, computed the same as the forage ratio of Jacobs (1974), was calculated as the proportion of stems of a species illegally harvested, relative to the proportion of all surviving planted individuals of that species on the plots in 2012. Two databases were examined to determine what the harvested trees might have been used for: Plant Resources of Tropical Africa (http://www.prota.org/) and the Useful Tropical Plants Database (http://tropical.theferns.info/).

Ordinary least squares linear regression (OLS) was used to examine correlations between biodiversity metrics, growth rates and other plot variables. The influence of enrichment plantings on total species richness (S) was estimated with the model: $S = \beta_0 + \beta_1 P$, where P is the proportion of total species found on a monitoring plot that were planted. β_1 estimates the change in total richness as a function of planted species richness and β_0 estimates the average species per plot without the enrichment plantings. ANOVA was used to test for significant differences in plot variables between different initial conditions. All analyses were accomplished using functions and packages in the R statistical environment (R Development Core Team, 2011).

2.4. Arthropod data collection and analysis

During the analysis of the vegetation data it was noticed that there were areas where *A. indica* had gained significant dominance over portions of the site (results described below). Since *A. indica* has known insecticidal properties, it was expected that plots which had high proportions of *A. indica* biomass, would also have lower arthropod populations. More specifically, the hypothesis was that ground-dwelling arthropods would be sensitive to changes in *A. indica* abundance, because of their limited mobility and the fact that they would be living amid the toxic litter (leafs, twigs, shed bark). Since there was a wide variation in the proportion of *A. indica* biomass across the plots, ground-dwelling arthropod abundance was sampled across this gradient. As control, the abundance of flying arthropods, which have greater mobility, and the ratio of flying to ground-dwelling arthropods were examined as possible indicators of arthropod community alterations by *A. indica*.

Arthropods were captured in nine of the twenty-nine monitoring plots in which vegetation data was recorded. In each sampled plot, flying insects were captured using both a standard two meter tall malaise trap and a SLAM malaise trap (BioQuip) suspended 2.5 m up in the canopy. Flying insects were also captured using yellow pan traps charged with soapy water (three per plot). Ground-dwelling arthropods were sampled using five 414 ml pitfall traps per plot; pitfalls were charged with soapy water and deployed with a central one placed near the malaise trap, and the remaining four placed 5 meters away from the center, with one in each cardinal direction.

Flying and ground-dwelling arthropods captured in the monitoring plots were brought back to be sorted at the Mwamba Field Station in Watamu, and specimens from select orders were preserved in 70% alcohol in glass vials. From captures in malaise traps (both types), flying insects from the orders Hymenoptera (excluding Formicidae), Coleoptera, and Diptera were counted and preserved. From captures in yellow pan traps, Hymenoptera (excluding Formicidae) and Coleoptera were counted and preserved. From captures in pitfall traps, ground-dwelling arthropods from the orders Coleoptera and Araneae were counted and preserved.

Ground-dwelling and flying arthropod abundance and flying to ground-dwelling ratios were regressed against relative *A. indica* AGB in linear models (using OLS) to determine the effect of *A. indica* on arthropod community structure. Structural complexity and basal area were also examined as covariates, to determine if forest structure or stand density might be additional or alternative determinants of arthropod community structure.

3. Results

3.1. Survival of planted trees under different initial conditions

After an average period of 18 years since planting, 54% of trees planted were still alive, with a slightly higher mean survival rate for trees inter-planted in areas where natural re-vegetation had begun (Table 1). However, the existence of woody vegetation at the time of planting had no statistically-significant lasting effect on the odds of a planted tree surviving ($p = 0.236$), relative to the initially bare areas, including plots where large relic trees existed.

3.2. Continued illegal harvesting of trees

Despite protective fencing and education programs, illegal cutting of trees was still evident. When surveyed in 2012, 52% of all plots had at least one planted tree illegally harvested (Table 1). While only 3% of all planted trees were illegally harvested, this

Table 1
Mean (std) number of planted trees per plot and survival rates (%) for trees planted under different initial conditions.

Attribute	Initial plot conditions			Total
	Insignificant woody vegetation	Significant woody vegetation	Relic trees	
Years since planting	17.8 (1.0)	17.0 (0.0)	18.0 (0.8)	17.8 (0.8)
# Planted	34.2 (7.5)	35.1 (6.5)	17.5 (0.0)	33.5 (7.1)
# Alive	17.4 (7.4)	19.8 (5.2)	9.0 (3.5)	18.1 (6.3)
# Dead	16.8 (1.6)	15.3 (1.0)	8.5 (1.4)	15.4 (1.3)
% Survival	51%	56%	51%	54%
# Illegally harvested	1.5 (1.6)	1.0 (1.4)	0.7 (1.0)	1.1 (1.3)
% Illegally harvested	4%	2%	6%	3%

represented 7% of all planted tree mortality recorded in 2012. Since some of the "dead" planted trees were recorded as "missing", this estimate is likely conservative. Nonetheless, most of the illegally harvested trees observed in the monitoring plots had since re-sprouted around their stumps. Because of this re-sprouting, the species of the trees removed could be identified, allowing for determination of preferred species and for inferences to be drawn regarding the likely use of the illegally harvested trees (Table 2). This information, combined with the relatively small size of the trees removed (average = 5.6 cm DBH; max 11.5 cm), suggests that the trees were being taken mainly to supply local people with poles for building, tool handles, utensils, and similar small wooden tools, and to a lesser extent wood carvings for tourists.

