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

2

3 Authors: Marshall, A.R.^{1,2,3*}, Coates, M.A.¹, Archer, J.^{1,2,4}, Kivambe, E.³, Mnendendo, H.³,

4 Mtoka, S.^{3,5}, Mwakisoma, R.^{3,6}, Lemos de Figueiredo, R.J.R.¹, Njilima, F.M.³

5

6 Addresses

7 ¹ CIRCLE, Environment Department, University of York, York YO10 5DD, UK.

8 ² Flamingo Land Ltd., Kirby Misperton, North Yorkshire YO10 6UX, UK.

9 ³ Udzungwa Forest Project, PO Box 99, Mang'ula, Morogoro, Tanzania.

10 ⁴ School of Geography, University of Leeds, Leeds, North Yorkshire LS2 9JT, UK.

11 ⁵ Tanzania Wildlife Research Institute, Kingupira Wildlife Research Centre, PO Box 16,

12 Utete-Rufiji, Tanzania.

13 ⁶ Udzungwa Ecological Monitoring Centre, PO Box 99, Mang'ula, Morogoro, Tanzania.

14

15 * Correspondence: E-mail: andy.marshall@york.ac.uk

16

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18

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23

1 Abstract

2 Liana growth following forest disturbance is threatening the tropical carbon sink by delaying
3 or preventing recovery. Tree growth can be stimulated by liana cutting, however its
4 applicability for conservation management remains uncertain, particularly in Africa (the
5 least-studied continent for ecological restoration) and against pervasive barriers such as
6 wildfires. We conducted a small-scale trial to investigate tree sapling regeneration following
7 liana cutting in a lowland African forest prone to low intensity wildfires. We employed a
8 BACI design comprising eighteen 25m² plots of sapling trees in liana-infested areas. After
9 five years of liana cutting we saw greater recruitment, stem growth and net biomass.

10 Wildfires caused 51% mortality and probably masked liana cutting influences on species and
11 survival, but may have encouraged stem recruitment through interaction with liana cutting.

12 Incorporating our data into a first quantitative review of previous studies, we found that tree
13 growth, recruitment and net growth rates were all consistently higher where lianas were either
14 absent or removed (respectively: 80%, 215%, 633%; n=14, 3, 4). Tree growth impacts were
15 approximately equivalent across size-classes and continents. We give recommendations for
16 improved plot and sample sizes, but conclude that liana cutting is a promising restoration
17 method for lowland tropical forests, including Africa.

18

19

1 Introduction

2

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

14

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

22

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

1 reduced growth, sap flow, fecundity, leaf production and survival (Hegarty, 1991; Álvarez-
2 Cansino et al., 2015; Toledo-Aceves, 2015) and ultimately biomass accumulation and carbon
3 sequestration (Schnitzer et al., 2014). Consequently, forest succession may be slowed or
4 arrested (Schnitzer, Dalling & Carson, 2000; Tymen et al., 2015). Accordingly, the global
5 distribution of lianas is negatively related to carbon stocks (Durán & Gianoli, 2013).
6 Increasing tropical forest degradation has stimulated 1.7-4.6% annual increase in liana
7 abundance, threatening the tropical carbon sink (Phillips et al., 2002; Schnitzer & Bongers,
8 2011; van der Heijden et al., 2013).

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

22
23 Studies of tree regeneration following liana cutting in the palaeotropics have been limited to
24 focal species in combination with other forestry techniques. Africa is the least-studied
25 continent for ecological restoration (Wortley, Hero & Howes, 2013) despite having the most
26 degraded forest (Minnemeyer et al., 2011) and huge restoration opportunity cost for rural

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

11

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

23

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

1 may trigger conversion to scrub or savanna (Cochrane et al., 1999). Forest fires are 94%
2 unplanned (FAO, 2010) and human-induced increases have reduced global tree basal area
3 (Lehmann et al., 2014), releasing carbon equivalent to 41% of global fossil fuels (Cochrane,
4 2003). Wildfires burned >85% of sub-Saharan Africa between 1996-2009 (Krawchuk &
5 Moritz, 2014) including >37Mha of forest (FAO, 2010).

6

7 While prescribed fire can maintain forest by removing deadwood and thicket, evidence from
8 Bolivia suggests that fire is inappropriate for managing lianas because it stimulates rapid
9 regrowth (Gerwing, 2001), especially for small lianas (Pinard, Putz & Licona, 1999).

10 Furthermore, the biggest impact of wildfires is on sapling trees, causing >50% annual
11 mortality, increasing with fire intensity and frequency (Balch et al., 2011). Therefore
12 prevention of wildfires is often deemed essential for tropical forest restoration (Holl, 2002).

13 However, wildfires have affected most terrestrial ecosystems throughout their history
14 (Marlon et al., 2008) including many tropical forests (Chazdon, 2003). For example, the East
15 African Coastal Forests have survived conversion to woodland for >150,000 years of low
16 frequency fires (Clarke & Karoma, 2000). Hence restoration strategies are required that do
17 not assume complete fire exclusion. However fire-vegetation dynamics remain poorly known,
18 prompting calls for more explicit inclusion in conservation research and planning (Krawchuk
19 et al., 2009).

20

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

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

1 Material and Methods

2 *Study site*

3 The study was conducted in Magombera Forest, southern Tanzania (Fig. 1; 11km²; elevation
4 270m; annual rainfall 1514mm; wet season March-May; sandy-loam pH 4.7; C:N 8.6). The
5 habitat was semi-deciduous Zanzibar Inhumbane forest with an understorey comprising small
6 herbs, vines, sparse evergreen shrubs and lianas predominant in disturbed areas. Magombera
7 Forest has high biodiversity value, including a remarkable proportion of threatened trees and
8 a unique plant community comprising both lowland and montane species typical of the
9 Eastern Arc Mountains and Coastal Forests of East Africa (Rodgers, Homewood & Hall,
10 1980; Marshall, 2008). The area supports several regionally endemic species including the
11 Udzungwa red colobus monkey (*Procolobus gordonorum*) and Magombera chameleon
12 (*Kinyongia magomberae*). Magombera Forest had no legal protection at the time of study, but
13 with interim management by a conservation collaboration, which ensured limited disturbance
14 to research sites.

15

16 Magombera Forest was chosen for its restoration potential following timber-felling in the
17 1970s/80s, and widespread pole-sized tree removal for local domestic use and sale. The area
18 comprised ~20% “secondary forest” (≥90% canopy loss with mostly stunted/damaged trees
19 and isolated tall trees) and ~80% “degraded primary forest” (<90% canopy loss with a mostly
20 heavily degraded understorey; Fig. 1). Most primary and secondary forest comprised a high
21 density of understorey lianas, particularly *Uncaria africana* G.Don, forming thickets fastened
22 by hooked spines (Fig. 2). Across the region, many of these thickets had persisted for ≥30
23 years, similar to liana forest elsewhere in East Africa (Chapman & Chapman, 1997).
24 Tanzanian forest habitats were mostly not actively managed at the time of study. However in
25 Magombera Forest, managers and villagers maintained fire-breaks and extinguished some
26 wildfires, reducing the extent of burning by ~50%. Wildfires were typical of lowland forests

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

3

4 *Plots*

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

20

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

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

7

8 *Analysis*

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

19

$$20 \quad \text{Above-ground biomass (kg)} = 0.0509 \times \rho D^2 H$$

21 Equation 1: Biomass calculation for moist forest trees using WSG (ρ ; g.cm⁻³), dbh (D; cm)

22 and height (H; m) (Chave et al., 2005).

23

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

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

12

13 For regeneration indicators dependent on year 1 biomass (all except recruitment), we
14 preferred proportional over absolute measures of change to reduce bias from variation in year
15 1 stem size and density. For these models using proportions, we excluded either one or two
16 plots with zero values in year 1 (i.e. infinite proportional change). To address this removal of
17 plots we also calculated means and 95% bootstrapped confidence intervals (10,000 iterations;
18 95CI) for absolute measurements, for comparison to proportional changes.

19

20 To avoid Type I errors we used False Discovery Rate correction of alpha values (α_{FDR} ;
21 Benjamini & Hochberg, 1995). To determine sampling adequacy for significant indicators we
22 used power analysis to calculate the proportion of discernible change, under our sampling
23 level and increased sampling to fifteen or twenty plots per treatment (80% power; Crawley,
24 2005).

25

26

1 Results

2 *Biomass*

3 Net biomass increase among stems 1-4.9cm dbh was higher in plots managed by liana cutting
4 than unmanaged plots (total 129.9 versus 9.6kg respectively; Fig. 3; Table 1). The increase in
5 biomass comprising recruitment of new stems was higher in managed plots (total 31.6kg;
6 0.42stems.m^{-2} , 95CI 0.16-0.75) than unmanaged plots (total 5.7kg; 0.10stems.m^{-2} , 0.03-0.18)
7 (Table 1). In year 1 we measured 107 stems, with no significant difference between managed
8 and unmanaged plots prior to management ($W=59$; $p=0.098$; managed: $0.4\text{-}5.6\text{stems.}10\text{m}^{-2}$;
9 unmanaged: $0.0\text{-}3.2\text{stems.}10\text{m}^{-2}$). Stem numbers increased with recruitment to 171 in year 5,
10 with significantly more stems in managed plots ($W=65.5$; $p=0.026$; managed: 0.8-
11 $17.2\text{stems.}10\text{m}^{-2}$; unmanaged $0.0\text{-}4.0\text{stems.}10\text{m}^{-2}$).

