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Title: Liana cutting for restoring tropical forests: a rare palaeotropical trial

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Abstract

Liana growth following forest disturbance is threatening the tropical carbon sink by delaying or preventing recovery. Tree growth can be stimulated by liana cutting, however its applicability for conservation management remains uncertain, particularly in Africa (the least-studied continent for ecological restoration) and against pervasive barriers such as wildfires. We conducted a small-scale trial to investigate tree sapling regeneration following liana cutting in a lowland African forest prone to low intensity wildfires. We employed a BACI design comprising eighteen 25m^2 plots of sapling trees in liana-infested areas. After five years of liana cutting we saw greater recruitment, stem growth and net biomass. Wildfires caused 51% mortality and probably masked liana cutting influences on species and survival, but may have encouraged stem recruitment through interaction with liana cutting. Incorporating our data into a first quantitative review of previous studies, we found that tree growth, recruitment and net growth rates were all consistently higher where lianas were either absent or removed (respectively: 80%, 215%, 633%; n=14, 3, 4). Tree growth impacts were approximately equivalent across size-classes and continents. We give recommendations for improved plot and sample sizes, but conclude that liana cutting is a promising restoration method for lowland tropical forests, including Africa.

Introduction

Restoration of degraded tropical forests is vital for averting substantial impacts on biodiversity, carbon sinks, and global economy. An estimated 33-60% of tropical forests have been degraded by logging (Asner et al., 2009; FAO, 2010) with 1.4Bha identified for potential restoration (Minnemeyer et al., 2011). Despite this potential, attempts at ecological restoration have addressed only a meagre proportion of tropical forests. Tropical forest management has even failed to prevent biodiversity loss within and around protected areas (Laurance et al., 2012). Attempts at improved management through restoration must use site-specific biological and social conditions to develop tailored approaches (Stanturf, Palik & Dumroese, 2014). Passive restoration is possible where soils, seeds and plant dispersal are conducive (Barnes & Chapman, 2014), but succession from heavily degraded tropical forest is significantly slower without active management (Chazdon, 2003).

Landscape-scale restoration methods for tropical forests are needed that are practical and affordable for developing nations. Tree-planting has considerable demands on time, expertise and cost (Chazdon, 2008). Planted trees may even grow slower than naturally regenerating trees (Omeja, Chapman & Obua, 2009) and will affect genetic diversity unless sourced from a range of parent trees at the immediate locality. One promising alternative for conservation management widely employed by commercial forestry (Putz, 1991) is to temporarily exclude lianas (woody climbers) by cutting.

Lianas are a disturbance-favouring guild (Ledo & Schnitzer, 2014), growing rapidly in canopy gaps or edges of tropical forest (Schnitzer & Bongers, 2011). While various non-climbing plants compete with forest trees, those that climb are particularly rigorous (Paul & Yavitt, 2011). Lianas physically restrict trees and compete for light and nutrients, causing

reduced growth, sap flow, fecundity, leaf production and survival (Hegarty, 1991; Álvarez-Cansino et al., 2015; Toledo-Aceves, 2015) and ultimately biomass accumulation and carbon sequestration (Schnitzer et al., 2014). Consequently, forest succession may be slowed or arrested (Schnitzer, Dalling & Carson, 2000; Tymen et al., 2015). Accordingly, the global distribution of lianas is negatively related to carbon stocks (Durán & Gianoli, 2013). Increasing tropical forest degradation has stimulated 1.7-4.6% annual increase in liana abundance, threatening the tropical carbon sink (Phillips et al., 2002; Schnitzer & Bongers, 2011; van der Heijden et al., 2013).

In selectively logged neotropical forests, liana cutting has improved growth, survival and recruitment of tree saplings (Gerwing, 2001; Campanello et al., 2012). Focal timber species have also shown increased growth and survival of saplings following liana cutting (Graul & Putz, 2004) and increased growth of mature trees by 9-64% (Pérez-Salicrup & Barker, 2000; Peña-Claros et al., 2008). The only studies outside of timber concessions or plantation have focussed on Panama, where liana cutting has improved tree growth, recruitment, net carbon uptake and community composition (Schnitzer et al., 2014; Álvarez-Cansino et al., 2015; van der Heijden, Powers & Schnitzer, 2015; Wright et al., 2015), whereas pioneer species may benefit from liana presence (Schnitzer & Carson, 2010). Liana cutting also has positive effects on leaf, fruit and seed production, damage caused by treefall, and reduced subsequent liana colonisation of canopy gaps (Parren & Bongers, 2005; Nabe-Nielsen, Kollmann & Peña-Claros, 2009).

Studies of tree regeneration following liana cutting in the palaeotropics have been limited to focal species in combination with other forestry techniques. Africa is the least-studied continent for ecological restoration (Wortley, Hero & Howes, 2013) despite having the most degraded forest (Minnemeyer et al., 2011) and huge restoration opportunity cost for rural

livelihoods (Chamshama & Vyamana, 2010). The value of liana cutting for restoration has been questioned for Africa because of insufficient logging degradation (Bongers, Schnitzer & Traore, 2002). Accordingly, liana removal did not affect tree size or density in Cameroon (Schnitzer, Parren & Bongers, 2004), nor tree species or growth in Uganda (Duncan & Chapman, 2003). Conversely, tree growth elsewhere in Uganda was slow in liana-dominated areas (Babaasa et al., 2004). Tree seedling growth also declined 19% when planted with lianas in Ghana (Toledo-Aceves & Swaine, 2007) and increased five-fold after liana cutting in Côte d'Ivoire (Schnitzer, Kuzee & Bongers, 2005). Liana cutting combined with liberation thinning also increased timber tree growth in Côte d'Ivoire (Parren & Doumbia, 2005), Malaysia (Putz, Lee & Goh, 1984) and Nigeria (Lowe & Walker, 1977).

While liana cutting may encourage tree growth, it may harm ecosystem functioning. Lianas contribute up to 44% of biodiversity and ~25% of stem density in tropical forests (Schnitzer & Bongers, 2002) and are important for structure (Gentry, 1991) and animals (Emmons & Gentry, 1983; Arroyo- Rodríguez et al., 2015). Cutting large lianas also damages regenerating trees (Campanello et al., 2007). Importantly for ecosystem functioning, liana cutting does not negatively affect subsequent liana regrowth, species composition or tree:liana ratio (Parren & Bongers, 2005; Parren & Doumbia, 2005; Campanello et al., 2012). However, few liana cutting studies have presented data for small trees (Gerwing, 2001; Pérez-Salicrup, 2001; Duncan & Chapman, 2003; Schnitzer et al., 2004; Wright et al., 2015), thus overlooking recruitment (and hence succession) and compromising ecosystem function through removal of large lianas.

Limited evidence suggests that tree growth following liana cutting may be robust to periodic wildfires (Peña-Claros et al., 2008). This is an important consideration because fire risk increases following heavy tropical forest degradation (Chazdon, 2003; Blate et al., 2005) and

may trigger conversion to scrub or savanna (Cochrane et al., 1999). Forest fires are 94% unplanned (FAO, 2010) and human-induced increases have reduced global tree basal area (Lehmann et al., 2014), releasing carbon equivalent to 41% of global fossil fuels (Cochrane, 2003). Wildfires burned >85% of sub-Saharan Africa between 1996-2009 (Krawchuk & Moritz, 2014) including >37Mha of forest (FAO, 2010).

While prescribed fire can maintain forest by removing deadwood and thicket, evidence from Bolivia suggests that fire is inappropriate for managing lianas because it stimulates rapid regrowth (Gerwing, 2001), especially for small lianas (Pinard, Putz & Licona, 1999). Furthermore, the biggest impact of wildfires is on sapling trees, causing >50% annual mortality, increasing with fire intensity and frequency (Balch et al., 2011). Therefore prevention of wildfires is often deemed essential for tropical forest restoration (Holl, 2002). However, wildfires have affected most terrestrial ecosystems throughout their history (Marlon et al., 2008) including many tropical forests (Chazdon, 2003). For example, the East African Coastal Forests have survived conversion to woodland for >150,000 years of low frequency fires (Clarke & Karoma, 2000). Hence restoration strategies are required that do not assume complete fire exclusion. However fire-vegetation dynamics remain poorly known, prompting calls for more explicit inclusion in conservation research and planning (Krawchuk et al., 2009).

This study employs liana cutting in a before-after-control-impact design to determine its effectiveness for regenerating sapling trees in an East African forest. The study is small scale and designed as a precursor for later work, but provides a rare palaeotropical trial that is unique in that we test (1) the combined influence of liana cutting on growth, recruitment, mortality, biomass and species for sapling trees, and (2) the robustness of the method by incorporating covariance with pervasive low frequency wildfires. The results are combined

with previous studies to make a first quantitative review of liana influence on tropical forest tree growth, and to discuss practicalities for liana cutting as a conservation tool.