3.3. Restoring forest structure

Despite the death of about half of the planted trees and significant illegal harvesting, the restoration effort, combined with natural succession, regenerated a high density of stems; about 2600 woody stems per ha ⩾ 2.5 cm DBH, in the 20 years since the area was deforested/degraded (Table 3). About 17% of the stems were planted and 83% from natural regeneration. About 21% were multi-stemmed, with an average of 1.3 stems (⩾2.5 cm DBH) per planted individual. The naturally-regenerated plants had a much higher proportion of multi-stemmed individuals (46%), with about 2.0 stems per individual. Overall, there were more individuals with more stems in the naturally regenerated population than in the planted one, which explained why the bulk of the stems regenerated were of natural origin.

The average size of a stem was about 6.8 and 6.9 cm DBH, respectively, for planted and naturally-regenerated trees, with a large range of stem sizes up to a 45.5 cm DBH planted specimen of *Ficus sansibarica* (Fig. 1a & b). The average tree size varied depending on canopy position, with an average DBH of 4.2, 6.2, 9.3, 14.0, and 21.8, for suppressed, moderately suppressed, co-dominant, dominant and emergent trees, respectively. This translated into DBH growth rates ranging from 0.2 cm yr^{-1} for suppressed trees to about 1.2 cm yr^{-1} for emergents. In general, the shape of the DBH distribution was about the same for both planted and naturalized trees, with many smaller diameter stems and fewer larger ones (Fig. 1a & b). So, most of the trees were small and in the shade of the canopy co/dominants.

Table 3
Summary statistics for the regenerating forest.

Forest attribute[a]	Mean (std)
Trees per ha^{-1}	2626 (653)
Basal area (m^2 ha^{-1})	15.4 (4.8)
Above-ground biomass (Mg ha^{-1})	56.8 (21.3)
Maximum height (m)	14.8 (2.6)
Complexity[b]	19.2 (12.4)
Shannon index	2.9 (0.3)
Species richness[c]	94 (na)

[a] Trees ⩾ 2.5 cm DBH.
[b] As described in Murphy and Lugo, 1986.
[c] Total species on 1.16 ha.

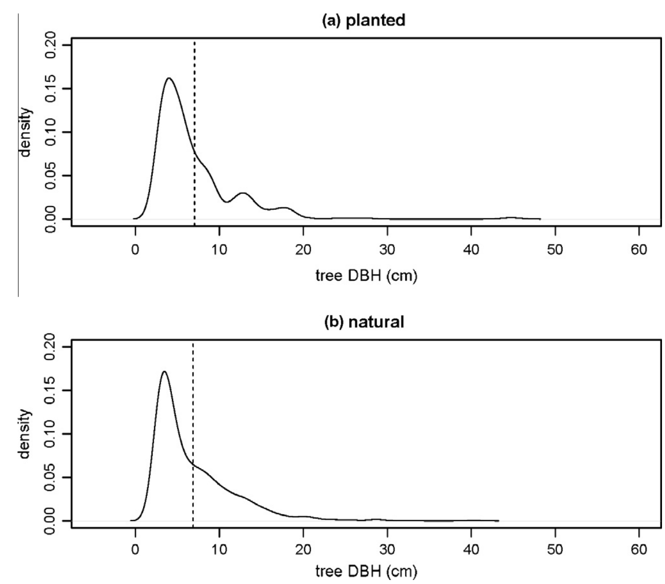

Fig. 1. Diameter at breast height (DBH) probability density functions (pdf) for (a) planted and (b) naturalized trees. Density (*y*-axis) is the probability that any tree's DBH is approximately equal to the value on the *x*-axis. The vertical dashed line is the mean DBH.

Table 2
Characteristics of, and preference for, illegally harvested tree species.

Species	Live[a]	Harvested[b]	H-ratio[c]	Uses[d]
Afzelia quanzensis	0.067	0.032	0.479	Heavy construction, flooring, exterior joinery, furniture and carvings
Combretum schumannii	0.087	0.065	0.738	Durable wood used widely. Popular for use in the carving industry
Grewia plagiophylla	0.015	0.032	2.214	Poles, posts, tool handles, bows, arrows, knobkerries and for carving
Cassia afrofistula	0.011	0.032	2.952	Medicinal use
Berchemia discolor	0.031	0.097	3.125	Furniture, poles, pestles and hair combs
Lepisanthes senegalensis	0.035	0.226	6.525	Furniture, poles and for making small utensils
Lecaniodiscus fraxinifolius scassellattii	0.009	0.065	7.084	Building poles, domestic utensils, tool handles, grain mortars
Millettia usaramensis	0.009	0.065	7.084	Hard and heavy. Used for building poles, pestles and withies
Carpodiptera africana	0.027	0.226	8.265	Construction and for poles, bows, tool handles and spoons. It is also used as firewood and for fiber (bark) and medicine

[a] Proportion of remaining live individuals of that species in 2012.
[b] Proportion of illegally harvested individuals of that species in 2012.
[c] The ratio of illegally harvested to all remaining live individuals of a species in 2012.
[d] Tree use data obtained from Plant Resources of Tropical Africa: http://www.prota.org/ and the Useful Tropical Plants Database: http://tropical.theferns.info/.