12

13 The net biomass increase also comprised growth of year 1 stems, again higher in managed
14 plots (total 116.7kg; 3.4kg.stem^{-1} , 95CI 1.8-5.5; $17.7\text{mm dbh.stem}^{-1}$, 95CI 12.3-23.4) than
15 unmanaged plots (total 21.3kg; 1.6kg.stem^{-1} , 0.1-4.4; $7.9\text{mm dbh.stem}^{-1}$, 0.5-18.4) (Table 1).
16 Biomass loss from mortality was no different between managed plots (total 18.5kg;
17 0.17stems.m^{-2} , 95CI 0.10-0.24) and unmanaged plots (total 17.4kg; 0.12stems.m^{-2} , 0.07-0.17)
18 (Table 1).

19

20 At 80% power our sample size was sufficient for detecting $\geq 152\%$ change in recruitment,
21 $\geq 267\%$ proportion growth, and $\geq 35\%$ proportion net biomass. Increasing the sample size 15-
22 20 plots per treatment would have increased the expected detection to $\geq 102\text{-}87\%$, $\geq 180\text{-}152\%$
23 and $\geq 24\text{-}20\%$ respectively.

24

25

26

1 *Species*

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

12

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

21

22 *Wildfire*

23 Pervasive wildfire frequency was 1.61plot^{-1} (range $1.0\text{-}3.0\text{plot}^{-1}$; 0.32yr^{-1} , $0.20\text{-}0.60$) and
24 equivalent between managed (1.60plot^{-1} , 95CI $1.00\text{-}2.10$) and unmanaged plots (1.63plot^{-1} ,
25 $0.63\text{-}2.50$). Wildfires killed ~55 year 1 stems (91.7% of deaths), but wildfire frequency did
26 not directly influence growth, recruitment, mortality or net biomass change ($r^2\leq 0.08$; $p\geq 0.27$)

1 and hence was not confidently retained in models (Table 1). Interaction was seen between
2 wildfire frequency and liana cutting management for recruitment (greater cutting influence at
3 high wildfire frequency; Fig. 4a) but with no significant improvement on liana cutting alone
4 (Table 1). Increasing wildfire frequency explained 29% of variation in proportional species
5 loss, enhancing a univariate liana cutting model but not significant at the 95% level (Table 1;
6 Fig. 4b). Plots with zero to one wildfire showed increased proportional community change
7 (0.23, 95CI -0.27-0.73), while those with two to three wildfires decreased (-0.3, 95CI -0.52 to
8 -0.13).

9

10

1 Discussion

2

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

7

8 *Biomass*

9 Our observed growth rate increase for liana cutting compared to unmanaged plots (dbh:
10 119%; biomass: 109%) is greater than most previous studies comparing tree dbh,
11 circumference or height with/without lianas (mean 66%, 95CI 39-99, n=12 [including this
12 study: 69%, 43-100, n=20]), but more typical of studies comparing biomass or basal area
13 (80%, 35-150, n=13 [83%, 39-147, n=14]) (Table 2). Previous studies have been biased
14 towards low elevation (median 200m; mean 215m), with the only high elevation study
15 showing no significant influence of liana and shrub removal on tree growth (Duncan &
16 Chapman, 2003). Our 350% increase in recruitment with liana cutting is higher than the only
17 two comparable studies of stems ≤ 5 cm dbh, both in Panama, which increased by 46% (stems
18 ≥ 1.3 m tall; Schnitzer & Carson, 2010) and 250% (stems < 1 cm dbh; Graul & Putz, 2004),
19 giving a mean of 215% across studies. Two further studies showed (a) comparable stem size
20 and density between liana cut and control plots in Cameroon (Schnitzer et al., 2004) and (b)
21 increased sapling density with liana cutting and liberation thinning after 19 years (but not 42
22 years) in Malaysia (Addo-Fordjour, Rahmad & Asyraf, 2013), but did not present pre-
23 treatment measurements for calculation of % increases.

24

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

1 palaeotropics combined (dbh/circ/h: +28%, -18-77, n=5; ba/bio: +92%, 26-197, n=8) did not
2 differ from the more extensive neotropical studies (dbh/circ/h: +83%, 54-119, n=15; ba/bio:
3 +71%, 37-112, n=6). This provides a first quantitative indication that lianas (and presumably
4 liana removal) have approximately equivalent pantropical impact on biomass.

5

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

18

19 Bringing together growth, recruitment and mortality, our observed 765% increase in relative
20 net biomass gain from 0.32kg.kg⁻¹ in managed plots to 2.77kg.kg⁻¹ in unmanaged plots is of
21 similar magnitude to two previous estimates from Panama of 370% (stems >1.3m height;
22 unmanaged 0.23kg.kg⁻¹; managed 1.08kg.kg⁻¹; Schnitzer et al., 2014) and 646% (stems
23 ≥10cm dbh; unmanaged 0.017kg.kg⁻¹; managed 0.11kg.kg⁻¹; van der Heijden et al., 2015). A
24 similar magnitude of increase (750%) was seen for basal area in Brazil (stems >5cm dbh;
25 unmanaged 64cm².m⁻²; managed 544cm².m⁻²; Gerwing, 2001). The mean 633% increase
26 across these studies suggests increasing pantropical liana growth will have increasing impact

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

6

7 The reason for our generally high regeneration is uncertain. Variation within previous studies
8 has been ascribed to shade and liana density (Ingwell et al., 2010; Schnitzer & Carson, 2010).
9 Variation across studies may also have arisen from inconsistencies in tree size, measurement
10 units and timespan. Across studies, the growth increase without lianas was unrelated to tree
11 size and most variable for small stems (<5cm dbh: 135% [95CI: 47-250], n=7; >5cm dbh:
12 75% [51-104], n=20; unspecified size: 75% [36-124], n=5). Regarding units, dbh narrowly
13 predominates over biomass in the literature, presumably because of its relevance to forestry
14 and uncertainty regarding biomass calculation. Indeed, region-specific biomass estimation
15 methods are lacking across the tropics, particularly for saplings. Regarding timespan, the
16 impact of liana cutting in isolation is unknown beyond 10 years and 71% of all restoration
17 studies have spanned ≤ 15 years (Wortley et al., 2013).

18

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

24

25 *Species*

1 Our difference in species between sapling and mature stems suggests typical negative density
2 dependent growth (Wright, 2002). However, our high sapling species richness shows good
3 restoration potential. Our data are inconclusive regarding liana cutting impacts on community
4 restoration, perhaps a result of limited scale. In Panama, tree species richness increased 65%
5 following liana cutting (Schnitzer & Carson, 2010) and tree-liana competition was similar
6 between species (Álvarez-Cansino et al., 2015). Conversely, liana cutting in Brazil caused
7 both increases and decreases across species (Gerwing, 2001). Community change following
8 liana cutting remains unverified for Africa, however pioneer trees recruited faster than mid-
9 successional species following liana/shrub removal in Uganda (Duncan & Chapman, 2003).
10 Moreover, tropical forest recovery often requires establishment of single species (Chazdon,
11 2003) or several “framework species” (Goosem & Tucker, 1995) before soil fertility, seed
12 dispersal and shade are sufficient to stimulate succession. Hence longer-term monitoring is
13 required.

14

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

22

23 *Practicalities*

24 An important practical consideration is cost. Using a cutting rate of sixteen person-hours ha⁻¹
25 (Grauel & Putz, 2004) it would take four people eighteen months to manage the 11km²
26 Magombera Forest. However, given our flat topography this could be achievable within

1 twelve months (one person-day.ha⁻¹). This would cost ~US\$6,000yr⁻¹ for labour and
2 equipment (US\$5.45ha⁻¹), compared to US\$1-4ha⁻¹ for West Africa (Bongers et al., 2002)
3 and mean \$11ha⁻¹ for Bolivia and Brazil (range \$1-16ha⁻¹; Vidal et al., 1997; Pérez-Salicrup
4 et al., 2001; Dauber, Fredericksen & Peña, 2005). The equivalent cost for alternative tree-
5 planting in neighbouring Uganda was more than 44 times more expensive (US\$1,200ha⁻¹.5yr⁻¹;
6 Omeja et al., 2009).

7
8 Future monitoring of saplings would benefit from increased sampling. Plots used previously
9 for stems <5cm dbh have varied in size and number per treatment (Duncan & Chapman,
10 2003: 25m², n=19; Schnitzer et al., 2005: 108m², n=10; Gerwing, 2001: 400m², n=6). Our
11 own sampling enabled statistically verifiable conclusions for biomass. However, larger plots
12 would reduce zero values and improve precision. Increased samples would further improve
13 precision, with our power analysis suggesting twenty plots per treatment would have nearly
14 doubled our ability to detect biomass change. While our plots were too small to estimate an
15 optimal size for measuring biodiversity, previous work suggests 300-400 stems per plot
16 (Gimaret-Carpentier et al., 1998). At our observed sapling density, this would need plots of
17 ~790-1,053m², similar to stems 1-9.9cm dbh in Amazonia (0.1ha; Magnusson et al., 2005).

18
19 Thirdly, lianas (and cutting) may not influence regeneration where light or liana abundance is
20 low, e.g. shaded forest or small canopy gaps (Toledo-Aceves & Swaine, 2008; van der
21 Heijden & Phillips, 2009; Ingwell et al., 2010). Liana removal may even be damaging to
22 healthy forests, e.g. maintaining small canopy gaps can preserve biodiversity by supporting
23 pioneers and lianas (Schnitzer & Carson, 2000). Hence liana cutting is best employed on a
24 tree-by-tree basis (Schnitzer & Bongers, 2002) with focus on abundant species (Sfair et al.,
25 2011) in large canopy gaps/thickets (Schnitzer & Carson, 2010) and heavily degraded
26 understorey (this study). Cutting must also be temporary to allow liana recovery (Campanello

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

3

4 Accurate assessment of liana cutting is also hindered because, for geographic completeness
5 our review of previous work includes liana presence/absence through natural growth or
6 planting. These studies may suffer from species bias in host tree preferences (Putz et al.,
7 1984; Campanello et al., 2007) or choice of planted seedlings. Indeed, the increase in growth
8 without lianas was higher among cutting studies (mean 90%; n=19) than the rest (57%;
9 n=10), but not significant (95CI 53-139 and 23-108 respectively). A previous comparison of
10 growth between liberated and naturally liana-free trees found ambiguous results for timber
11 species in Bolivia (Villegas et al., 2009). Therefore more liana cutting studies are needed
12 across stem sizes in natural forest, especially regarding recruitment and biodiversity.