Material and Methods

Study site

The study was conducted in Magombera Forest, southern Tanzania (Fig. 1; 11km^2; elevation 270m; annual rainfall 1514mm; wet season March-May; sandy-loam pH 4.7; C:N 8.6). The habitat was semi-deciduous Zanzibar Inhumbane forest with an understorey comprising small herbs, vines, sparse evergreen shrubs and lianas predominant in disturbed areas. Magombera Forest has high biodiversity value, including a remarkable proportion of threatened trees and a unique plant community comprising both lowland and montane species typical of the Eastern Arc Mountains and Coastal Forests of East Africa (Rodgers, Homewood & Hall, 1980; Marshall, 2008). The area supports several regionally endemic species including the Udzungwa red colobus monkey (*Procolobus gordonorum*) and Magombera chameleon (*Kinyongia magomberae*). Magombera Forest had no legal protection at the time of study, but with interim management by a conservation collaboration, which ensured limited disturbance to research sites.

Magombera Forest was chosen for its restoration potential following timber-felling in the 1970s/80s, and widespread pole-sized tree removal for local domestic use and sale. The area comprised ~20% "secondary forest" (≥90% canopy loss with mostly stunted/damaged trees and isolated tall trees) and ~80% "degraded primary forest" (<90% canopy loss with a mostly heavily degraded understorey; Fig. 1). Most primary and secondary forest comprised a high density of understorey lianas, particularly *Uncaria africana* G.Don, forming thickets fastened by hooked spines (Fig. 2). Across the region, many of these thickets had persisted for ≥30 years, similar to liana forest elsewhere in East Africa (Chapman & Chapman, 1997). Tanzanian forest habitats were mostly not actively managed at the time of study. However in Magombera Forest, managers and villagers maintained fire-breaks and extinguished some wildfires, reducing the extent of burning by ~50%. Wildfires were typical of lowland forests

in the region, comprising creeping low intensity ground fires spreading from neighbouring agriculture and woodland management.

Plots

In July 2007 (year 1) we established eighteen 5m×5m plots in areas with lianas touching or obstructing all "sapling" tree stems 1-4.9cm diameter at breast height (130cm; dbh). Plots were placed at 100m intervals along a transect to ease relocation, randomly offsetting 100m north or south to avoid disturbance. We did not randomise across the forest as dense thickets would have precluded relocation of plots and required extensive cutting for access. Instead the transect location was selected for its representation of the Magombera Forest tree species community (Marshall, 2008). One randomised plot location had few lianas and hence was repositioned. The plot size and number were chosen to allow rapid survey while giving sufficient sample size to assess growth following a previous East African study (Duncan & Chapman, 2003). Among the 18 plots we managed ten alternate plots by cutting lianas. We used secateurs to cut liana stems or branches (mostly <1cm dbh) that either touched or obstructed "seedling" (<1cm dbh) or sapling trees, leaving cut vegetation in situ. Cuts were made at ground level and around 1.5m. Annually in February and July, any new liana growth was cut again. The sample size was uneven (ten managed by liana cutting; eight unmanaged) because two intended plot locations had few lianas anywhere nearby.

In year 1 we measured, marked and identified all sapling tree stems, and painted the point of measurement (re-labelling annually if deteriorated). To ease relocation in subsequent years, we dug L-shaped ditches at plot corners (15cm deep × 30cm long) and marked nearby trees with paint and tags. In July 2012 (year 5) we re-measured all surviving year 1 stems, plus any new "recruited" stems. Height was measured using a tape measure (stems 1.3-2.5m), wooden pole (2.5-7m), or Bushnell Yardage Pro rangefinder (≥7m). We measured dbh using a

girthing tape, adjusting the point of measurement for deformed trees (Kuebler, 2003). Specimens were collected for identification at the Royal Botanic Gardens, Kew. To determine potential for future restoration of the mature tree community, we also made basic quantitative comparison (% species overlap) of the sapling species composition to "mature" stems ≥10cm dbh along the same transect (0.875ha; 5m×1,750m), and to a species inventory of mature stems ≥10cm dbh for the whole forest (Marshall, 2008 and unpublished data).

Analysis

Above-ground biomass was calculated using Equation 1 (Chave et al., 2005) as used previously for sapling stems (Holl & Zahawi, 2014; Schnitzer et al., 2014). We preferred this equation over alternatives excluding height because stature varies with climate (Marshall et al., 2012). We also preferred this method over less-tested alternatives following previous success in Africa (Vieilledent et al., 2012) and following trials with our own data that increased biomass estimates by 22-55% (Ngomanda et al., 2014; Mugasha et al., 2016). Wood specific gravity (WSG) was determined using mean catalogued values for each species (Zanne et al., 2009), or genus, family or Magombera Forest average for species lacking WSG data. In addition to biomass, we also present tree growth rate as $dbh.stem^{-1}.yr^{-1}$ for consistency with previous studies.

$$\text{Above-ground biomass (kg)} = 0.0509 \times \rho D^2 H$$

Equation 1: Biomass calculation for moist forest trees using WSG (ρ; $g.cm^{-3}$), dbh (D; cm) and height (H; m) (Chave et al., 2005).

We performed statistical analyses using R 3.0.2 (http://cran.r-project.org). To determine the impact of liana cutting, we used one-way Analysis of Variance (ANOVA) models to compare five regeneration indicators between managed and unmanaged plots: (a) new sapling stem

biomass (recruitment), (b) proportional biomass increase of year 1 stems (growth), (c) proportion of year 1 biomass lost through deaths (mortality), (d) proportional change in total biomass (net biomass change; recruitment plus growth minus mortality) and (e) proportional species richness change (community change). We did not manage fire, but included wildfire frequency per plot in ANOVA models, including its statistical interaction with liana cutting (ANCOVA). To ensure parsimony, wildfire frequency (and in one instance liana cutting) was dropped from models where it did not improve the effect size according to likelihood ratio tests (Crawley, 2005). For all modelling we employed transformations to remove skew, including twice natural log for recruitment and growth, and square root for proportional net biomass change (respectively adding one or two to address negative values). Residual diagnostics were used to verify normality.

For regeneration indicators dependent on year 1 biomass (all except recruitment), we preferred proportional over absolute measures of change to reduce bias from variation in year 1 stem size and density. For these models using proportions, we excluded either one or two plots with zero values in year 1 (i.e. infinite proportional change). To address this removal of plots we also calculated means and 95% bootstrapped confidence intervals (10,000 iterations; 95CI) for absolute measurements, for comparison to proportional changes.

To avoid Type I errors we used False Discovery Rate correction of alpha values (α_{FDR}; Benjamini & Hochberg, 1995). To determine sampling adequacy for significant indicators we used power analysis to calculate the proportion of discernible change, under our sampling level and increased sampling to fifteen or twenty plots per treatment (80% power; Crawley, 2005).

Results

Biomass

Net biomass increase among stems 1-4.9cm dbh was higher in plots managed by liana cutting than unmanaged plots (total 129.9 versus 9.6kg respectively; Fig. 3; Table 1). The increase in biomass comprising recruitment of new stems was higher in managed plots (total 31.6kg; 0.42stems.m^{-2}, 95CI 0.16-0.75) than unmanaged plots (total 5.7kg; 0.10stems.m^{-2}, 0.03-0.18) (Table 1). In year 1 we measured 107 stems, with no significant difference between managed and unmanaged plots prior to management (W=59; p=0.098; managed: 0.4-5.6stems.10m^{-2}; unmanaged: 0.0-3.2stems.10m^{-2}). Stem numbers increased with recruitment to 171 in year 5, with significantly more stems in managed plots (W=65.5; p=0.026; managed: 0.8-17.2stems.10m^{-2}; unmanaged 0.0-4.0stems.10m^{-2}).

The net biomass increase also comprised growth of year 1 stems, again higher in managed plots (total 116.7kg; 3.4kg.stem^{-1}, 95CI 1.8-5.5; 17.7mm dbh.stem^{-1}, 95CI 12.3-23.4) than unmanaged plots (total 21.3kg; 1.6kg.stem^{-1}, 0.1-4.4; 7.9mm dbh.stem^{-1}, 0.5-18.4) (Table 1). Biomass loss from mortality was no different between managed plots (total 18.5kg; 0.17stems.m^{-2}, 95CI 0.10-0.24) and unmanaged plots (total 17.4kg; 0.12stems.m^{-2}, 0.07-0.17) (Table 1).