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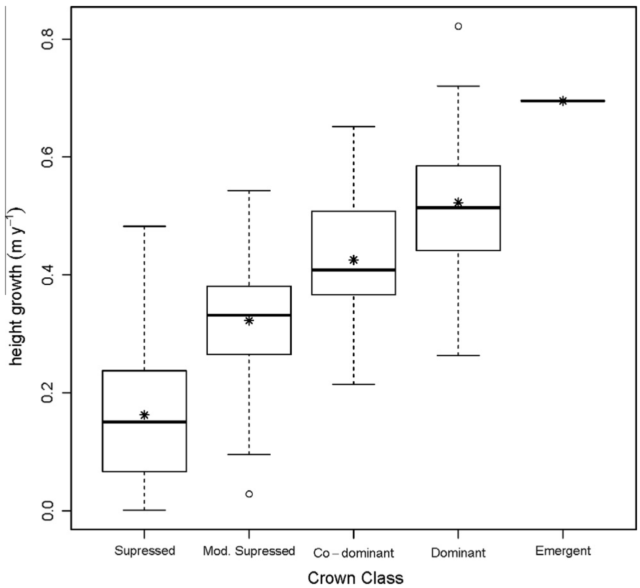

Fig. 2. Height growth rates for trees in restoration plantings, stratified by crown competition classes: (1) suppressed, (2) mostly suppressed, (3) co-dominant, (4) dominant, and (5) emergent.

Stratification of the canopy resulted from differential height growth of species. The average maximum tree height on a plot was 14.8 m (Table 3) and the average tree height was 9.8 m over all trees. The tallest trees on the site were emergent relic trees, including individual specimens of *Lonchocarpus bussei* (20.6 m) *Terminalia spinosa* (20.0 m), *Hyphaene compressa* (19.4 m) and *A. indica* (19.2 m). Mean height growth rates for planted trees were 0.16, 0.32, 0.42, 0.52, and 0.70 m yr^{-1} (Fig. 2) for suppressed, moderately suppressed, co-dominant, dominant and emergent trees, respectively. Average height growth rates are shown for a wide diversity of planted species in Table 4. The slowest growing species was a small understory tree/shrub, *Rinorea elliptica*, which did not grow detectably beyond the height it was when planted. The fastest growing species was *Erythrina sacleuxii*, a specimen of which was the only planted tree classed as emergent (Fig. 2).

Total woody plant AGB accumulated in the restoration area was estimated to be around 56.8 Mg ha^{-1} (Table 5). *A. indica* was the dominant species regenerating in the restoration area, as measured by the fraction of total AGB stocks (35% of all stocks, though it was only about 1% of the species represented). Both growth of enrichment plantings and natural regeneration were positively correlated with total biomass growth rate, but were not significantly influenced by each other ($p = 0.2696$), meaning that both were contributing independently to biomass plot gain. Overall, the enrichment plantings contributed about 17% to biomass growth, with the rest being from natural regeneration. Looking only at the plots that were initially non-vegetated, the relative contribution of natural versus planted trees to biomass accumulation was 15% and 85%, respectively, of AGB accumulated over about 18 years. From these latter plots, the human-assisted regeneration rate of the ZI forest after deforestation could be estimated to be about 2.8 Mg ha^{-1} yr^{-1}.

The restoration plot design allowed for examination of the effect of initial plot conditions on biomass accumulation. The highest amounts were found in areas where some biomass had already accumulated, in the form of relic trees, before the restoration project was established (Table 5). These areas also had the lowest proportion of planted tree biomass, because fewer trees were initially planted in those plots (Table 1) and shading slowed the growth of planted trees; they added only about 0.1 Mg ha^{-1} yr^{-1}. The initially non-vegetated areas accumulated the least AGB. However, planted tree biomass was a higher proportion (26%) of total accumulated AGB on the plots with initial woody vegetation, even though the average number of growing years was about 1 year less (Tables 1 and 5); this resulted in a biomass accumulation rate 1.7 times higher than the non-vegetated plots (0.7 Mg ha^{-1} yr^{-1} versus 0.4 Mg ha^{-1} yr^{-1}). ANOVA revealed that these mean trends were not statistically significant, however, due to the high variation in biomass from plot to plot, which likely reflects the myriad of other factors which effect biomass accumulation over time. One exception was that initial plot conditions had a statistically significant effect ($p = 0.021$) on the amount of *A. indica* AGB on the plots. *A. indica* made up the majority of AGB (63%) in plots with relic trees, because many of the relic trees were larger *A. indica* trees, and it made up the lowest proportion of AGB (23%) in plots that were initially non-vegetated.

3.4. Restoration of indigenous species diversity

Ninety-four woody plant species were found over all the study plots (Table 4), giving a species richness above the high end of the range considered typical for tropical dry forests (35–90 species, Murphy and Lugo, 1986), over a similar size area surveyed. Shannon diversity was also high, at around 2.9 (Magurran, 1988). Most interestingly, *A. indica* was the only species found in the monitoring plots that was not indigenous to East Africa, as determined from a variety of sources on East African flora (Beentje et al., 1994; Birch, 1963; Bridson, 1992; CABI, 2011; Gachathi et al., 1994. Gillett et al., 1971; Sleumer, 1975; Thulin, 2008; Verdcourt, 1999; Weiss, 1973; White and Verdcourt, 1996 and Whitehouse et al., 2001).