13

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

23

24

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2

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7

8

- 1 References
- 2
- 3 ADDO-FORDJOUR, P., RAHMAD, Z.B. & ASYRAF, M. (2013) Impacts of forest
4 management on liana abundance and liana–tree relationships in a tropical forest in
5 Malaysia and implications for conservation. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manage.*
6 9, 13-20.
- 7 ÁLVAREZ-CANSINO, L., SCHNITZER, S.A., REID, J.P. & POWERS, J.S. (2015) Liana
8 competition with tropical trees varies seasonally but not with tree species identity. *Ecology*
9 96, 39-45.
- 10 ARROYO-RODRÍGUEZ, V., ASENSIO, N., DUNN, J.C., CRISTÓBAL-AZKARATE, J. &
11 GONZALEZ-ZAMORA, A. (2015) Use of lianas by primates: more than a food source.
12 In: *Ecology of Lianas* (Eds. S.A. SCHNITZER, F. BONGERS, R.J. BURNHAM &
13 F.E.PUTZ). John Wiley and Sons, Ltd., Chichester.
- 14 ASNER, G.P., RUDEL, T.K., AIDE, T.M., DEFRIES, R. & EMERSON, R. (2009) A
15 contemporary assessment of change in humid tropical forests. *Cons. Biol.* 23, 1386-1395.
- 16 BABAASA, G.E., KASANGAKI, A., BITARIHO, R. & MCNEILAGE, A. (2004) Gap
17 characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *Afr. J.*
18 *Ecol.* 42, 217-224.
- 19 BALCH, J.K., NEPSTAD, D.C., CURRAN, L.M., BRANDO, P.M., PORTELAB, O.,
20 GUILHERMEG, P., REUNING-SCHERERA, J.D. & DE CARVALHO, JR. O. (2011)
21 Size, species, and fire behaviour predict tree and liana mortality from experimental burns
22 in the Brazilian Amazon. *Forest Ecol. Manag.* 261, 68-77.
- 23 BARNES, A.D. & CHAPMAN, H.M. (2014) Dispersal traits determine passive restoration
24 trajectory of a Nigerian montane forest. *Acta Oecol.* 56, 32-40.
- 25 BENJAMINI, Y. & HOCHBERG, Y. (1995) Controlling the false discovery rate: a practical
26 and powerful approach to multiple testing. *J. R. Stat. Soc. B.* 57, 289-300.

- 1 BLATE, G.M. (2005) Modest trade-offs between timber management and fire susceptibility
2 of a Bolivian semi-deciduous forest. *Ecol. Appl.* 15, 1649-1663.
- 3 BONGERS, F.J.J.M., SCHNITZER, S.A. & TRAORE, D. (2002) The importance of lianas
4 and consequences for forest management in West Africa. *BioTerre* Special Edition, 59-70.
- 5 CAMPANELLO, P.I., GARIBALDI, J.F., GATTI, M.G. & GOLDSTEIN, G. (2007) Lianas
6 in a subtropical Atlantic Forest: host preference and tree growth. *Forest Ecol. Manag.* 242,
7 250-259.
- 8 CAMPANELLO, P.I., VILLAGRA, M., GARIBALDI, J.F., RITTER, L.J., ARAUJO, J.J. &
9 GOLDSTEIN, G. (2012) Liana abundance, tree crown infestation, and tree regeneration
10 ten years after liana cutting in a subtropical forest. *Forest Ecol. Manag.* 284, 213-221.
- 11 CHAMSHAMA, S.A.O. & VYAMANA, V.G. (2010) Forests and forestry in Tanzania. In:
12 *Degraded Forests in East Africa: Management and Restoration* (Eds. F. BONGERS & T.
13 TENNIGKEIT). Earthscan, Washington DC.
- 14 CHAPMAN, C.A. & CHAPMAN, L.J. (1997) Forest regeneration in logged and unlogged
15 forests of Kibale National Park, Uganda. *Biotropica* 29, 396-412.
- 16 CHAVE, J., ANDALO, C., BROWN, S., CAIRNS, A., CHAMBERS, J.Q., EAMUS, D.,
17 FÖLSTER, H., FROMARD, F., HIGUCHI, N., KIRA, T., LESCURE, J.-P., NELSON,
18 B.W., OGAWA, H., PUIG, H., RIÉRA, B. & YAMAKURA, T. (2005) Tree allometry
19 and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145,
20 87-99.
- 21 CHAZDON, R.L. (2003) Tropical forest recovery: legacies of human impact and natural
22 disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6, 51-71.
- 23 CHAZDON, R.L. (2008) Beyond deforestation: restoring forests and ecosystem services on
24 degraded lands. *Science* 320, 1458-1460.

- 1 CLARKE, G.P. & KAROMA, N.J. (2000) History of anthropic disturbance. In: *Coastal*
2 *Forests of Eastern Africa* (Eds. N.D. BURGESS & G.P. CLARKE). IUCN, Gland,
3 Cambridge.
- 4 COCHRANE, M.A. (2003) Fire science for rainforests. *Nature* 421, 913-919.
- 5 COCHRANE, M.A., ALENCAR, A., SCHULZE, M.D., SOUZA, JR. C.M., NEPSTAD,
6 D.C., LEFEBVRE, P. & DAVIDSON, E.A. (1999) Positive feedbacks in the fire dynamic
7 of closed canopy tropical forests. *Science* 284, 1832-1835.
- 8 COCHRANE, M.A., SCHULZE, M.D. (1999) Fire as a recurrent event in tropical forests of
9 the eastern Amazon: effects on forest structure, biomass, and species composition.
10 *Biotropica* 31, 2-16.
- 11 CRAWLEY, M.J. (2005) *Statistics: An Introduction Using R*. John Wiley & Sons Ltd.,
12 Chichester.
- 13 DAUBER, E., FREDERICKSEN, T.S. & PEÑA, M. (2005) Sustainability of timber
14 harvesting in Bolivian tropical forests. *Forest Ecol. Manag.* 214, 294-304.
- 15 DUNCAN, R.S. & CHAPMAN, C.A. (2003) Tree–shrub interactions during early secondary
16 forest succession in Uganda. *Restor. Ecol.* 11, 198-207.
- 17 DURÁN, S.M. & GIANOLI, E. (2013) Carbon stocks in tropical forests decrease with liana
18 density. *Biol. Lett.* 9, 20130301.
- 19 EMMONS, L.H., GENTRY, A.H. (1983) Tropical forest structure and the distribution of
20 gliding and prehensile-tailed vertebrates. *Am. Nat.* 121, 513-524.
- 21 FAO (2010) *Global Forest Resources Assessment*. Food and Agriculture Organisation of the
22 United Nations, Rome.
- 23 GENTRY, A.H. (1991) The distribution and evolution of climbing plants. In: *The Biology of*
24 *Vines* (Eds. F.E. PUTZ & H.A. MOONEY). Cambridge University Press, Cambridge.
- 25 GERWING, J.J. (2001) Testing liana cutting and controlled burning as silvicultural
26 treatments for a logged forest in the eastern Amazon. *J. Appl. Ecol.* 38, 1264-1276.

- 1 GIMARET-CARPENTIER, C., PÉLISSIER, R., PASCAL, J.P. & HOULLIER, F. (1998)
2 Sampling strategies for the assessment of tree species diversity. *J. Veg. Sci.* 9, 161-172.
- 3 GOOSEM, S.P. & TUCKER, N.I.J. (1995) *Repairing the Rainforest – Theory and Practice*
4 *of Rainforest Re-establishment in North Queensland's Wet Tropics*. Wet Tropics
5 Management Authority, Cairns.
- 6 GRAUEL, W.T. & PUTZ, F.E. (2004) Effects of lianas on growth of *Prioria copaifera* in
7 Darien, Panama. *Forest Ecol. Manag.* 190, 99-108.
- 8 HEGARTY, E.E. (1991) Vine-host interactions. In: *The Biology of Vines* (Ed. F.E. PUTZ &
9 H.A. MOONEY). Cambridge University Press, Cambridge.
- 10 HOFFMANN, W.A., GEIGER, E.L., GOTSCH, S.G., ROSSATTO, D.R., SILVA, L.C.R.,
11 LAU, O.L., HARIDASAN, M. & FRANCO, A.C. (2012) Ecological thresholds at the
12 savanna-forest boundary: how plant traits, resources and fire govern the distribution of
13 tropical biomes. *Ecol. Lett.* 15, 759-768.
- 14 HOLL, K.D. (2002) Tropical moist forest. In: *Handbook of Ecological Restoration* (Ed. M.R.
15 Perrow & A.J. Davy). Cambridge University Press, Cambridge.
- 16 HOLL, K.D. & ZAHAWI, R.A. (2014) Factors explaining variability in woody above-ground
17 biomass accumulation in restored tropical forest. *Forest Ecol. Manag.* 319, 36-43.
- 18 INGWELL, L.L., WRIGHT, S.J., BECKLUND, K.K., HUBBELL, S.P. & SCHNITZER,
19 S.A. (2010) The impact of lianas on 10 years of tree growth and mortality on Barro
20 Colorado Island, Panama. *J. Ecol.* 98, 879-887.
- 21 ITTO (2002) *ITTO Guidelines for the Restoration, Management and Rehabilitation of*
22 *Degraded and Secondary Tropical Forests*. ITTO Policy Development Series No 13.
23 International Tropical Timber Organisation, Yokohama, Japan.
- 24 KINNAIRD, M.F. & O'BRIEN, T.G. (1998) Ecological effects of wildfire on lowland
25 rainforest in Sumatra. *Cons. Biol.* 12, 954-956.