At 80% power our sample size was sufficient for detecting ≥152% change in recruitment, ≥267% proportion growth, and ≥35% proportion net biomass. Increasing the sample size 15-20 plots per treatment would have increased the expected detection to ≥102-87%, ≥180-152% and ≥24-20% respectively.

Species

Four species were recruited to plots that were absent in year 1, but seven species were lost, resulting in a net loss (2007: 29 species; 2012: 26 species). The proportional loss of species was not significantly different between managed and unmanaged plots (Table 1). Community composition was similar between treatments, with 76% of stems from species found in both managed and unmanaged plots. However, managed and unmanaged plots shared only five of their top ten species in year 1 (four in year 5; Table S1). This difference did not account for the proportional net biomass increase in managed plots, which persisted using only stems from species found in both treatments ($F=6.79$; $r^2=0.31$; $p=0.020$). Precision for assessing relative species abundance within and between plots was limited, as seen from frequent zero values and complete overlap in 95CIs (Table S1).

Out of 86 tree species known to reach 10cm dbh across the forest, we identified 38 sapling species in restoration plots, compared to 29 mature tree species along the transect. Only 48% of mature tree species were found among saplings. The top ten sapling species included only one of the top ten mature trees and only three of the top ten from the whole forest (Table S1; two and three year 5 species respectively). Nearly all stems (>99%) were species typical of the Eastern Arc Mountains and Coastal Forests (EAMCF) of eastern Africa, with drier woodland species comprising <1% of stems. Mature trees were dominated by canopy species, whereas restoration plots were dominated by understorey/midstrata species (Table S1).

Wildfire

Pervasive wildfire frequency was 1.61plot^{-1} (range 1.0-3.0plot^{-1}; 0.32yr^{-1}, 0.20-0.60) and equivalent between managed (1.60plot^{-1}, 95CI 1.00-2.10) and unmanaged plots (1.63plot^{-1}, 0.63-2.50). Wildfires killed ~55 year 1 stems (91.7% of deaths), but wildfire frequency did not directly influence growth, recruitment, mortality or net biomass change ($r^2 \leq 0.08$; $p \geq 0.27$)

and hence was not confidently retained in models (Table 1). Interaction was seen between wildfire frequency and liana cutting management for recruitment (greater cutting influence at high wildfire frequency; Fig. 4a) but with no significant improvement on liana cutting alone (Table 1). Increasing wildfire frequency explained 29% of variation in proportional species loss, enhancing a univariate liana cutting model but not significant at the 95% level (Table 1; Fig. 4b). Plots with zero to one wildfire showed increased proportional community change (0.23, 95CI -0.27-0.73), while those with two to three wildfires decreased (-0.3, 95CI -0.52 to -0.13).

Discussion

The results suggest that liana cutting is a promising restoration strategy, expanding its potential beyond the geographic bias of previous studies. We here compare our tree regeneration rates to previous liana cutting studies, and to studies comparing liana presence/absence through natural growth or planting.

Biomass

Our observed growth rate increase for liana cutting compared to unmanaged plots (dbh: 119%; biomass: 109%) is greater than most previous studies comparing tree dbh, circumference or height with/without lianas (mean 66%, 95CI 39-99, n=12 [including this study: 69%, 43-100, n=20]), but more typical of studies comparing biomass or basal area (80%, 35-150, n=13 [83%, 39-147, n=14]) (Table 2). Previous studies have been biased towards low elevation (median 200m; mean 215m), with the only high elevation study showing no significant influence of liana and shrub removal on tree growth (Duncan & Chapman, 2003). Our 350% increase in recruitment with liana cutting is higher than the only two comparable studies of stems ≤5cm dbh, both in Panama, which increased by 46% (stems ≥1.3m tall; Schnitzer & Carson, 2010) and 250% (stems <1cm dbh; Graul & Putz, 2004), giving a mean of 215% across studies. Two further studies showed (a) comparable stem size and density between liana cut and control plots in Cameroon (Schnitzer et al., 2004) and (b) increased sapling density with liana cutting and liberation thinning after 19 years (but not 42 years) in Malaysia (Addo-Fordjour, Rahmad & Asyraf, 2013), but did not present pre-treatment measurements for calculation of % increases.

The impact of liana absence on tree stem growth in Africa (dbh/circ/h: +28%, -18-77, n=5; ba/bio: +122%, 21-288, n=5), Asia (dbh/circ/h: no data; ba/bio: +41%, 9-73, n=3) and the

palaeotropics combined (dbh/circ/h: +28%, -18-77, n=5; ba/bio: +92%, 26-197, n=8) did not differ from the more extensive neotropical studies (dbh/circ/h: +83%, 54-119, n=15; ba/bio: +71%, 37-112, n=6). This provides a first quantitative indication that lianas (and presumably liana removal) have approximately equivalent pantropical impact on biomass.

Our lack of liana cutting influence on mortality is inconsistent with neotropical studies showing greater mortality with lianas present (Ingwell et al., 2010; Schnitzer & Carson, 2010; van der Heijden et al., 2015). However, wildfires were not present in these studies, and may have masked a positive impact of liana cutting on survival. Accordingly, our 56-64% stem mortality (57-68% biomass loss) is within the range of other tropical forests impacted by wildfires (Woods, 1989: >80%, Malaysia; Pinard et al., 1999: 74%, Bolivia; Kinnaird & O'Brien, 2008: 25-70%, Sumatra). However, without controlling for fire the expected positive influence of liana cutting on survival remains uncertain. Previous African studies of tree mortality with/without lianas have found only ambiguous (Schnitzer et al., 2005; Toledo-Aceves & Swaine, 2007) or zero relationships (Toledo-Aceves & Swaine, 2008). Liana cutting also did not influence seedling survival for two tree species in Bolivia (Pérez-Salicrup, 2001).

Bringing together growth, recruitment and mortality, our observed 765% increase in relative net biomass gain from 0.32kg.kg^{-1} in managed plots to 2.77kg.kg^{-1} in unmanaged plots is of similar magnitude to two previous estimates from Panama of 370% (stems >1.3m height; unmanaged 0.23kg.kg^{-1}; managed 1.08kg.kg^{-1}; Schnitzer et al., 2014) and 646% (stems ≥10cm dbh; unmanaged 0.017kg.kg^{-1}; managed 0.11kg.kg^{-1}; van der Heijden et al., 2015). A similar magnitude of increase (750%) was seen for basal area in Brazil (stems >5cm dbh; unmanaged 64cm^2.m^{-2}; managed 544cm^2.m^{-2}; Gerwing, 2001). The mean 633% increase across these studies suggests increasing pantropical liana growth will have increasing impact

on biomass loss beyond existing estimates of 9-76% (Schnitzer et al., 2014; van der Heijden et al., 2015). Liana influence can vary with initial tree biomass (Schnitzer et al., 2014), hence we have made these comparisons using biomass (or basal area) increase per pre-treatment stem size, i.e. $kg.kg^{-1}$ and $cm^2.m^{-2}$, to control for initial differences in and plot and stem size between studies.

The reason for our generally high regeneration is uncertain. Variation within previous studies has been ascribed to shade and liana density (Ingwell et al., 2010; Schnitzer & Carson, 2010). Variation across studies may also have arisen from inconsistencies in tree size, measurement units and timespan. Across studies, the growth increase without lianas was unrelated to tree size and most variable for small stems (<5cm dbh: 135% [95CI: 47-250], n=7; >5cm dbh: 75% [51-104], n=20; unspecified size: 75% [36-124], n=5). Regarding units, dbh narrowly predominates over biomass in the literature, presumably because of its relevance to forestry and uncertainty regarding biomass calculation. Indeed, region-specific biomass estimation methods are lacking across the tropics, particularly for saplings. Regarding timespan, the impact of liana cutting in isolation is unknown beyond 10 years and 71% of all restoration studies have spanned ≤15 years (Wortley et al., 2013).

Importantly, wildfires in Magombera Forest have not obscured the positive influence of liana cutting on biomass. Furthermore, the observed positive interaction between liana cutting and wildfire frequency provides weak evidence that liana cutting is more effective for encouraging recruitment in the presence of fire. However, our observed lack of biomass gain in the absence of liana cutting does not suggest a positive "prescribed burn" influence.