The enrichment plantings had a significant positive effect on increasing woody plant species richness (Fig. 3); explaining 56% of variation in total richness observed between monitoring plots. Conversely, since the proportion of natural species on plots ($1 - P$) is the complement of the proportion of planted ones, the relationship shown in Fig. 3 is exactly reversed for plots with a higher proportion of natural colonists, which were lower in diversity. The average species per plot without the enrichment plantings was estimated to be $\beta_0 \approx 13$ (Table 6). The slope of the increase in species richness with more planted species seemed insensitive to the initial plot conditions (compare β_1 values in Table 6). However, the presence of existing woody vegetation seemed to reduce the natural species colonization rate ($\beta_0 \approx 11$ in Table 6) (see Fig. 3). Overall, the average richness per plot was about 31 species (min = 21 max = 44), about half of which were planted species (mean = 15 per plot) and the other half naturalized (mean = 16 per plot). About 25 species per plot were planted, on average, so about 10 planted species per plot were lost over the last 20 years, and about 16 species per plot were added through natural regeneration processes. Over all the monitoring plots observed, the total richness of planted individuals that survived to 2012 was 54 species, compared to a total of 65 naturalized species. However, 25 species that naturalized were also the same species as those planted, giving the total of 94 unique species found across the plots (Table 4). That left a net contribution of about 29 additional species to the restored area through the enrichment plantings, beyond that which naturalized, or about 31% of the total species observed.

Natural forest regeneration processes, as measured by AGB growth from naturalized species, had a strong negative effect on the Shannon index (Fig. 4a) and a weak negative effect on species richness (Fig. 4b). By contrast, Shannon diversity showed a trend of increasing when the AGB growth of planted species was low and then decreasing where productivity of the plantings was higher (Fig. 4c); a similar but much weaker trend was shown for species richness (Fig. 4d). With an average of 33 individuals and

Table 4
Naturalized (N) and Planted (P) species found in the restoration monitoring plots in 2012. I/E means indigenous/exotic.

spp.	N	P	I/E	Mean height growth (m y^{-1})
Adansonia digitata		x	I	0.26
Afzelia quanzensis		x	I	0.39
Allophylus rubifolius	x		I	–
Annona senegalensis	x		I	–
Antiaris toxicaria	x	x	I	0.29
Antidesma venosum	x		I	–
Azadirachta indica	x		E	–
Balanites wilsoniana		x	I	0.38
Berchemia discolor		x	I	0.31
Bourreria petiolaris	x	x	I	0.30
Bridelia cathartica	x	x	I	0.24
Canthium glaucum	x		I	–
Carpodiptera africana		x	I	0.24
Carpolobia goetzei		x	I	0.10
Cassia afrofistula	x	x	I	0.27
Cassipourea euryoides	x		I	–
Catunaregam nilotica	x		I	–
Combretum schumannii	x	x	I	0.32
Commiphora zanzibarica	x	x	I	0.29
Cordyla africana		x	I	0.23
Cussonia zimmermannii	x	x	I	0.33
Dalbergia melanoxylon	x	x	I	0.14
Deinbollia borbonica	x		I	–
Dichrostachys cinerea	x		I	–
Diospyros squarrosa	x		I	–
Dovyalis abyssinica	x		I	–
Drypetes natalensis		x	I	0.29
Drypetes reticulata		x	I	0.29
Ehretia bakeri	x		I	–
Elaeodendron schweinfurthianum	x		I	–
Erythrina sacleuxii		x	I	0.70
Euclea natalensis	x		I	–
Feretia apodanthera	x		I	–
Ficus bubu		x	I	0.30
Ficus bussei		x	I	0.25
Ficus lingua		x	I	0.22
Ficus sansibarica		x	I	0.37
Ficus tremula		x	I	0.36
Flacourtia indica	x		I	–
Flueggea virosa	x	x	I	0.27
Grewia holstii	x		I	–
Grewia micrantha	x		I	–
Grewia plagiophylla	x	x	I	0.39
Grewia vaughanii	x		I	–
Gyrocarpus americanus	x	x	I	0.13
Haplocoelum inoploeum	x	x	I	0.17
Harrisonia abyssinica	x		I	–
Hoslunida opposita	x		I	–
Hymenaea verrucosa	x		I	–
Hyphaene compressa	x		I	–
Kigelia africana		x	I	0.32
Lannea schweinfurthii stuhlmannii	x	x	I	0.25
Lannea welwitschii		x	I	0.36
Lecaniodiscus fraxinifolius	x	x	I	0.29
Lepisanthes senegalensis	x	x	I	0.17
Lonchocarpus bussei	x	x	I	0.13
Maerua angolensis	x		I	–
Manilkara sansibarensis	x		I	–
Markhamia zanzibarica		x	I	0.29
Millettia usaramensis	x	x	I	0.29
Mimusops obtusifolia		x	I	0.25
Monodora grandidieri		x	I	0.27
Ormocarpum kirkii	x		I	–
Pleurostylia africana	x		I	–
Premna chrysoclada	x		I	–
Psydrax faulknerae	x		I	–
Rinorea elliptica		x	I	0.00
Sclerocarya birrea	x		I	–
Sclerocarya caffra		x	I	0.12
Sideroxylon inerme		x	I	0.30
Sorindeia madagascariensis	x	x	I	0.27
Sterculia africana	x	x	I	0.05
Sterculia appendiculata		x	I	0.34
Strychnos madagascariensis	x		I	–