- 1 KRAWCHUK, M.A. & MORITZ, M.A. (2014) Burning issues: statistical analyses of global
2 fire data to inform assessments of environmental change. *Environmetrics* 25, 472-481.
- 3 KRAWCHUK, M.A., MORITZ, M.A., PARISIEN M-A., VAN DORN, J. & HAYHOE, K.
4 (2009) Global pyrogeography: the current and future distribution of wildfire. *Plos ONE* 4,
5 e5102.
- 6 KUEBLER, C. (2003) *Standardized Vegetation Monitoring Protocol*. Tropical Ecology,
7 Assessment, and Monitoring Initiative. Conservation International, Washington, D.C.
- 8 LAURANCE, W.F. et al. [multi-author] (2012) Averting biodiversity collapse in tropical
9 forest protected areas. *Nature* 489, 290-294.
- 10 LEDO, A. & SCHNITZER, S.A. (2014) Disturbance and clonal reproduction determine liana
11 distribution and maintain liana diversity in a tropical forest. *Ecology* 95, 2169-2178.
- 12 LEHMANN, C.E.R., ANDERSON, T.M., SANKARAN, M., HIGGINS, S.I., ARCHIBALD,
13 S., HOFFMAN, W.A., HANAN, N.P., WILLIAMS, R.J., FENSHAM, R.J., FELFILI, J.,
14 HUTLEY, L.B., RATNAM, J., SAN JOSE, J., MONTES, R., FRANKLIN, D., RUSSEL-
15 SMITH, J., RYAN, C.M., DURIGAN, G., HIERNAUX, P., HAIDAR, R., BOWMAN,
16 D.M.J.S. & BOND, W.J. (2014) Savanna vegetation-fire-climate relationships differ
17 among continents. *Science* 343, 548-552.
- 18 LOWE, R.G. & WALKER, P. (1977) Classification of canopy, stem, crown status and
19 climber infestation in natural tropical forest in Nigeria. *J. Appl. Ecol.* 14, 897-903.
- 20 MAGNUSSON, W.E., LIMA, A.P., LUIZÃO, R., LUIZÃO, F., COSTA, F.R.C., DE
21 CASTILHO, C.V. & KINUPP, V.F. (2005) RAPELD: A modification of the Gentry
22 method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica* 5.
- 23 MARLON, J.R., BARTLEIN, P.J., CARCAILLET, C., GAVIN, D.G., HARRISON, S.P.,
24 HIGUERA, P.E., JOOS, F., POWER, M.J. & PRENTICE, I.C. (2008) Climate and human
25 influences on global biomass burning over the past two millennia. *Nat. Geosci.* 1, 697-
26 702.

- 1 MARSHALL, A.R. (2008) Assessing and restoring biodiversity in Tanzania's forests: the
2 case of Magombera. *Proceedings of the 6th TAWIRI Scientific Conference, December*
3 *2007*. Tanzania Wildlife Research Institute, Arusha.
- 4 MARSHALL, A.R., JØRGENSENBYE, H.I., ROVERO, F., PLATTS, P.J., WHITE, P.C.L. &
5 LOVETT, J.C. (2010) The species-area relationship and confounding variables in a
6 threatened monkey community. *Am. J. Primatol.* 72, 325-336.
- 7 MARSHALL, A.R., WILLCOCK, S., PLATTS, P.J., LOVETT, J.C., BALMFORD, A.,
8 BURGESS, N.D., LATHAM, J.E., MUNISHI, P.K.T., SALTER, R., SHIRIMA, D.D. &
9 LEWIS, S.L. (2012) Measuring and modelling above-ground carbon and tree allometry
10 along a tropical elevation gradient. *Biol. Conserv.* 154, 20-33.
- 11 MINNEMEYER, S., LAESTADIUS, L., SIZER, N., SAINT-LAURENT, C. & POTAPOV,
12 P. (2011) *A World of Opportunity*. The Global Partnership on Forest Landscape
13 Restoration, Bonn.
- 14 MUGASHA, W.A., MWAKALUKWA, E.E., LUOGA, E., MALIMBWI, R.E., ZAHABU,
15 E., SILAYO, D.S., SOLA, G., CRETE, P., HENRY, M. & KASHINDYE, A. (2016)
16 Allometric models for estimating tree volume and aboveground biomass in lowland forests
17 of Tanzania. *Int. J. Forestry Research* (in press).
- 18 NABE-NEILSEN, J., KOLLMANN, J. & PEÑA-CLAROS, M. (2009) Effects of liana load,
19 tree diameter and distances between conspecifics on seed production in tropical timber
20 trees. *Forest Ecol. Manag.* 257, 987-993.
- 21 NGOMANDA, A., OBIANG, N.L.E., LEBAMBA, J., MAVOUROULOU, Q.M., GOMAT,
22 H., MANKOU, G.S., LOURNETO, J., IPONGA, D.M., DITSOUGA, F.K., KOUMBA,
23 R.Z., BOBÉ, K. H. B. B., OKOUYI, C.M., NYANGADOUMA, R., LÉPENGUE, N.,
24 MBATCHI, B. & PICARD, N. (2014) Site-specific versus pantropical allometric
25 equations: Which option to estimate the biomass of a moist central African forest? *Forest*
26 *Ecol. Manag.* 312, 1-9.

- 1 OMEJA, P.A., CHAPMAN, C.A. & OBUA, J. (2009) Enrichment planting does not improve
2 tree restoration when compared with natural regeneration in a former pine plantation in
3 Kibale National Park, Uganda. *Afr. J. Ecol.* 47, 650-657.
- 4 PARREN, M.P.E. & BONGERS, F. (2005) Management of climbers in the forests of West
5 Africa. In: *Forest Climbing Plants of West Africa* (Eds. F. BONGERS, M. PARREN & D.
6 TRAORÉ). CABI Publishing, Wallingford, UK.
- 7 PARREN, M.P.E. & DOUMBIA, F. (2005) Logging and lianas in West Africa. In: *Forest*
8 *Climbing Plants of West Africa* (Eds. F. BONGERS, M. PARREN & D. TRAORÉ). CABI
9 Publishing, Wallingford, UK.
- 10 PAUL, G.S. & YAVITT, J.B. (2011). Tropical vine growth and the effects on forest
11 succession: A review of the ecology and management of tropical climbing plants. *Bot.*
12 *Rev.* 77, 11-30.
- 13 PEÑA-CLAROS, M., FREDERICKSEN, T.S., ALARCÓN, A., BLATE, G.M., CHOQUE,
14 U., LEAÑO, C., LICONA, J.C., MOSTACEDO, B., PARIONA, W., VILLEGAS, Z. &
15 PUTZ, F.E. (2008) Beyond reduced-impact logging: Silvicultural treatments to increase
16 growth rates of tropical trees. *Forest Ecol. Manag.* 256, 1458-1467.
- 17 PÉREZ-SALICRUP, D. (2001) Effect of liana cutting on tree regeneration in a liana forest in
18 Amazonian Bolivia. *Ecology* 82, 389-396.
- 19 PÉREZ-SALICRUP, D.R. & BARKER, M.G. (2000) Effect of liana cutting on water
20 potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian
21 tropical forest. *Oecologia* 124, 469-475.
- 22 PÉREZ-SALICRUP, D.R., CLAROS, A., GUZMAN, R., LICONA, J.C., LEDEZMA, F.,
23 PINARD, M.A. & PUTZ, F.E. (2001) Cost and efficiency of cutting lianas in a lowland
24 liana forest of Bolivia. *Biotropica* 33, 324-329.
- 25 PHILLIPS, O.L., MARTÍNEZ, R.V., ARROYO, L., BAKER, T.R., KILLEEN, T., LEWIS,
26 S.L., MALHI, Y., MENDOZA, M., NEILL, D., VARGAS, P.N., ALEXIADES, M.,

- 1 CERÓN, C., DI FIORE, A., ERWIN, T., JARDIM, A., PALACIOS, W., SALDIAS, M.,
2 VINCETI, B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*
3 418, 770-774.
- 4 PINARD, M.A., PUTZ, F.E. & LICONA, J.C. (1999) Tree mortality and vine proliferation
5 following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecol. Manag.*
6 116, 247-252.
- 7 PLATTS, P.J., BURGESS, N., GEREAU, R.E., LOVETT, J.C., MARSHALL, A.R.,
8 MCCLEAN, C., PELLIKA, P., SWETNAM, R. & MARCHANT, R. (2011) Delimiting
9 tropical mountain ecoregions for conservation. *Environ. Conserv.* 38, 312-324.
- 10 PUTZ, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology*
11 65, 1713-1724.
- 12 PUTZ, F.E. (1991) Silvicultural effects of lianas. In: *The Biology of Vines* (Ed. F.E. PUTZ,
13 F.E. & H.A. MOONEY). Cambridge University Press, Cambridge.
- 14 PUTZ, F.E., LEE, H.S. & GOH, R. (1984) Effects of post-felling silvicultural treatments on
15 woody vines in Sarawak. *The Malaysian Forester* 47, 214-226.
- 16 RODGERS, W.A., HOMEWOOD, K.M. & HALL, J.B. (1980) The railway and a rare
17 colobus monkey. *Oryx* 25, 491-495.
- 18 SCHNITZER, S.A. & BONGERS, F. (2002) The ecology of lianas and their role in forests.
19 *Trends Ecol. Evol.* 17, 223-230.
- 20 SCHNITZER, S.A. & BONGERS, F. (2011) Increasing liana abundance and biomass in
21 tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.* 14, 397-406.
- 22 SCHNITZER, S.A. & CARSON, W.P. (2000) Have we forgotten the forest because of the
23 trees? *Trends Ecol. Evol.* 15, 375-376.
- 24 SCHNITZER, S.A. & CARSON, W.P. (2010) Lianas suppress tree regeneration and diversity
25 in treefall gaps. *Ecol. Lett.* 13, 849-857.