Species

Our difference in species between sapling and mature stems suggests typical negative density dependent growth (Wright, 2002). However, our high sapling species richness shows good restoration potential. Our data are inconclusive regarding liana cutting impacts on community restoration, perhaps a result of limited scale. In Panama, tree species richness increased 65% following liana cutting (Schnitzer & Carson, 2010) and tree-liana competition was similar between species (Álvarez-Cansino et al., 2015). Conversely, liana cutting in Brazil caused both increases and decreases across species (Gerwing, 2001). Community change following liana cutting remains unverified for Africa, however pioneer trees recruited faster than mid-successional species following liana/shrub removal in Uganda (Duncan & Chapman, 2003). Moreover, tropical forest recovery often requires establishment of single species (Chazdon, 2003) or several "framework species" (Goosem & Tucker, 1995) before soil fertility, seed dispersal and shade are sufficient to stimulate succession. Hence longer-term monitoring is required.

Similar to mortality, our lack of liana cutting influence on species composition may have been confounded by wildfires, which can favour pioneers (Cochrane & Schulze, 1999) or drought-resistant species with thick bark (Uhl & Kauffman, 1990). However our observed prevalence of forest species gives no evidence for wildfire-driven conversion to woodland. Yet while our regression was weak, wildfires caused ≥51% stem mortality and net species loss where they exceeded one per five years. As saplings grow their resilience to fire improves, with increasing evidence for a bark resistance threshold (Hoffman et al., 2012).

Practicalities

An important practical consideration is cost. Using a cutting rate of sixteen person-hours ha^{-1} (Grauel & Putz, 2004) it would take four people eighteen months to manage the $11km^2$ Magombera Forest. However, given our flat topography this could be achievable within

twelve months (one person-day.ha^{-1}). This would cost ~US$6,000yr^{-1} for labour and equipment (US$5.45ha^{-1}), compared to US$1-4ha^{-1} for West Africa (Bongers et al., 2002) and mean $11ha^{-1} for Bolivia and Brazil (range $1-16ha^{-1}; Vidal et al., 1997; Pérez-Salicrup et al., 2001; Dauber, Fredericksen & Peña, 2005). The equivalent cost for alternative tree-planting in neighbouring Uganda was more than 44 times more expensive (US$1,200ha^{-1}.5yr^{-1}; Omeja et al., 2009).

Future monitoring of saplings would benefit from increased sampling. Plots used previously for stems <5cm dbh have varied in size and number per treatment (Duncan & Chapman, 2003: 25m^2, n=19; Schnitzer et al., 2005: 108m^2, n=10; Gerwing, 2001: 400m^2, n=6). Our own sampling enabled statistically verifiable conclusions for biomass. However, larger plots would reduce zero values and improve precision. Increased samples would further improve precision, with our power analysis suggesting twenty plots per treatment would have nearly doubled our ability to detect biomass change. While our plots were too small to estimate an optimal size for measuring biodiversity, previous work suggests 300-400 stems per plot (Gimaret-Carpentier et al., 1998). At our observed sapling density, this would need plots of ~790-1,053m^2, similar to stems 1-9.9cm dbh in Amazonia (0.1ha; Magnusson et al., 2005).

Thirdly, lianas (and cutting) may not influence regeneration where light or liana abundance is low, e.g. shaded forest or small canopy gaps (Toledo-Aceves & Swaine, 2008; van der Heijden & Phillips, 2009; Ingwell et al., 2010). Liana removal may even be damaging to healthy forests, e.g. maintaining small canopy gaps can preserve biodiversity by supporting pioneers and lianas (Schnitzer & Carson, 2000). Hence liana cutting is best employed on a tree-by-tree basis (Schnitzer & Bongers, 2002) with focus on abundant species (Sfair et al., 2011) in large canopy gaps/thickets (Schnitzer & Carson, 2010) and heavily degraded understorey (this study). Cutting must also be temporary to allow liana recovery (Campanello

et al., 2012). Trees were bent by lianas in Magombera up to ~2cm dbh, and we estimate that six to seven years of cutting would allow 50% of recruited stems to reach this size.

Accurate assessment of liana cutting is also hindered because, for geographic completeness our review of previous work includes liana presence/absence through natural growth or planting. These studies may suffer from species bias in host tree preferences (Putz et al., 1984; Campanello et al., 2007) or choice of planted seedlings. Indeed, the increase in growth without lianas was higher among cutting studies (mean 90%; n=19) than the rest (57%; n=10), but not significant (95CI 53-139 and 23-108 respectively). A previous comparison of growth between liberated and naturally liana-free trees found ambiguous results for timber species in Bolivia (Villegas et al., 2009). Therefore more liana cutting studies are needed across stem sizes in natural forest, especially regarding recruitment and biodiversity.

Finally, restoration must form part of a holistic strategy. Effective restoration benefits from legal and stakeholder support, economic value, improvement in soil, hydrology and water quality, and understanding the interactions between ecosystems and socio-political systems (ITTO, 2002; SER, 2004). Arguably no tropical forest restoration study has addressed situations where all of these factors have been true. This includes our study, where there was limited legal protection, little direct income from the forest, and no soil or hydrology data. Moreover, the persistence of wildfires emphasises that burning practices in adjacent areas were not employed with landscape management in mind. Nevertheless, liana cutting has here proved effective for regenerating biomass even without full wildfire control.

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Tables

Table 1 Comparison of mean (and 95CI) regeneration indicators following management of 25m^2 plots using liana cutting versus unmanaged plots (2007-2012). Significant models of liana cutting influence on regeneration per plot are summarised with significant results in bold (α_{FDR}=0.03) indicating direction of influence (+/–). Pervasive wildfire frequency and interaction covariates are also shown where retained following model reduction (α_{FDR}=0.01), including the reduction in effect size when each variable was removed (δr^2). Models without covariates (i.e. liana cutting alone) did not explain reduced variance to those including wildfire and interaction terms (F≤2.69; p≥0.103).

Regeneration measure	Unmanaged	Managed (lianas cut)	Models [and covariates]
Recruitment: Biomass recruited (g.m^{-2})*[1]	**28 (6-59)**	**126 (53-211)**	**** (a) F=6.2, r^2=0.28, p=0.024** (b) F=4.3, r^2=0.37, p=0.024 [liana cutting$^{(+)}$: δr^2=0.37, p=0.72; wildfires$^{(+)}$: δr^2=0.09, p=0.061; interaction$^{(+)}$: δr^2=0.18, p=0.038]
Growth: Proportional *(and g.m^{-2})* biomass growth of liberated year 1 saplings*[1]	**0.46 (-0.05-1.33)** *142 (-5-404)*	**1.98 (0.86-3.15)** *467 (168-793)*	**F=6.3, r^2=0.28, p=0.023**
Mortality: Proportion *(and g.m^{-2})* of year 1 biomass lost through deaths	0.68 (0.43-0.91) *116 (49-187)*	0.57 (0.36-0.77) *74 (33-119)*	F=0.39, r^2=0.03, p=0.541
Net biomass increase:	**-0.10**	**3.43**	**F=13.1, r^2=0.46, p=0.0026**

Proportion *(and g.m^{-2})* **change in total biomass (recruitment + growth - death)**^{*2}	**(-0.79-0.83)** *48* *(-118-269)*	**(1.92-4.95)** *520* *(205-859)*	
Community change: Proportional *(and absolute)* change in species richness per plot	-0.33 (-0.67-0.17) *0.00* *(-0.75-0.88)*	-0.06 (-0.32-0.24) *-0.70* *(-1.70-0.20)*	*** F=3.1, r^2=0.22, p=0.080 [liana cutting$^{(-)}$: δr^2=-0.08, p=0.502; wildfires$^{(-)}$: δr^2=0.17, p=0.038]

*Transformed for modelling: [1]twice ln; [2]square root. **Models (a) and (b) explained equivalent variance (F=2.69; p=0.103) and hence (a) preferred for parsimony. However model (b) also presented to highlight interaction. ***Model using wildfire frequency alone (Fig. 4b) preferred for parsimony (equivalent variance explained: F=0.48; p=0.503).

Table 2 Mean tree stem growth with and without competition from lianas, from all known studies in tropical forests. Unless stated, data show annual increments per stem and liana absence was due to cutting. Alternative measurements of the same stems using different units are shown in parentheses. Ba=basal area, cm^2; bio=biomass, kg; circ=rate of circumference increase, mm/mm; dbh, dbh_{15}=diameter at 1.3m or 1.5m, mm; dbh_{gr}=species-independent ten year growth residual derived from dbh, mm; h=height in m; $RGR_{c,d,h,b}$=relative growth rate (circumference at breast height, diameter at base, height, or biomass); %=percent increase in growth rate with lianas absent; Size=size of stems in the study (dbh, cm, unless stated); Years=duration of the study.