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Table 4 (*continued*)

spp.	N	P	I/E	Mean height growth (m y^{-1})
Strychnos spinosa	x		I	–
Suregada zanzibariensis	x	x	I	0.28
Tamarindus indica	x	x	I	0.20
Tarenna graveolens		x	I	0.14
Tarenna supra-axillaris	x		I	–
Teclea trichocarpa	x		I	–
Terminalia spinosa	x	x	I	0.41
Thespesia danis	x		I	–
Trichilia emetica	x	x	I	0.39
Turraea wakefieldii		x	I	0.39
Uvaria lucida		x	I	0.22
Uvariodendron kirkii		x	I	0.14
Vismia orientalis	x		I	–
Vitex keniensis	x		I	–
Vitex mombassae	x		I	–
Ximenia americana	x		I	–
Xylopia parviflora	x	x	I	0.34
Zanthoxylum chalybeum	x		I	–
Zanthoxylum holtzianum		x	I	0.01
Ziziphus mucronata	x	x	I	0.40

Table 5
Mean (std) of above-ground biomass (ABG, Mg ha^{-1}) for planted and naturally regenerated sub-populations under different initial plot conditions.

Regeneration type	Initial plot conditions			All plots
	Insignificant woody vegetation	Significant woody vegetation	Relic trees	
Planted	7.6 (8.1)	12.4 (10.3)	1.2 (0.2)	9.6 (9.4)
Natural[a]	42.7 (15.7)	47.9 (22.7)	68.5 (36.3)	47.2 (21)
Not *A. indica*	31.4 (15.1)	24.2 (11.4)	24.6 (5.3)	27.2 (13)
A. indica	11.4 (6.5)	23.7 (18.3)	43.9 (41.6)	20.0 (18)
Planted and Natural	50.3 (15.9)	60.2 (23.4)	69.7 (36.1)	56.8 (21.3)

[a] Natural is the sum of "*A. indica*" and "Not *A. indica* " components.

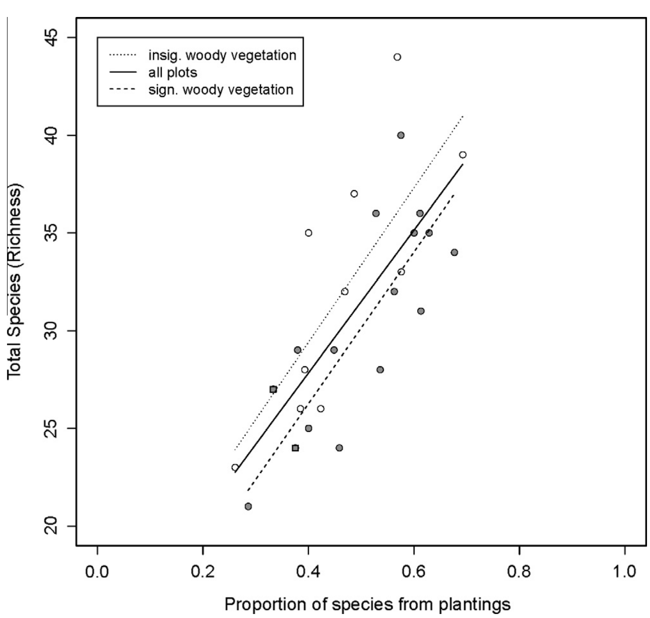

Fig. 3. The influence of the proportion of planted species (*P*) on total species richness (S) across all plots and plots with differing levels of initial woody vegetation cover. Regression lines are fitted with ordinary least squares regression. Shaded symbols are plots with significant initial woody vegetation. Square symbols are plots with relic trees.

24 species per plot, the restoration plantings assured a more even-then-natural condition and worked to offset the natural process of concentrating a greater proportion of biomass into fewer dominant species. However, the concavity of the relationships (Fig. 4c & d) also hints that the human-assisted boost to biodiversity may be declining over time as natural forest processes outweigh the legacy effect of the plantings. There was also a significant effect of initial conditions ($p = 0.049$) on the relationship between Shannon diversity and productivity of the plantings (Fig. 4c), such that the presence of established woody vegetation dampened the human-assisted boost to evenness.

Table 6
Models describing the influence of enrichment plantings on total species richness $S = \beta_0 + \beta_1 P$, where *P* is the proportion of total species found on monitoring plots that were planted. β_1 estimates the change in total richness as a function of planted species richness and β_0 is the average species per plot without any planted species.

Initial conditions	Coefficient	Estimate	Std	*p*	R^2
All	β_0	13.22	2.98	0.00	0.56
	β_1	36.53	6.03	0.00	
Insignificant woody vegetation	β_0	13.60	4.82	0.02	0.57
	β_1	39.52	10.09	0.00	
Significant woody vegetation	β_0	10.74	4.11	0.02	0.63
	β_1	38.81	7.85	0.00	

3.5. Influence of exotic species on tree structure, diversity and arthropod communities

When the restoration plots were put in, two exotic species were of concern: *L. camara* and *A. indica*. Twenty years later no individuals of *Lantana* were found on the monitoring plots. *A. indica* was abundant, though the proportion of total biomass that was from *A. indica* (% *A. indica*) varied widely from plot to plot, ranging from as low as 3% to as much as 77% of total AGB. There was a significant ($p = 0.00$), negative effect of increasing % *A. indica* biomass on Shannon diversity, indicating that *A. indica* was crowding out other species where abundant. However, *A. indica* growth was completely uncorrelated with the AGB accumulated from either the plantings or other natural (non – *A. indica*) regeneration, indicating that *A. indica* plot dominance was essentially random with respect to different mixtures of planted and other naturally regenerating species.