- 1 SCHNITZER, S.A., DALLING, J.W. & CARSON, W.P. (2000) The impact of lianas on tree
2 regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-
3 phase regeneration. *J. Ecol.* 88, 655-666.
- 4 SCHNITZER, S.A., KUZEE, M.E. & BONGERS, F. (2005) Disentangling above- and
5 below-ground competition between lianas and trees in a tropical forest. *J. Ecol.* 93, 1115-
6 1125.
- 7 SCHNITZER, S.A., PARREN, M.P. & BONGERS, F. (2004) Recruitment of lianas into
8 logging gaps and the effects of pre-harvest climber cutting in a lowland forest in
9 Cameroon. *Forest Ecol. Manag.* 190, 87-98.
- 10 SCHNITZER, S.A., VAN DER HEIJDEN, G., MASCARO, J. & CARSON, W.P. (2014)
11 Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology* 95, 3008-3017.
- 12 SER (2004) *The SER International Primer on Ecological Restoration*. Society for Ecological
13 Restoration International, Tucson, Arizona, USA
- 14 SFAIR, J.C., ROCHELLE, A.L.C., VAN MELIS, J., REZENDE, A.A., WEISER, V.L.,
15 MARTINS, F.R. (2011) Theoretical approaches to liana management: a search for a less
16 harmful method. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manage.* 11, 89-95.
- 17 STANLEY, W.G. (1997) Liana-tree interactions in a second-growth forest stand in Eastern
18 Amazonia. *Journal of the Tropical Resources Institute* 16, 15-17.
- 19 STANTURF, J.A., PALIK, B.J. & DUMROESE, R.K. (2014) Contemporary forest
20 restoration: A review emphasizing function. *Forest Ecol. Manag.* 331, 292-323.
- 21 TOLEDO-ACEVES, T. (2015) Above and below ground competition between lianas and
22 trees. In: *Ecology of Lianas* (Eds. S.A. SCHNITZER, F. BONGERS, R.J. BURNHAM &
23 F.E. PUTZ). John Wiley and Sons, Ltd., Chichester.
- 24 TOLEDO-ACEVES, T. & SWAINE, M.D. (2007) Effect of three species of climber on the
25 performance of *Ceiba pentandra* seedlings in gaps in a tropical forest in Ghana. *J. Trop.*
26 *Ecol.* 23, 45-52.

- 1 TOLEDO-ACEVES, T. & SWAINE, M.D. (2008) Effect of lianas on tree regeneration in
2 gaps and forest understorey in a tropical forest in Ghana. *J. Veg. Sci.* 19, 717-728.
- 3 TYMEN, B., RÉJOU-MÉCHAIN, M., DALLING, J.W., FAUSET, S., FELDPAUSCH, T.R.,
4 NORDEN, N., PHILLIPS, O.L., TURNER, B.L., VIERS, J. & CHAVE, J. (2015)
5 Evidence for arrested succession in a liana-infested Amazonian forest. *Ecology* 104, 149-
6 159.
- 7 UHL, C. & KAUFFMAN, J.B. (1990) Deforestation, fire susceptibility, and potential tree
8 responses to fire in the eastern Amazon. *Ecology* 71, 437-449.
- 9 VAN DER HEIJDEN, G.M.F. & PHILLIPS, O.L. (2009) Liana infestation impacts tree
10 growth in a lowland tropical moist forest. *Biogeosciences* 6, 2217-2226.
- 11 VAN DER HEIJDEN, G.M.F., SCHNITZER, S.A., POWERS, J.S. & PHILLIPS, O.L.
12 (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests.
13 *Biotropica* 45, 682-692.
- 14 VAN DER HEIJDEN, G.M.F., POWERS, J.S. & SCHNITZER, S.A. (2015) Lianas reduce
15 carbon accumulation and storage in tropical forests. *Proc. Natl. Acad. Sci. U.S.A.* 112,
16 13267-13271.
- 17 VIDAL, E., JOHNS, J., GENVING, J.J., BARRETO, P. & UHL, C. (1997) Vine
18 management for reduced-impact logging in eastern Amazonia. *Forest Ecol. Manag.* 98,
19 105-114.
- 20 VIEILLEDENT, G., VAUDRY, R., ANDRIAMANOHISOA, S.F.D., RAKOTONARIVO,
21 S.O., RANDRIANASOLO, Z.H., RAZAFINDRABE, H.N., RAKOTOARIVONY, C.B.,
22 EBELING, J. & RASAMOELINA, M. (2012) A universal approach to estimate biomass
23 and carbon stock in tropical forests using generic allometric models. *Ecol. Appl.* 22, 572-
24 583.
- 25 VILLEGAS, Z., PEÑA-CLAROS, M., MOSTACEDO, B., ALARCÓN, A., LICONA, J.C.,
26 LEAÑO, C., PARIONA, W. & CHOQUE, U. (2009) Silvicultural treatments enhance

- 1 growth rates of future crop trees in a tropical dry forest. *Forest Ecol. Manag.* 258, 971-
- 2 977.
- 3 WOODS, P. (1989) Effects of logging, drought, and wildfire on structure and composition of
- 4 tropical forests in Sabah, Malaysia. *Biotropica* 21, 290-298.
- 5 WORTLEY, L., HERO, J-M. & HOWES, M. (2013) Evaluating ecological restoration
- 6 success: a review of the literature. *Restor. Ecol.* 21, 537-543.
- 7 WRIGHT, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species
- 8 coexistence. *Oecologia* 130, 1-14.
- 9 WRIGHT, A., TOBIN, M., MANGAN, S. & SCHNITZER, S.A. (2015) Unique competitive
- 10 effects of lianas and trees in a tropical forest understory. *Oecologia* 177, 561-569.
- 11 ZANNE, A., LOPEZ-GONZALEZ, G., COOMES, D.A., ILIC, K., JANSEN, S., LEWIS,
- 12 S.L. & MILLER, R.B. (2009) *Global Wood Density Database*.
- 13 <http://www.datadryad.org/handle/10255/dryad.235>.

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1 Tables

2 **Table 1** Comparison of mean (and 95CI) regeneration indicators following management of
 3 25m² plots using liana cutting versus unmanaged plots (2007-2012). Significant models of
 4 liana cutting influence on regeneration per plot are summarised with significant results in
 5 bold ($\alpha_{FDR}=0.03$) indicating direction of influence (+/-). Pervasive wildfire frequency and
 6 interaction covariates are also shown where retained following model reduction ($\alpha_{FDR}=0.01$),
 7 including the reduction in effect size when each variable was removed (δr^2). Models without
 8 covariates (i.e. liana cutting alone) did not explain reduced variance to those including
 9 wildfire and interaction terms ($F \leq 2.69$; $p \geq 0.103$).

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

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

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

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1 **Table 2** Mean tree stem growth with and without competition from lianas, from all known
 2 studies in tropical forests. Unless stated, data show annual increments per stem and liana
 3 absence was due to cutting. Alternative measurements of the same stems using different units
 4 are shown in parentheses. Ba=basal area, cm²; bio=biomass, kg; circ=rate of circumference
 5 increase, mm/mm; dbh, dbh₁₅=diameter at 1.3m or 1.5m, mm; dbh_{gr}=species-independent ten
 6 year growth residual derived from dbh, mm; h=height in m; RGR_{c,d,h,b}=relative growth rate
 7 (circumference at breast height, diameter at base, height, or biomass); %=percent increase in
 8 growth rate with lianas absent; Size=size of stems in the study (dbh, cm, unless stated);
 9 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 ^{al}	Bolivia (500m ^k)	2.2 dbh	2.6 dbh	18	≥10	3-8
Dauber et al. (2005) site 2 ^{al}	Bolivia (250m ^k)	4.1 dbh	7.0 dbh	71	≥10	2-3
Dauber et al. (2005) site 3 ^{al}	Bolivia (300m ^k)	2.6 dbh	4.1 dbh	58	≥10	7
Dauber et al. (2005) site 4 ^{al}	Bolivia (250m ^k)	3.2 dbh	3.6 dbh	13	≥10	1-4
Schnitzer et al. (2005) ^{a2,c,e}	Cote d'Ivoire (30m ^l)	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) ^{al}	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

1 ^aLianas not removed, instead compared ^{a1}trees with/without lianas, or ^{a2}trees planted
2 with/without planted lianas. ^bLiana-cutting combined with other silvicultural treatments.
3 ^cPlantation. ^dIncrements estimated from empirical models. ^eMean of focal species, mostly
4 commercial except for Álvarez-Cansino et al. (2015) and Wright et al. (2015). ^fForest trees
5 regenerating in fire-managed pasture. ^gData cited from an unpublished conference
6 presentation; size class inferred. ^hTree growth benefitted from liana absence in large gaps
7 (mean RGR: +14%; bio: +28%) but not small gaps/understorey (mean RGR: -1, +5; bio: -12,
8 -12); Only RGR_h was significant, for just one tree species in large gaps. ⁱMean of low,
9 medium and high light levels (18, 36 and 89% growth increase without lianas). ^jBiomass data
10 from Schnitzer et al. (2014). ^kElevation estimated from online map. ^lContrary to other studies,
11 however the highest liana density had a negative impact. *not significant.