Study	Country (elevation)	Lianas	No lianas	%	Size	Years
This study	Tanzania (270m)	1.6 dbh (0.33 bio)	3.5 dbh (0.69 bio)	119 (109)	1-4.9	5
Lowe & Walker (1977) [b,d,e]	Nigeria (143m)	19.1 ba	22.9 ba	20	10.5-36.2	6
Putz (1984) [a1,d,e]	Panama (85m[k])	635 ba	893 ba	41	30-50	10
Putz et al. (1984) site 1 [b,e]	Malaysia (124m[k])	15.4 ba	26.6 ba	73	≥10	5
Putz et al. (1984) site 2 [b,e]	Malaysia (47m[k])	23.9 ba*	26.0 ba*	9	≥10	4
Putz et al. (1984) site 3 [b,e]	Malaysia (200m[k])	28.2 ba	40.1 ba	42	≥10	4
Stanley (1997) [a1,f]	Brazil (30m[k])	2.1 dbh* (0.17 h)	2.4 dbh* (0.23 h)	14 (35)	≥2.0 h	9

Pérez-Salicrup & Barker (2000) [e]	Bolivia (200m)	0.2 circ	0.4 circ	100	10-20	1
Gerwing (2001)	Brazil (50m[k])	1.3 dbh	3.0 dbh	131	>5	2
Gerwing (2001)	Brazil (50m[k])	0.8 dbh	2.5 dbh	213	2-5	2
Pérez-Salicrup (2001) [e]	Bolivia (200m)	0.18 RGR_h	0.28 RGR_h	54	Seedlings	1.5
Duncan & Chapman (2003) [c]	Uganda (1500)	0.2 h*	0.1 h*	-50	<1.6 h	6
Grauel & Putz (2004) [e]	Panama (50m[k])	1.1 dbh*	1.9 dbh*	73	4-15	5
Grauel & Putz (2004) [e]	Panama (50m)	2.8 dbh	6.0 dbh	114	≥15	5
Dauber et al. (2005) site 1 [a1]	Bolivia (500m[k])	2.2 dbh	2.6 dbh	18	≥10	3-8
Dauber et al. (2005) site 2 [a1]	Bolivia (250m[k])	4.1 dbh	7.0 dbh	71	≥10	2-3
Dauber et al. (2005) site 3 [a1]	Bolivia (300m[k])	2.6 dbh	4.1 dbh	58	≥10	7
Dauber et al. (2005) site 4 [a1]	Bolivia (250m[k])	3.2 dbh	3.6 dbh	13	≥10	1-4
Schnitzer et al. (2005) [a2,c,e]	Cote d'Ivoire (30m[j])	0.22 bio	1.18 bio	436	Seedlings	2

Parren & Doumbia (2005) [e,g]	Cote d'Ivoire (125m[k])	6.0 dbh	9.0 dbh	50	5-50	3
Campanello et al. (2007)	Argentina (200m[k])	3.6 RGR_c	6.4 RGR_c	78	≥10	1.75
Peña-Claros et al. (2008)	Bolivia (300m[k])	0.24 dbh	0.52 dbh	116	≥10	4
Toledo-Aceves & Swaine (2007) [a2,c,e]	Ghana (210m)	0.062 RGR_d (0.064 RGR_h) (0.119 RGR_b*)	0.069 RGR_d (0.076 RGR_h) (0.144 RGR_b*)	11 (19) (21)	Seedlings	1
Toledo-Aceves & Swaine (2008) [a2,e,h]	Ghana (210m)	0.037 RGR_d* (0.040 RGR_h) (0.014 bio*)	0.041 RGR_d* (0.044 RGR_h) (0.017 bio*)	10 (9) (22)	Seedlings	1-1.25
Van der Heijden & Phillips (2009) [a1,d,i]	Peru (260m)	2.8 dbh (2.92 bio Mg ha^{-1})	4.6 dbh (3.30 bio Mg ha^{-1})	63 (13)	≥10	3
Villegas et al. (2009) [e]	Bolivia (450m)	2.0 dbh	3.0 dbh	50	10-50	4
Ingwell et al. (2010) [a1]	Panama (145m)	Sun 0.004 dbh_{gr} Shade -0.02 dbh_{gr}	0.022 dbh_{gr} -0.04 dbh_{gr} [l]	450 100	4-193	10
Schnitzer & Carson (2010) [j]	Panama (30m[k])	0.09 dbh (1.12 bio m^{-2})	0.14 dbh (2.23 bio m^{-2})	56 (99)	>1.3 h	8
Álvarez-Cansino et al. (2015) [e]	Panama (30m[k])	1.98 ba	5.18 ba	162	10-20	1
Van der Heijden	Panama	3.79 bio	5.50 bio	45	≥10	3

et al. (2015)	(30m[k])	Mg ha^{-1}	Mg ha^{-1}			
Wright et al. (2015)	Panama (30m[k])	2.08 RGR_b	2.69 RGR_b	29	≥0.5	3
Wright et al. (2015) [e]	Panama (30m[k])	-0.115 RGR_b	0.006 RGR_b	105	Seedlings	3

[a]Lianas not removed, instead compared [a1]trees with/without lianas, or [a2]trees planted with/without planted lianas. [b]Liana-cutting combined with other silvicultural treatments. [c]Plantation. [d]Increments estimated from empirical models. [e]Mean of focal species, mostly commercial except for Álvarez-Cansino et al. (2015) and Wright et al. (2015). [f]Forest trees regenerating in fire-managed pasture. [g]Data cited from an unpublished conference presentation; size class inferred. [h]Tree growth benefitted from liana absence in large gaps (mean RGR: +14%; bio: +28%) but not small gaps/understorey (mean RGR: -1, +5; bio: -12, -12); Only RGR_h was significant, for just one tree species in large gaps. [i]Mean of low, medium and high light levels (18, 36 and 89% growth increase without lianas). [j]Biomass data from Schnitzer et al. (2014). [k]Elevation estimated from online map. [l]Contrary to other studies, however the highest liana density had a negative impact. *not significant.

Figure Legends

Fig. 1 Map showing the location of forest within the Eastern Arc Mountains (top left), Kilombero valley including digital elevation model (top right, including greyscale digital elevation model 270-2100m), and the Magombera Conservation Area showing the location of plots (red rectangle) and Kilombero Sugar Company land (dashed black line) (Kilombero District, Morogoro Region; bottom map). Dark green = degraded primary forest (<90% canopy loss; heavily degraded understorey/midstrata), mid green = secondary forest (canopy ≥90% canopy loss), pale green = woodland, pale yellow = grassland, grey = agriculture/human settlement (bottom). Map by Nicolas Deere and Freddie Sutton, based on ground-truthing (bottom) and data from Marshall et al. (2010; top right) and Platts et al. (2011; top left).