Populations of ground-dwelling arthropods were significantly ($p = 0.05$), negatively correlated (Pearson's $r = -0.59$) with % *A. indica* biomass, while populations of flying arthropods were not influenced by it ($p = 0.21$), supporting the hypothesis that *A. indica* was having a localized impact on the arthropod community.

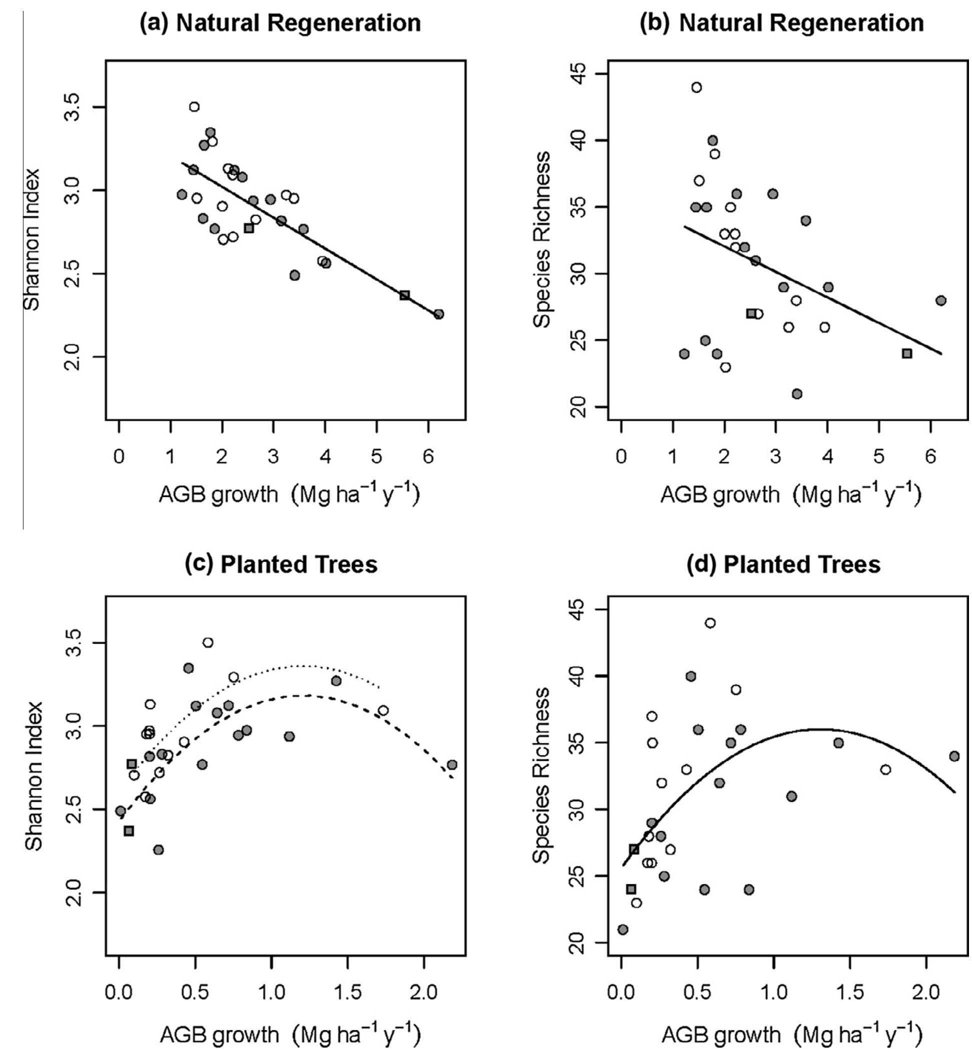

Fig. 4. Influence of productivity (above-ground biomass (AGB) growth) of naturalized (a and b) and planted (c and d) trees on two metrics of diversity, Shannon index and Species Richness, respectively. Lines are fitted with ordinary least squares regression (solid lines = all plots, dotted lines = insignificant woody vegetation, dashed lines = significant woody vegetation). Shaded symbols are plots with significant initial woody vegetation. Square symbols are plots with relic trees.

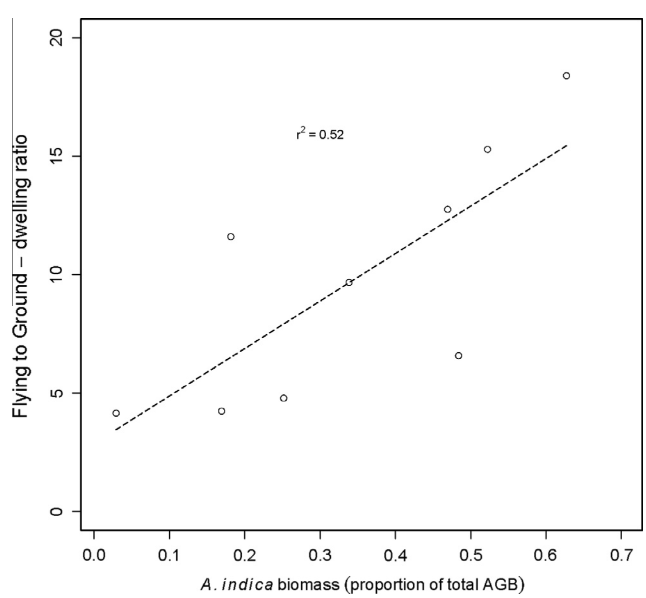

Fig. 5. Influence of *Azadirachta indica* dominance (proportion of total above-ground biomass (AGB)) on the ratio of flying to ground-dwelling arthropods. Regression line is fitted with ordinary least squares regression.