12

13

1 Figure Legends

2 **Fig. 1** Map showing the location of forest within the Eastern Arc Mountains (top left),

3 Kilombero valley including digital elevation model (top right, including greyscale digital

4 elevation model 270-2100m), and the Magombera Conservation Area showing the location of

5 plots (red rectangle) and Kilombero Sugar Company land (dashed black line) (Kilombero

6 District, Morogoro Region; bottom map). Dark green = degraded primary forest (<90%

7 canopy loss; heavily degraded understorey/midstrata), mid green = secondary forest (canopy

8 $\geq 90\%$ canopy loss), pale green = woodland, pale yellow = grassland, grey =

9 agriculture/human settlement (bottom). Map by Nicolas Deere and Freddie Sutton, based on

10 ground-truthing (bottom) and data from Marshall et al. (2010; top right) and Platts et al.

11 (2011; top left).

12 **Fig. 2** Forest understorey dominated by lianas (mostly *Uncaria africana* G.Don, known by

13 the local Hehe tribe as “mtonasimba” (“lion’s grasp” in English), because of its hooked

14 spines [inset]).

15 **Fig. 3** Mean (and 95CI) biomass of stems 1-4.9cm dbh in plots managed by liana cutting

16 (n=10) and unmanaged (n=8), spanning 2007-2012.

17 **Fig. 4** Potential confounding influences on the effectiveness of liana cutting for sapling

18 regeneration per 25m² plot: (a) ANCOVA interaction between wildfire frequency and liana

19 cutting for the prediction of biomass recruitment in liana managed (solid line, closed points;

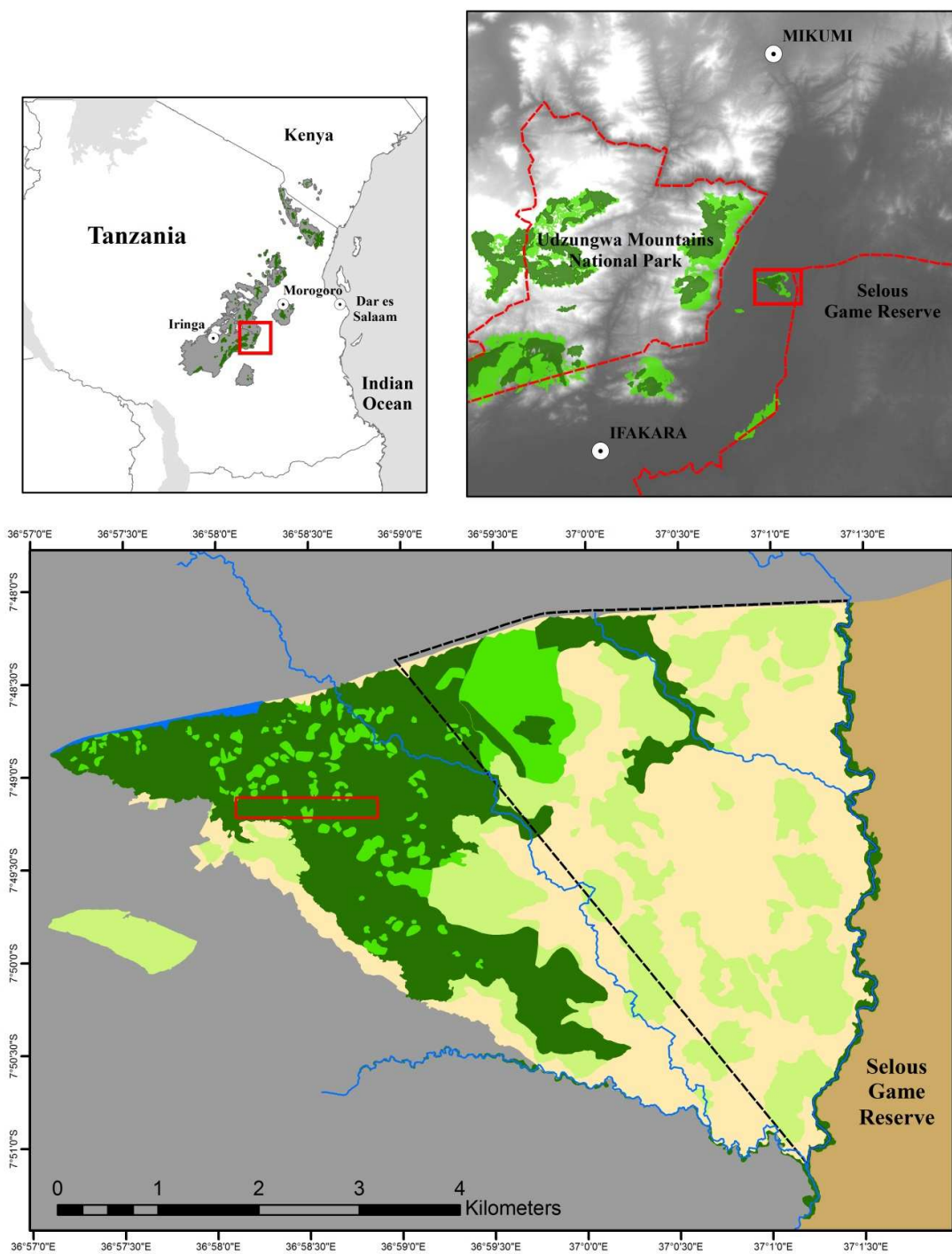
20 $p=0.06$) and unmanaged plots (dashed line, open points; $p=0.72$) ($\delta r^2=0.09$; Table 1), and (b)

21 proportional change in species richness decreasing with wildfire frequency (offset by ≤ 0.05

22 to reveal overlapping points; regression: $r^2=0.29$, $p=0.029$, $\alpha_{FDR}=0.01$).

23

1 Figures



2

3 Fig. 1

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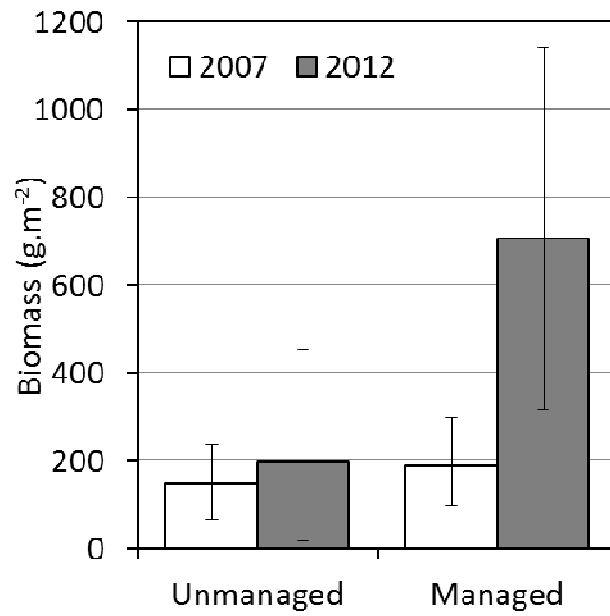
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3 Fig. 2

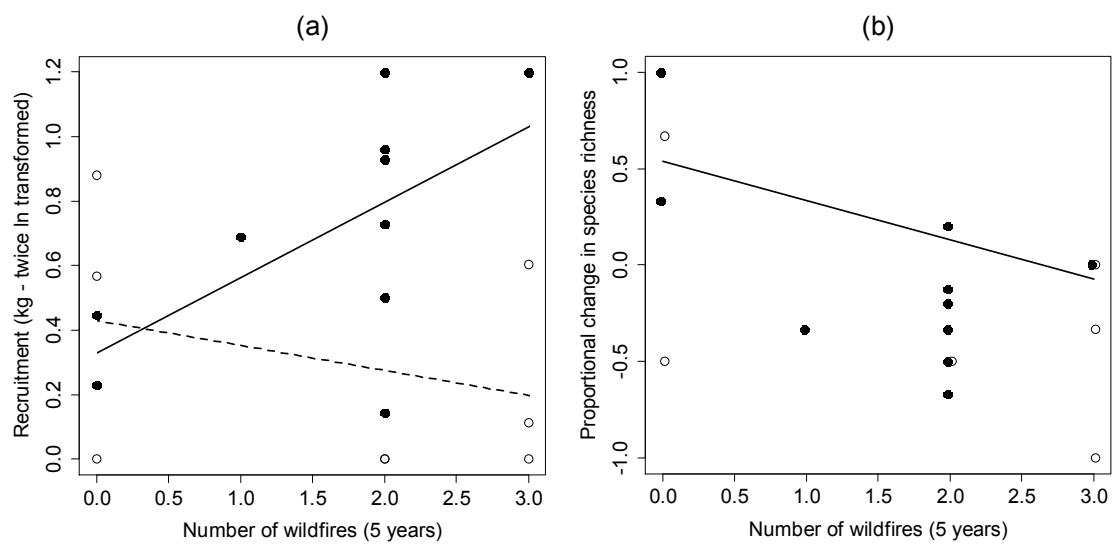
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3 Fig. 3