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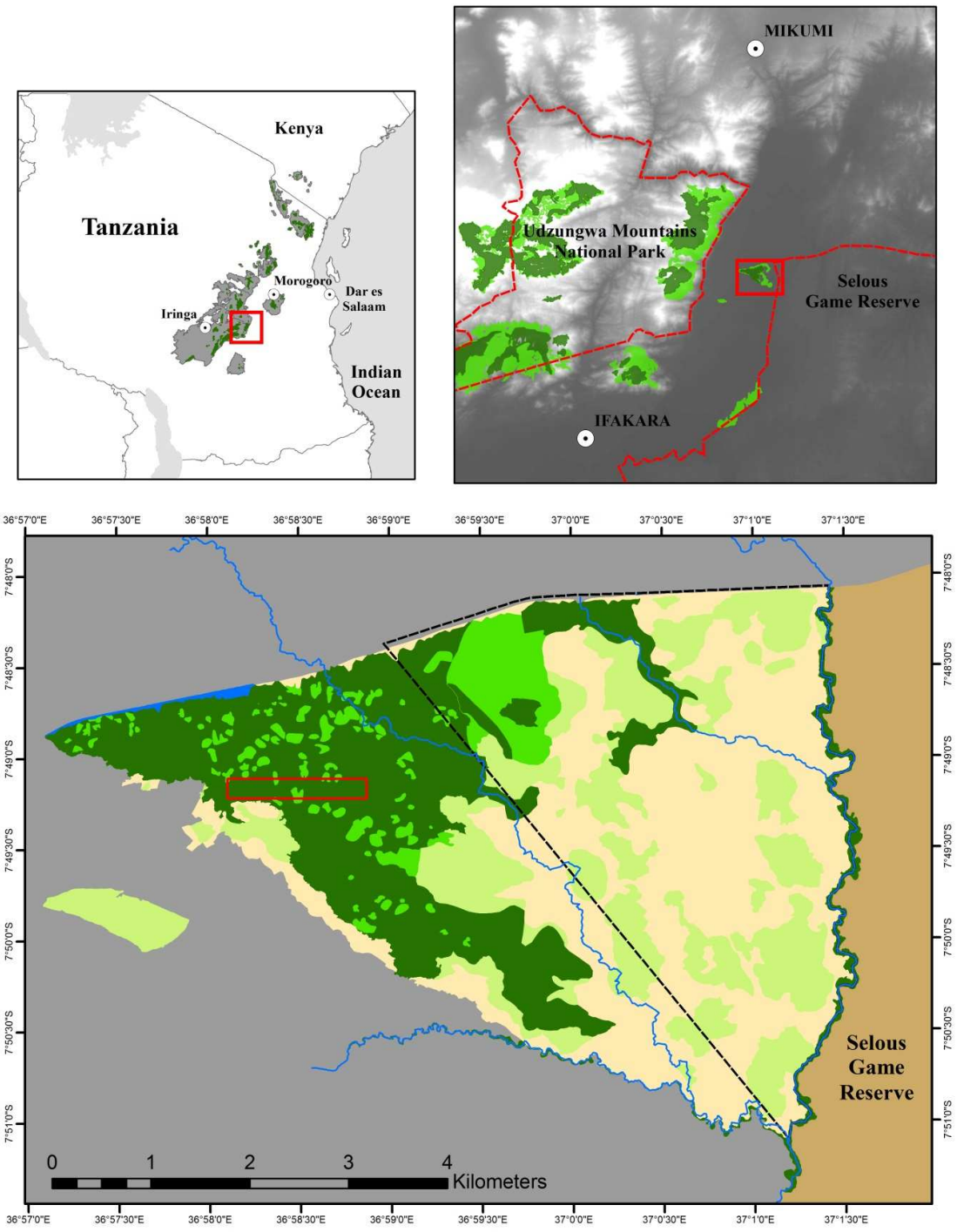
Fig. 4 Potential confounding influences on the effectiveness of liana cutting for sapling regeneration per $25m^2$ plot: (a) ANCOVA interaction between wildfire frequency and liana cutting for the prediction of biomass recruitment in liana managed (solid line, closed points; p=0.06) and unmanaged plots (dashed line, open points; p=0.72) (δr^2=0.09; Table 1), and (b) proportional change in species richness decreasing with wildfire frequency (offset by ≤0.05 to reveal overlapping points; regression: r^2=0.29, p=0.029, α_{FDR}=0.01).

1 Figures



2

3 Fig. 1

4

Fig. 2

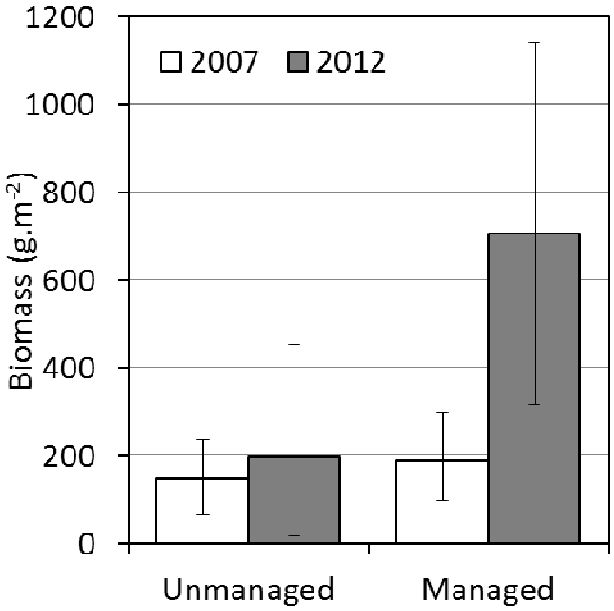
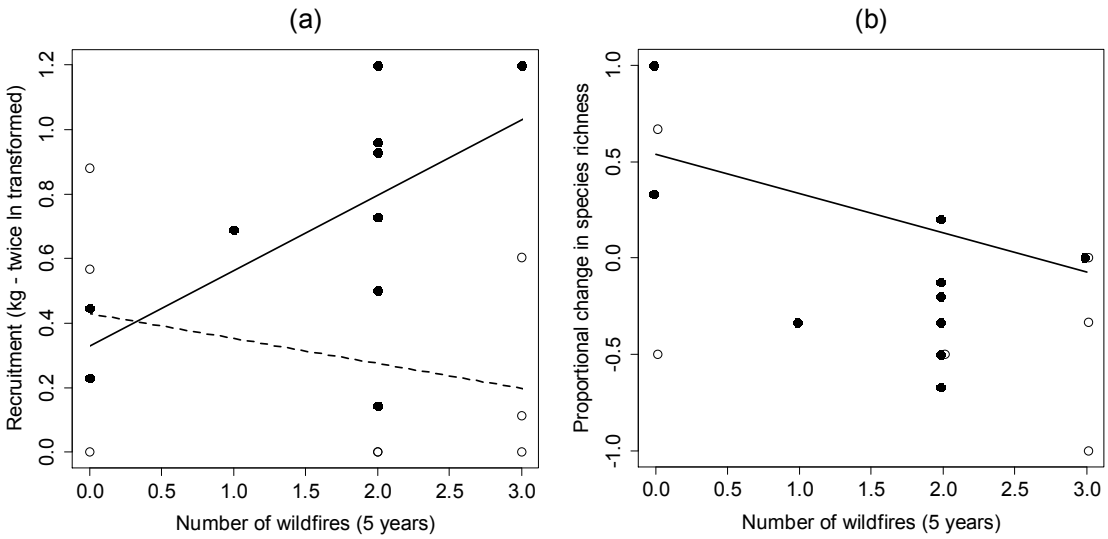

1200
1000
800
600
400
200
0
Biomass (g.m-2)
2007
2012
Unmanaged
Managed

Fig. 3

1


(a)
Recruitment (kg - twice ln transformed)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Number of wildfires (5 years)
(b)
Proportional change in species richness
-1.0
-0.5
0.0
0.5
1.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Number of wildfires (5 years)