Ground-dwelling versus flying arthropod populations were completely uncorrelated with each other (r = 0.00), suggesting they were reacting to different forest attributes. While ground-dwelling arthropods were most strongly correlated with % *A. indica* biomass, flying arthropods were most strongly correlated with plot basal area (p = 0.03, r = 0.73). Flying arthropod biomass was also significantly, positively correlated (p = 0.04, r = 0.69) with structural complexity, but ground-dwelling arthropods appeared not to be significantly influenced by it. Looking at the relative shift in both populations, there was a statistically significant (p = 0.02), moderately-strong relationship between the flying to ground-dwelling arthropod ratio and% *A. indica* biomass, over the subset of nine plots sampled that spanned the *A. indica* gradient (Fig. 5). Overall, the results suggest that the largest shifts in the arthropod community structure occurred in areas where large *A. indica* trees dominated.

4. Discussion

The results of this study provide useful data for understanding the potential to conserve and regenerate fragments of ZI forest in Kenya and similar remnants of coastal dry forest throughout East Africa. These insights can be separated into three major categories:

(i) consequences of specific restoration strategies, (ii) the role of exotic versus indigenous tree species in providing ecosystems services to local people, and (iii) recovery of the indigenous forest in response to coupled human-natural regeneration; each is discussed below.

4.1. Consequences of forest restoration strategies

This study allowed for examination of the consequences of different restoration approaches in a rare tropical dry forest ecosystem, where growth and regeneration potential of indigenous species are poorly documented and there have been few, if any, similar manipulative experiments to facilitate greater understanding of them.

The choice by Robertson et al. (2002) to inter-plant within existing woody regeneration reflected their knowledge of earlier studies that suggested a possible benefit for seedling establishment in South Africa Fynbos fragments (Milton et al., 1999) and dry forest in the Caribbean (Ray and Brown, 1995). A recent review by Vieira and Scariot (2006) noted that sapling growth in tropical dry forests is typically better in the sun than in the shade, as the data from this study shows, but the water balance of the plants, particularly early in establishment, is also important. In the seasonally hot and dry conditions of the Kenya coast, water limitation could explain the boost in productivity observed for trees planted in ground that was not bare, but had no high shade (the plots with significant initial woody cover).

The choice to plant many different species in the same plots increased both species richness and evenness. However, such a strategy could cause some species not to grow as well in mixtures with other species as they could if they seeded in naturally, at a stage of forest development that matches their life history evolution. This could explain why species like *Gyrocarpus americanus* and *Sterculia appendiculata* had fairly slow average growth rates (Table 4), even though they are typically considered as fast-growing 'pioneer' species. Leaving relic trees on the plots created initially shady conditions, which appeared not to effect survival, but substantially reduced growth rates of survivors. These latter results have implications relevant to the practice of establishing plantations as "nurse" trees for forest regeneration (Löf et al., 2014), particularly non-native species, the role of which are among the most vigorously debated issues in restoration ecology (Ewel and Putz, 2004; Schlaepfer et al., 2011).

The choice to leave exotic species (*L. camara* and *A. indica*) in areas where they were established was influenced by evidence that they might function effectively as nurse trees for indigenous species (Ray and Brown, 1995; Parrota, 1995), but also because there was insufficient manpower to remove them (it was hoped that the plantings would crowd them out, Robertson et al., 2002). It is notable that *L. camara* was eradicated from the restoration plots, as it has proven to be an aggressive, invasive species, adept at crowding out natives in other ecosystems, and is considered to be one of the world's ten worst weeds (Sharma et al., 2005). Duggin and Gentle (1998) found that shading by intact canopies is an effective barrier against *Lantana* invasion, so accelerating canopy development through the plantings and leaving relic trees may have made a difference in arresting the spread of this species. By contrast, *A. indica* became abundant across the site. The fact that *A. indica* dominance appeared random, with respect to species composition on the plots, suggests an ability of this species to take a foothold across a broad spectrum of tree species assemblages. Given the relative ubiquity of seed sources for *A. indica* in the surrounding villages and its success in the initially non-vegetated plots, it is unlikely that anything short of an aggressive removal campaign would have excluded this species from the regenerating forest. A recent campaign to eradicate *A. indica* from tropical forests in Tanzania showed the challenges of removal, in part, because of the ability of the species to re-sprout vigorously after girdling (Silayo and Kiwango, 2010).