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2 Fig. 4

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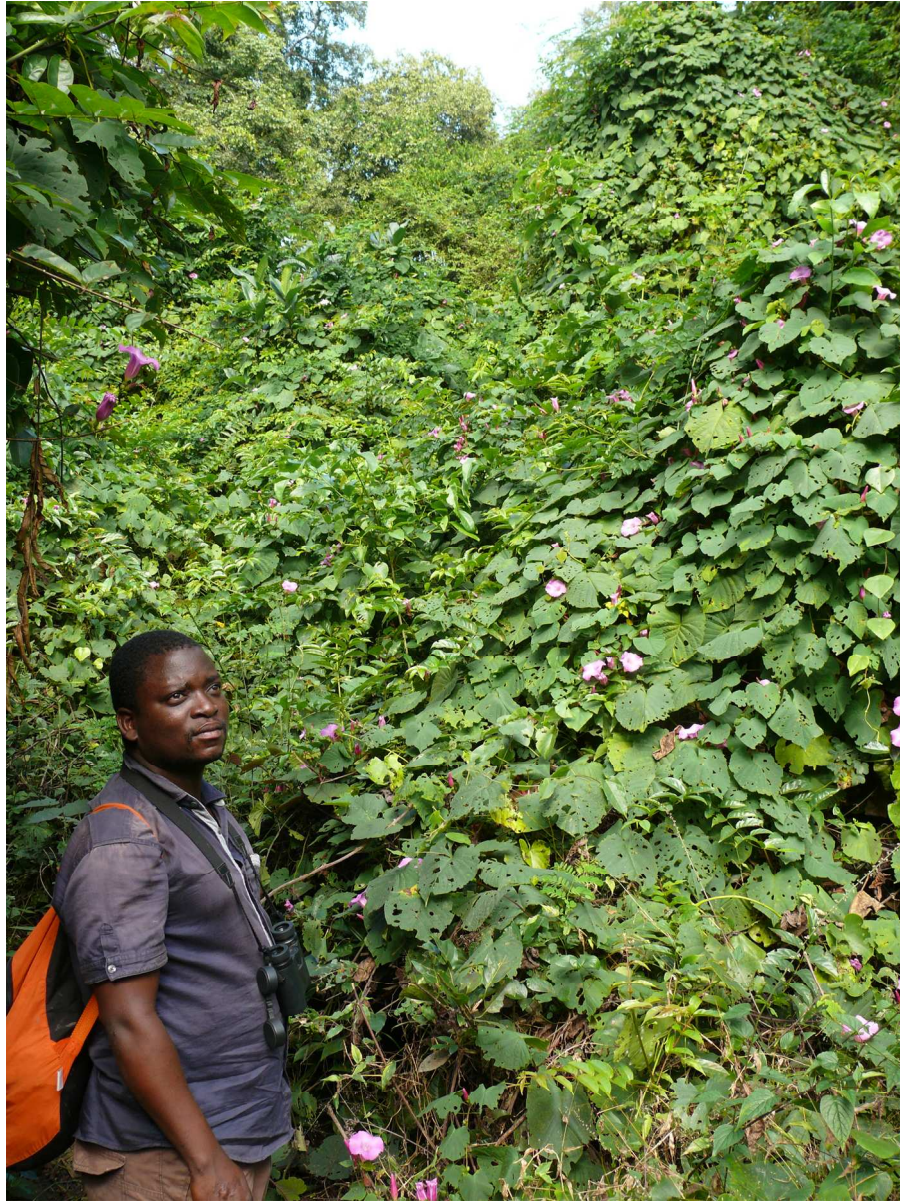
1 Supporting Information

2 **Table S1** Mean percentage of stems comprising the ten most common tree species (and 95CI) per unmanaged and liana-managed 5m×5m
 3 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
<i>Rothmannia macrosiphon</i> (K.Schum. ex Engl.) Bridson	37.5 (0.0-93.8)	<i>Mallotus oppositifolius</i> Müll.Arg.	30.9 (0.0-89.9)	<i>Lettowianthus stellatus</i> Diels* <i>Isoberlinia scheffleri</i> (Harms) Greenway*
<i>Calycosiphonia spathicalyx</i> (K.Schum.) Robbr.	18.8 (0.0-56.3)	<i>Leptactina platyphylla</i> (Hiern) Wernham	8.6 (0.0-25.9)	<i>Tapura fischeri</i> Engl. <i>Ochna holstii</i> Engl.*
<i>Tabernaemontana pachysiphon</i> Stapf	12.5 (0.0-37.5)	<i>Rawsonia lucida</i> Harv. & Sond.	6.5 (0.0-19.4)	<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan* <i>Lettowianthus stellatus</i> Diels*
<i>Markhamia lutea</i> K.Schum.*	6.3 (0.0-18.8)	<i>Aoranthe penduliflora</i> (K.Schum.) Somers	5.8 (0.0-14.4)	<i>Xylopia longipetala</i> De Wild. & T.Durand* <i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan*
<i>Tapura fischeri</i> Engl.	6.3 (0.0-12.5)	<i>Tapura fischeri</i> Engl.	5.8 (0.0-13.7)	<i>Pseudobersama mossambicensis</i> (Sim) Verdc.* (K.Schum.) Robbr. <i>Calycosiphonia spathicalyx</i> (K.Schum.) Robbr.
<i>Antiaris toxicaria</i> Lesch.*	3.1 (0.0-9.4)	<i>Rothmannia macrosiphon</i> (K.Schum. ex Engl.) Bridson	5.0 (0.0-15.1)	<i>Isoberlinia scheffleri</i> (Harms) Greenway* <i>Diospyros abyssinica</i> (Hiern) F.White *
<i>Blighia unijugata</i> Baker*	3.1 (0.0-9.4)	<i>Voacanga Africana</i> Stapf ex Scott Elliot	5.0 (0.0-11.5)	<i>Dracaena mannii</i> Baker <i>Tapura fischeri</i> Engl.
<i>Dialium holtzii</i> Harms*	3.1 (0.0-9.4)	<i>Tabernaemontana pachysiphon</i> Stapf	4.3 (0.0-10.8)	<i>Diospyros abyssinica</i> (Hiern) F.White * <i>Craterispermum schweinfurthii</i> Hiern
<i>Leptactina platyphylla</i> (Hiern) Wernham	3.1 (0.0-9.4)	<i>Croton sylvaticus</i> Hochst.*	3.6 (0.0-10.8)	<i>Aoranthe penduliflora</i> (K.Schum.) Somers <i>Xylopia longipetala</i> De Wild. & T.Durand *
<i>Mallotus oppositifolius</i> Müll.Arg.	3.1 (0.0-9.4)	<i>Diospyros kabuyeana</i> F.White	3.6 (0.0-7.2)	<i>Tabernaemontana elegans</i> Stapf <i>Tabernaemontana pachysiphon</i> Stapf
<i>Tricalysia pallens</i> Hiern	3.1 (0.0-9.4)			<i>Diospyros zombensis</i> (B.L.Burt) F.White

4 * Canopy species

5



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)

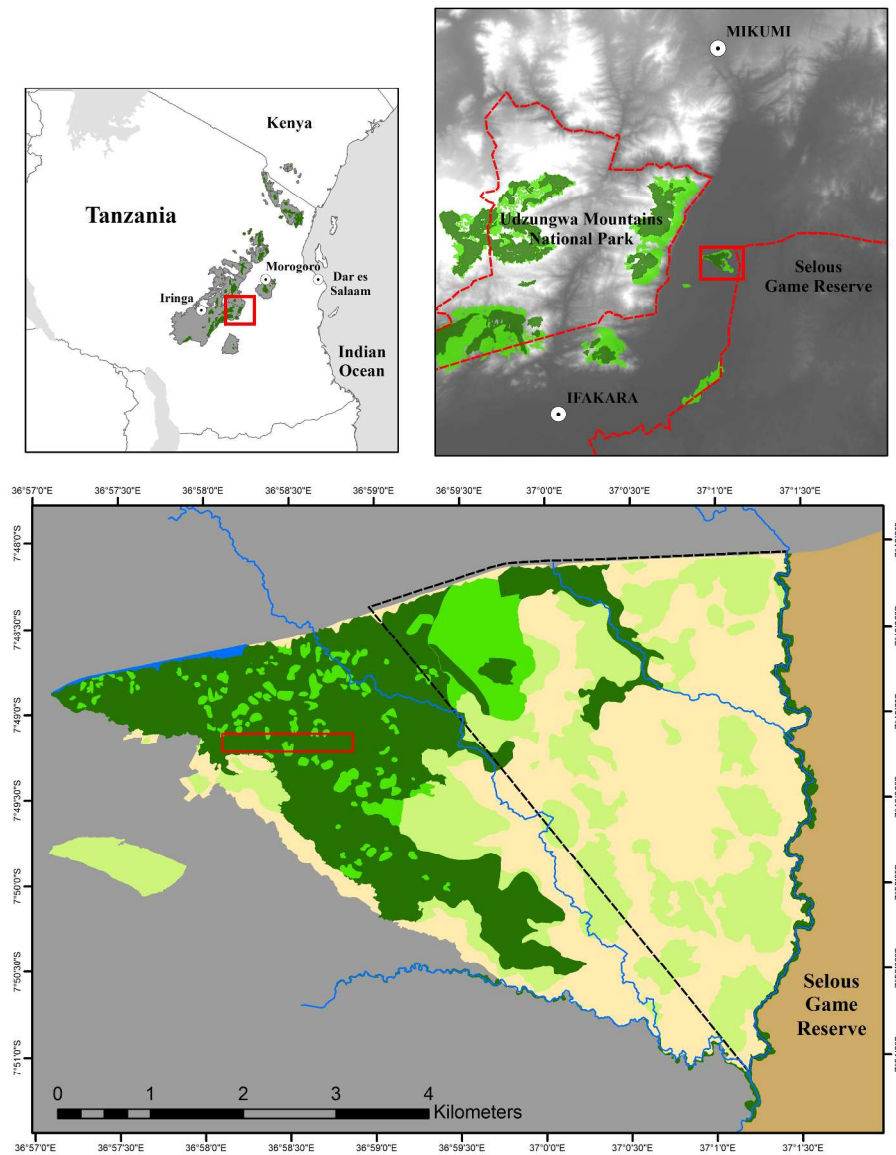


Fig. 1 Map showing the location of forest within the Eastern Arc Mountains (top left), Kilombero valley including digital elevation model (top right, including greyscale digital elevation model 270-2100m), and the Magombera Conservation Area showing the location of plots (red rectangle) and Kilombero 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 \geq 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).
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)