2 Fig. 4

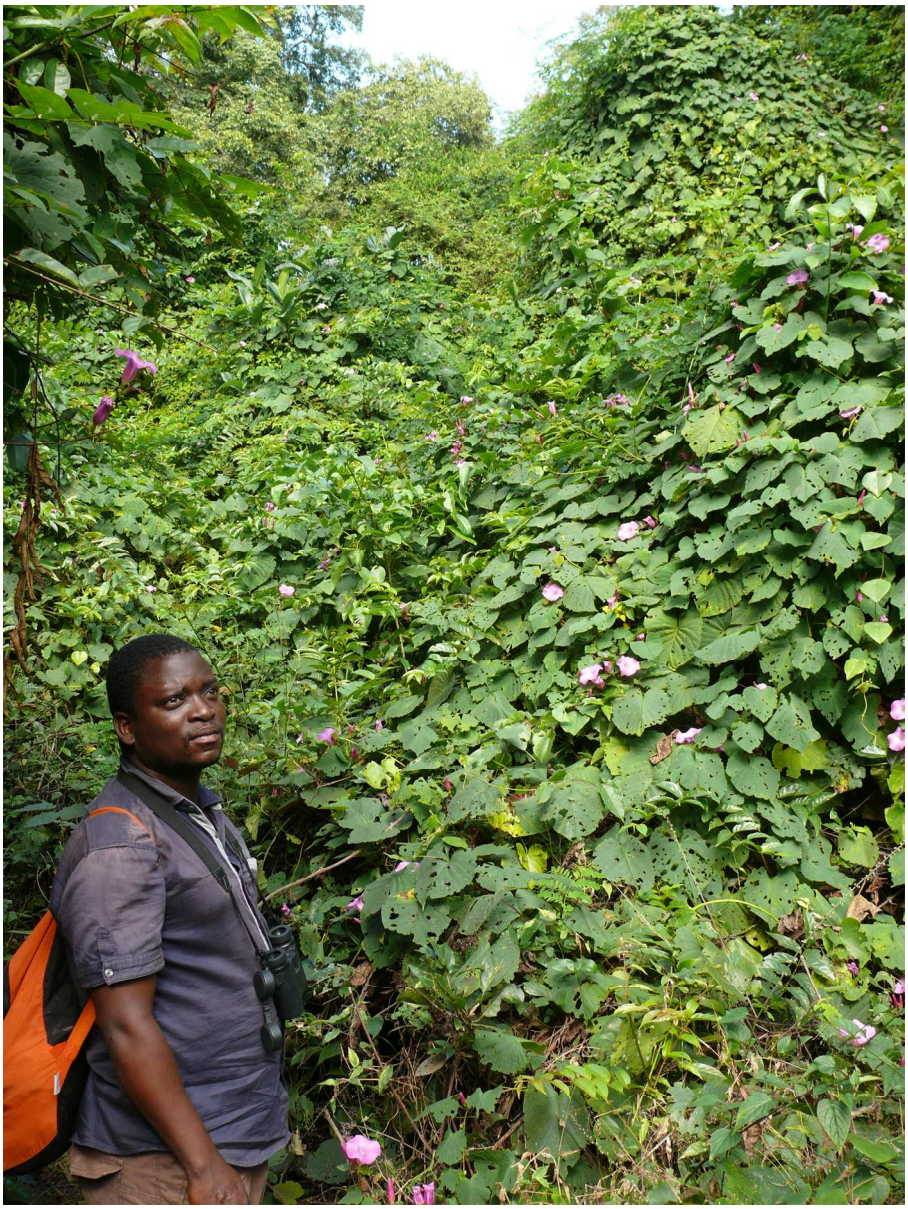
3

Supporting Information

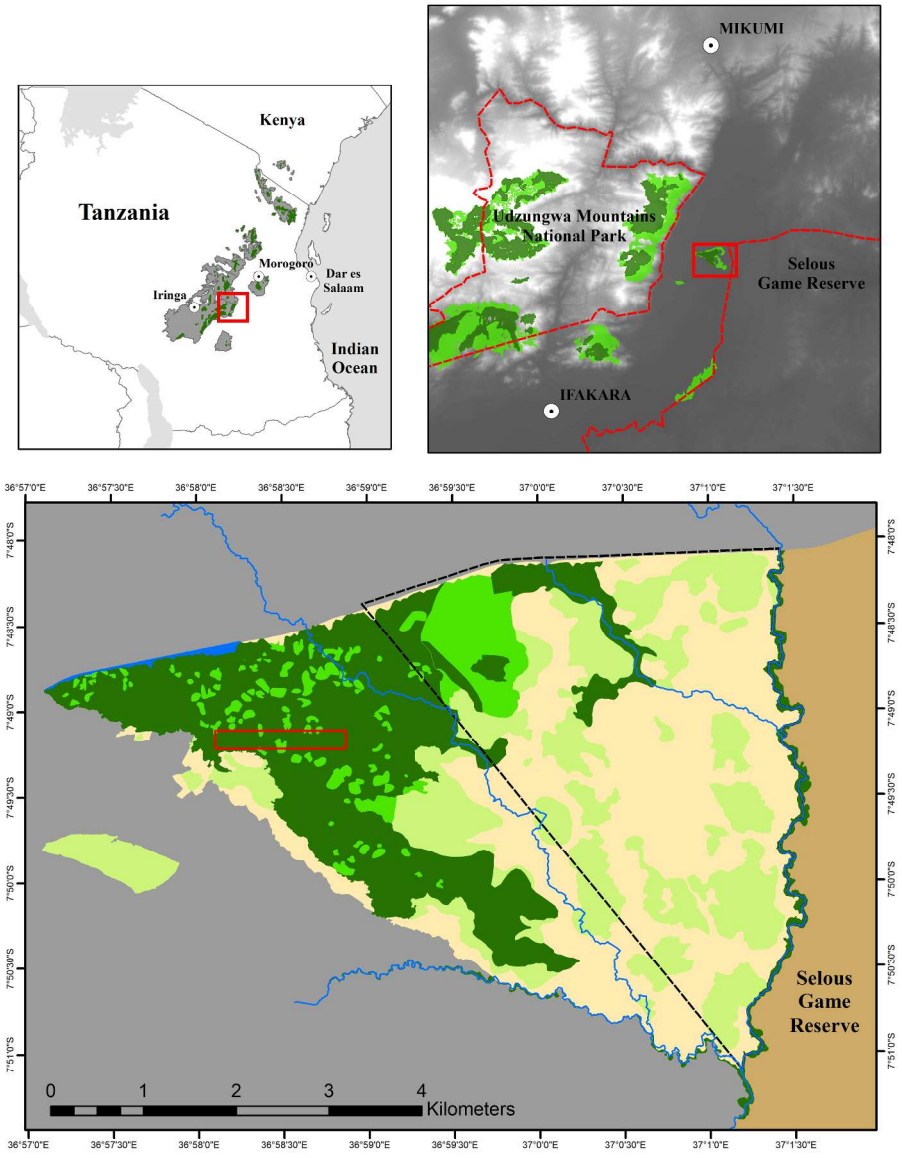
Table S1 Mean percentage of stems comprising the ten most common tree species (and 95CI) per unmanaged and liana-managed 5m×5m restoration plot after five years (2007-2012), compared to trees ≥10cm dbh in nearby mature forest and in the whole forest.

Unmanaged (n=32 stems, eight plots)		Managed (n=139 stems, ten plots)		Nearby mature	Whole forest
Rothmannia macrosiphon (K.Schum. ex Engl.) Bridson	37.5 (0.0-93.8)	*Mallotus oppositifolius* Müll.Arg.	30.9 (0.0-89.9)	*Lettowianthus stellatus* Diels*	*Isoberlinia scheffleri* (Harms) Greenway*
Calycosiphonia spathicalyx (K.Schum.) Robbr.	18.8 (0.0-56.3)	*Leptactina platyphylla* (Hiern) Wernham	8.6 (0.0-25.9)	*Tapura fischeri* Engl.	*Ochna holstii* Engl.*
Tabernaemontana pachysiphon Stapf	12.5 (0.0-37.5)	*Rawsonia lucida* Harv. & Sond.	6.5 (0.0-19.4)	*Erythrophleum suaveolens* (Guill. & Perr.) Brenan*	*Lettowianthus stellatus* Diels*
Markhamia lutea K.Schum.*	6.3 (0.0-18.8)	*Aoranthe penduliflora* (K.Schum.) Somers	5.8 (0.0-14.4)	*Xylopia longipetala* De Wild. & T.Durand*	*Erythrophleum suaveolens* (Guill. & Perr.) Brenan*
Tapura fischeri Engl.	6.3 (0.0-12.5)	*Tapura fischeri* Engl.	5.8 (0.0-13.7)	*Pseudobersama mossambicensis* (Sim) Verdc.*	*Calycosiphonia spathicalyx* (K.Schum.) Robbr.
Antiaris toxicaria Lesch.*	3.1 (0.0-9.4)	*Rothmannia macrosiphon* (K.Schum. ex Engl.) Bridson	5.0 (0.0-15.1)	*Isoberlinia scheffleri* (Harms) Greenway*	*Diospyros abyssinica* (Hiern) F.White *
Blighia unijugata Baker*	3.1 (0.0-9.4)	*Voacanga Africana* Stapf ex Scott Elliot	5.0 (0.0-11.5)	*Dracaena mannii* Baker	*Tapura fischeri* Engl.
Dialium holtzii Harms*	3.1 (0.0-9.4)	*Tabernaemontana pachysiphon* Stapf	4.3 (0.0-10.8)	*Diospyros abyssinica* (Hiern) F.White *	*Craterispermum schweinfurthii* Hiern
Leptactina platyphylla (Hiern) Wernham	3.1 (0.0-9.4)	*Croton sylvaticus* Hochst.*	3.6 (0.0-10.8)	*Aoranthe penduliflora* (K.Schum.) Somers	*Xylopia longipetala* De Wild. & T.Durand *
Mallotus oppositifolius Müll.Arg.	3.1 (0.0-9.4)	*Diospyros kabuyeana* F.White	3.6 (0.0-7.2)	*Tabernaemontana elegans* Stapf	*Tabernaemontana pachysiphon* Stapf
Tricalysia pallens Hiern	3.1 (0.0-9.4)			*Diospyros zombensis* (B.L.Burtt) F.White	

* Canopy species



Cover photo: Udzungwa Forest Project Co-ordinator Fadhili Njilima and degraded forest in Tanzania, where lianas have prevented forest tree regeneration for >30 years. Credit: Andrew R. Marshall.
150x199mm (300 x 300 DPI)



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269x349mm (300 x 300 DPI)

Fig. 2 Forest understorey dominated by lianas (mostly Uncaria africana G.Don, known by the local Hehe tribe as "mtonasimba" ("lion's grasp" in English), because of its hooked spines [inset]).
254x190mm (96 x 96 DPI)