The main impacts of the decision to let native species compete with *A. indica* were a local reduction in diversity in patches of the new forest and an apparent shift in make-up of the forest arthropod community. The latter may have spillover effects on ecosystem services such as pollination (which relies heavily on hymenopteran vectors) and biological control in the forest-agroecosystem mosaic around Gede National Monument (Tscharntke et al., 2007, 2008). These results also highlight the possible value of using multiple species or functional guilds to quantify the effects of anthropogenic influences on habitats and landscapes (Oldekop et al., 2012), rather than focusing on a single indicator taxon. Other studies have shown reductions in small mammal biodiversity due to high densities of invading *A. indica* (Decher and Bahian, 1999), so there is prior evidence that it influences animal communities where abundant. The long-term fate of *A. indica* is not clear, as it is considered a pioneer, but one that can grow in its own shade (Silayo and Kiwango, 2010). In our data, we found that the number of suppressed and moderately-suppressed *A. indica* trees found on a plot was significantly, positively correlated with the number of co-dominant and dominant individuals of that species ($r = 0.81$), indicating that *A. indica* can grow in its own shade in these forests. In general, more studies like this one are needed to document the impact of this broadly-naturalized invasive species on the indigenous biotic communities of tropical dry forests.

In understanding these results, it is important to acknowledge that this study lacked explicit control areas where forests were not being restored. This is true of many studies of ecological restoration ecology (e.g., Kiehl et al., 2006), because of the general rarity of the areas under study or because suitable reference sites have been not been left alone to recover naturally. So, it is not possible here to say what would have happened to the degraded forest without direct human assistance. Nonetheless, a recent study of degraded tropical dry forest in Hawaii, USA (Medeiros et al., 2014) showed that control areas remained essentially unchanged, while native shrub cover increased and exotics declined in restored areas. Further, the authors of the latter study concluded that, without implementation of appropriate management strategies, Hawaiian dry forest would likely disappear in the next century.

4.2. The role of exotic versus indigenous tree species in providing ecosystems services

This study raises questions about the role of exotic species versus indigenous species in providing ecosystems services (Ewel and Putz, 2004) and highlights the difficulty of developing conservation approaches that may need to balance biodiversity goals with improving livelihoods of local people (Lamb et al., 2005). The results clearly showed that local people preferred certain indigenous species (Table 2), despite the abundance of *A. indica*, which likely reflects historic and cultural ties to tree species that cannot be easily erased (Dahdouh-Guebas et al., 2000). On the other hand, *A. indica* is also valued by local people, particularly for its medicinal properties, which is apparently why it was introduced to East Africa by Indian immigrants (Silayo and Kiwango, 2010). In a recent study in South Africa, Shackleton et al. (2015) concluded that the negative impacts of invasive *Prosopis* spp., which was purposely introduced to help to local communities, exceeded the benefits. They found that households preferred using products from native species to that from *Prosopis*, and that the combined demand for native species and their displacement by *Prosopis* was exacerbating loss of native species. One possible solution is to encourage local farmers/landowners to grow native species instead of exotic ones on their own land, which requires (a) overcoming cultural and technical barriers to planting trees (Meijer et al., 2015) and (b) providing direct technical assistance to landowners to plant native trees (Garen et al., 2009). In Kenya, there have been recent efforts to provide technical guidelines to help farmers to grow native tree species for their timber needs (e.g., *Melia volkensii*, Muok et al., 2010). Increasing knowledge of propagation methods for and growth rates of many of the species indigenous to ZI forests was a major goal of the restoration project described here (Robertson et al., 2002). Overall, this study suggests an important role for endemic tree species in providing ecosystems services to local, forest-dependent people, which should be considered as a critical component of efforts to conserve and restore tropical dry forest fragments in East Africa.

4.3. Recovery of the indigenous forest in response to coupled human-natural regeneration

The forest regenerating in the restoration area appears to be recovering much of its original structure and biodiversity, despite the success of *A. indica*. A combination of traits, including a relatively low canopy, many small stems, and a very high biodiversity suggested a moderate structural complexity of the regenerating forest (Table 3), measured on a scale for tropical dry forests (ranging from 5 to 45, Murphy and Lugo, 1986). Right now, the restoration area could best be classed as a coastal mixed forest "thicket", based on the biomass accumulated and the stature of the trees (Glenday, 2008). The high degree of multi-stemmed individuals found in the plots is typical of tropical dry forests, whose species are naturally prone to sprouting due to selection pressure from both natural and anthropogenic mortality (Murphy and Lugo, 1986), but also likely reflects tree-cutting in the recent past. Based on the size and growth rates of the trees in the monitoring plots and measurements taken on some of the very old trees in the GNM (the tallest tree was a 30 m tall *S. appendiculata*, growing amid the ruins), it is expected that this forest will continue to grow into a "tall" coastal mixed forest, similar to that found in the last largest remaining fragment of East African dry forest, the Arabuko-Sokoke Forest (Glenday, 2008), if allowed to continue to regenerate.

The relatively high contribution of indigenous species regeneration from natural sources supports the assertion that tropical dry forests can have a resilient flora and a high taxonomic recovery rate after disturbance (Murphy and Lugo, 1986; Vieira and Scariot, 2006), despite the relative isolation of this fragment. However, the enrichment plantings constituted a considerable densification of the indigenous biodiversity in the restored area, and will likely make a long-term contribution to sustaining biodiversity in the region. Research has shown that even very small forest fragments can make a large contribution to conservation of biological diversity (Arroyo-Rodriguez et al., 2009). More studies of coupled human-natural regeneration of indigenous forest fragments are needed globally, to help determine how human action can help sustain healthy human-forest mutualisms into the future.

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