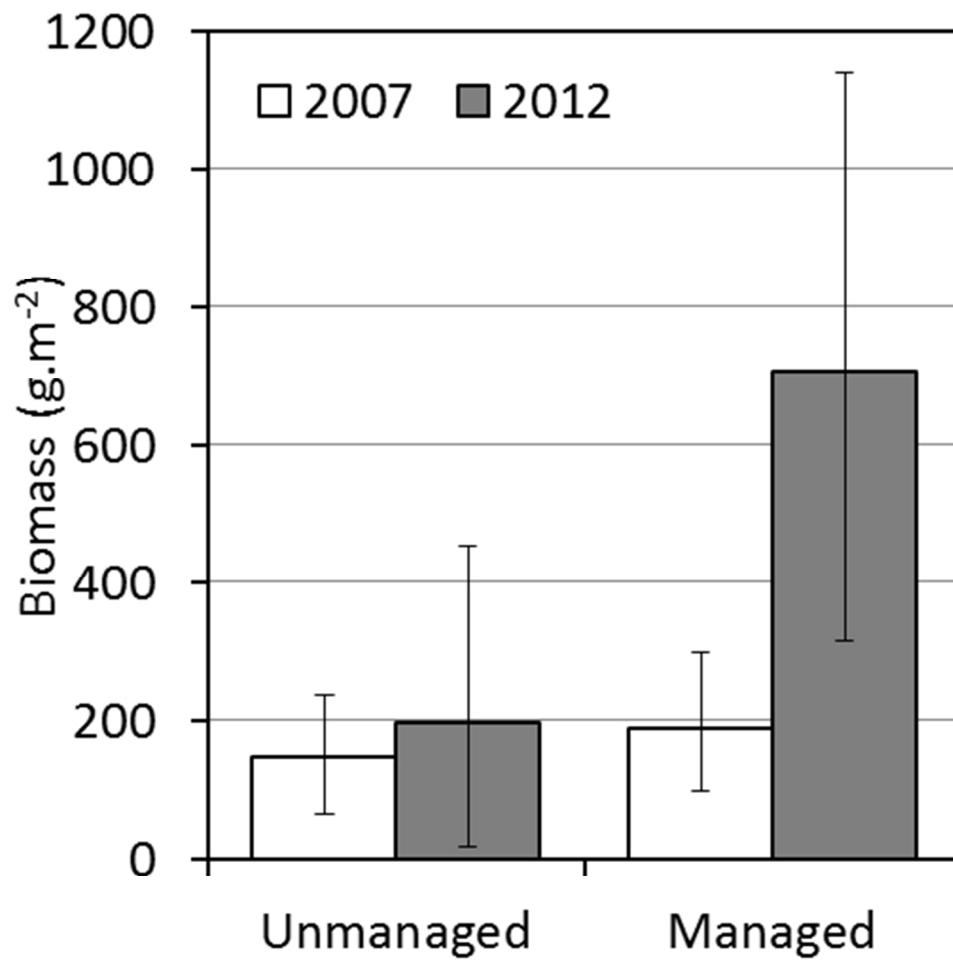


Fig. 3 Mean (and 95CI) biomass of stems 1-4.9cm dbh in plots managed by liana cutting (n=10) and unmanaged (n=8), spanning 2007-2012.
90x89mm (149 x 149 DPI)

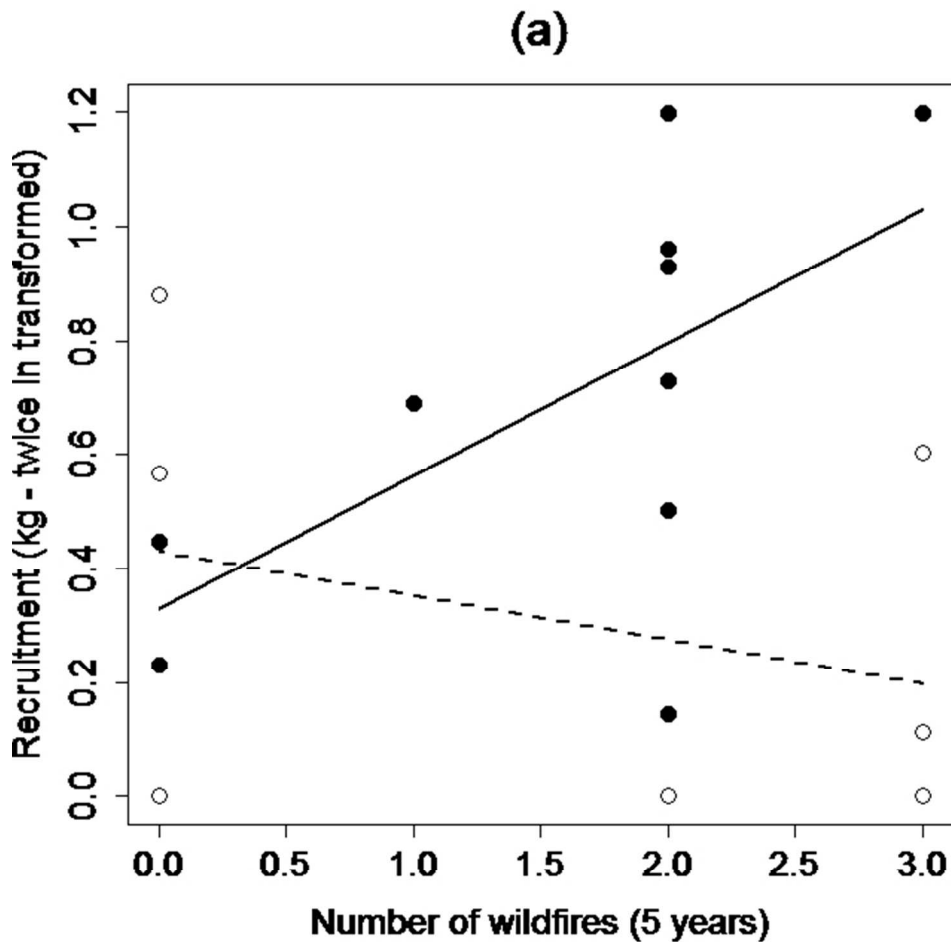
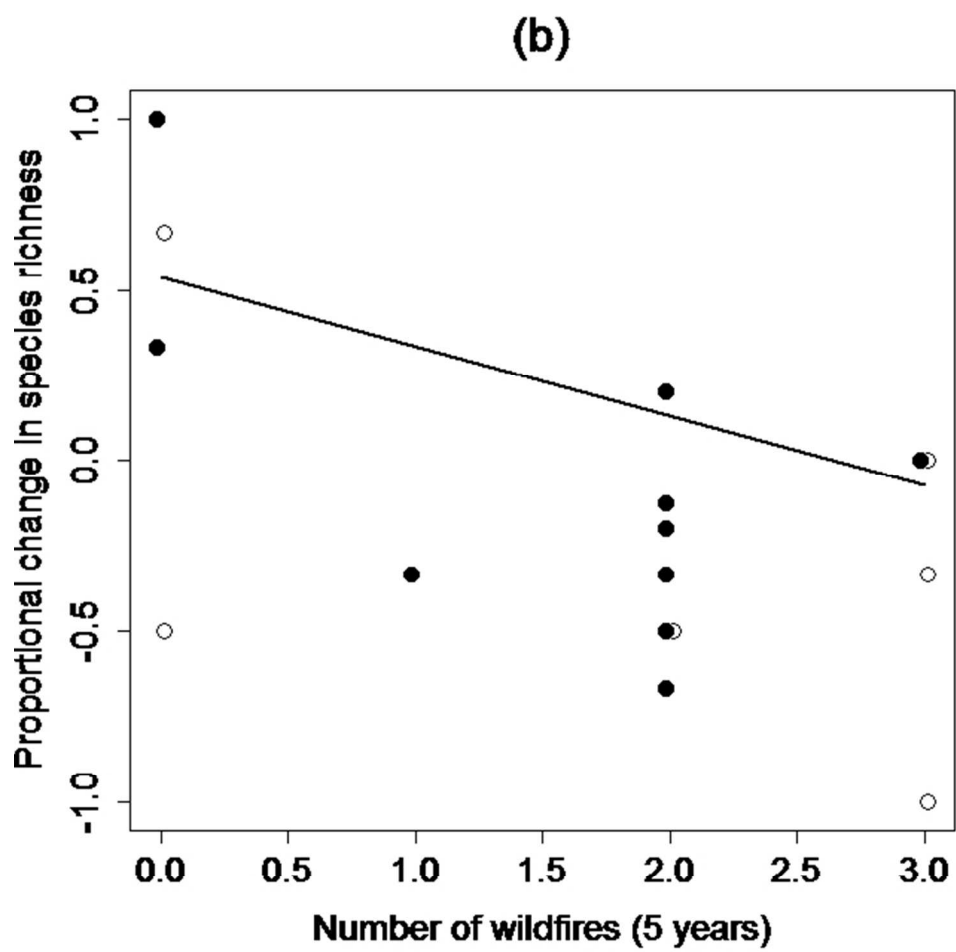


Fig. 4 Potential confounding influences on the effectiveness of liana cutting for sapling regeneration per 25m² plot: (a) ANCOVA interaction between wildfire frequency and liana cutting for the prediction of biomass recruitment in liana managed (solid line, closed points; $p=0.06$) and unmanaged plots (dashed line, open points; $p=0.72$) ($\delta r^2=0.09$; Table 1), and (b) proportional change in species richness decreasing with wildfire frequency (offset by ≤ 0.05 to reveal overlapping points; regression: $r^2=0.29$, $p=0.029$, $\alpha_{FDR}=0.01$).
143x143mm (119 x 119 DPI)



Same as Fig. 4a
143x143mm (119 x 119 DPI)