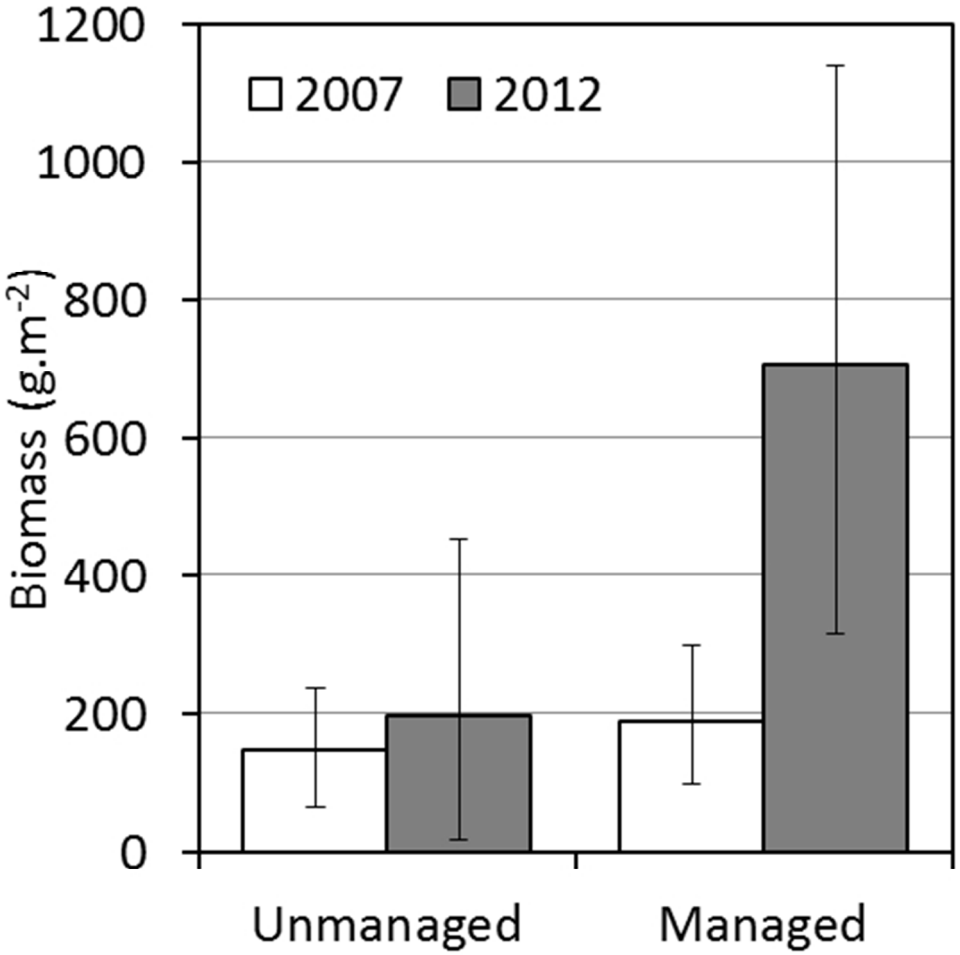

Fig. 3 Mean (and 95CI) biomass of stems 1-4.9cm dbh in plots managed by liana cutting (n=10) and unmanaged (n=8), spanning 2007-2012.
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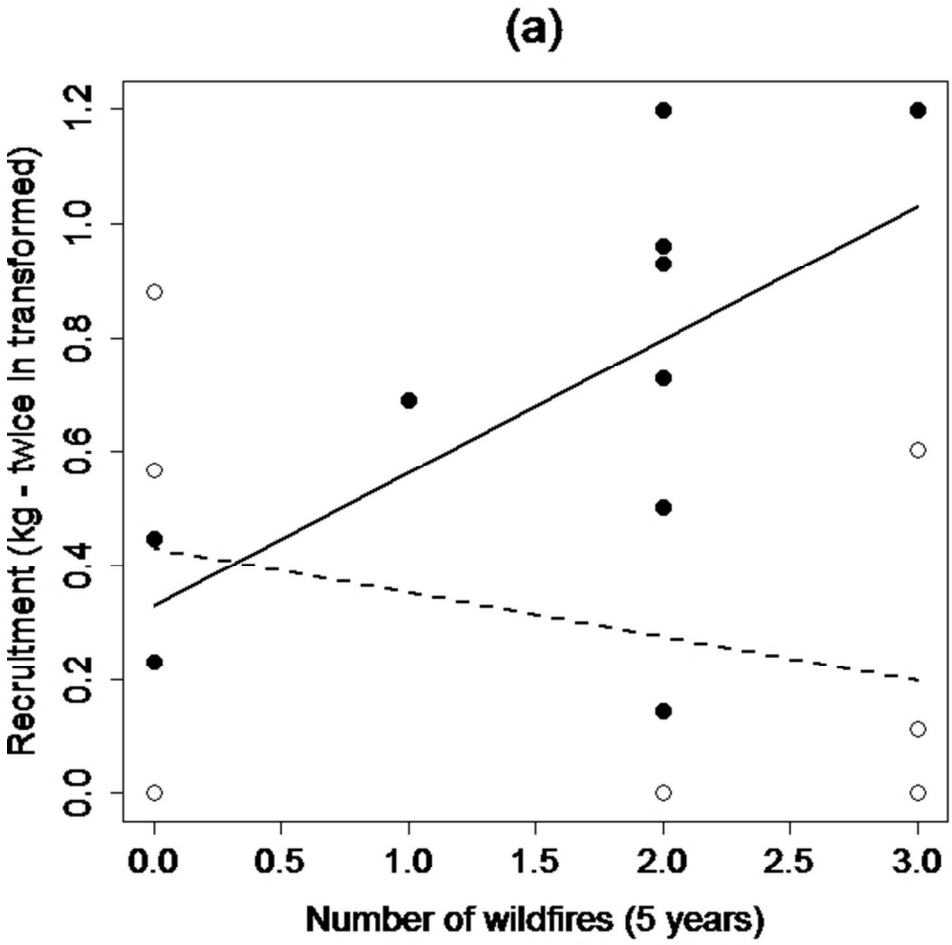

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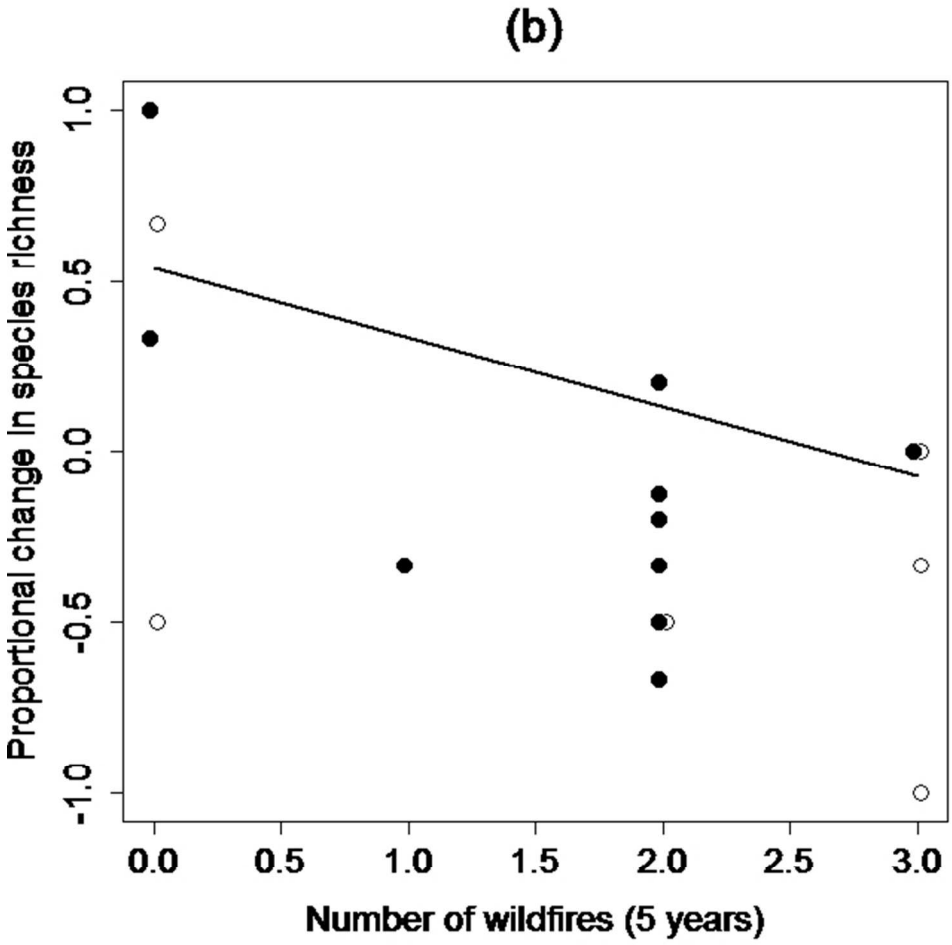

Same as Fig. 4a
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