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Positive effects of liana cutting on seedlings are reduced during El Niño-induced drought

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Abstract

1. Liana cutting is a management practice currently applied to encourage seedling regeneration and tree growth in some logged tropical forests. However, there is limited empirical evidence of its effects on forest demographic rates in Southeast Asia.
2. We used 22 four-hectare plots in the Sabah Biodiversity Experiment (a reduced impact logging site) enrichment line planted with 16 dipterocarp species to assess the effects of complete liana cutting on tree growth and survival. We compared plots where lianas were only cut along planting lines (standard enrichment line planting) with those with one (2014) or two rounds (2011 and 2014) of complete liana cutting.
3. We found increased seedling growth following the first complete liana cut in 2011 relative to the enrichment line planting, consistent with previous studies. The response after three years to the cutting in 2014 depended on whether lianas had been previously cut or not: in twice-cut plots, seedling growth was not significantly different from the standard enrichment planting controls, whereas growth in plots with only one complete cut in 2014 was significantly slower. Seedling survival decreased through time for both once- and twice-cut liana treatments but remained stable in controls.

4. Sapling growth after the 2014 liana cutting showed a similar pattern to seedling growth, while tree growth following the 2014 liana cutting was significantly lower than controls regardless of whether lianas were cut twice (2011 and 2014) or once (2014).
5. Differences in response between the two rounds of liana cutting were likely due to changes in precipitation - 2011 was followed by consistent rainfall while 2014 was followed by two severe droughts within two years.
6. *Synthesis and applications.* Our results generally support the widely-reported positive effects of liana cutting on tree growth and survival. However, reduced growth and survival after the 2015/16 El Niño suggests that drought may temporarily undermine the benefits of liana cutting in logged tropical forests. Managers of similar areas in SE Asia should consider halting liana cutting during El Niño events. In other tropical areas, seedling survival should be monitored to assess to what extent results from SE Asia are transferable.

Keywords

Logged forest, tree demography, climate change, forest restoration, forest conservation, plant–climate interactions, tropical forest, liana

Introduction

Lianas and climbing bamboo (hereafter lianas) are important structural components of tropical rainforests that influence forest productivity and dynamics (Durán, Sánchez-Azofeifa, Rios, & Gianoli, 2015), and their relative abundance in tropical forests increases with dry season length and decreasing rainfall (DeWalt et al., 2010; Schnitzer, 2005;

Schnitzer & Bongers, 2011). Liana abundance also seems to be increasing in tropical forests globally (Schnitzer & Bongers, 2011) likely due to increasing drought frequency and severity under climate change (Cai et al., 2014; Dai, 2013; Walsh & Newbery, 1999) and logging, both of which promote liana proliferation (DeWalt et al., 2010; Laurance et al., 2001; Ledo & Schnitzer, 2014). This increase in liana abundance may enhance the negative impacts on tree demographic rates (i.e. reproduction, regeneration, growth and survival) in aseasonal and seasonal tropical forests alike (Magrach et al., 2016; S. J. Wright, Sun, Pickering, Fletcher, & Chen, 2015). Although the effect of lianas on forest dynamics has been studied in more seasonal tropical forests (Estrada-Villegas & Schnitzer, 2018; van der Heijden, Powers, & Schnitzer, 2015), empirical support for the effect of lianas on tree growth and survival remains limited in aseasonal forests of Southeast Asia, which are important biodiversity hotspots of both flora and fauna (Estrada-Villegas & Schnitzer, 2018; Myers, Fonseca, Mittermeier, Fonseca, & Kent, 2000; S. J. Wright et al., 2015).

Lianas affect forest dynamics through impacts on seedlings, saplings and trees (Estrada-Villegas & Schnitzer, 2018). Seedling regeneration — both growth and survival — is negatively impacted by liana abundance, especially in gaps where lianas can inhibit establishment of non-pioneer tree species (Schnitzer & Carson, 2010; Schnitzer, Dalling, & Carson, 2000). Growth and survival of saplings and trees are also commonly inhibited by lianas (Campanello, Genoveva Gatti, Ares, Montti, & Goldstein, 2007; Clark & Clark, 1990; Ingwell, Wright, Becklund, Hubbell, & Schnitzer, 2010; van der Heijden & Phillips, 2009; S. J. Wright et al., 2015). Seedlings and saplings, in particular, may experience strong competition for below-ground resources with lianas (Dillenburg, Whigham, Teramura, & Forseth, 1993; Schnitzer, Kuzee, & Bongers, 2005; Toledo-Aceves & Swaine, 2008). These results suggest nearly ubiquitous negative effects of lianas on tree demographic rates — i.e. growth, survival and reproduction (Estrada-Villegas & Schnitzer, 2018). Furthermore, these negative effects may increase with increasing drought (due to climate change) and logging (DeWalt et al., 2010; Laurance et al., 2001; Magrach et al., 2016).

While lianas are a natural component of tropical forests, land-use change by humans and increases in the frequency and severity of drought are promoting liana abundance and biomass (DeWalt et al., 2010; Ingwell et al., 2010; Laurance et al., 2001; Magrach et al., 2016; Phillips et al., 2002; Schnitzer & Bongers, 2011). The interaction between these global change drivers may enhance the negative effects of lianas on tree establishment, growth and survival, which presents a developing issue for tropical forest conservation (Magrach et al., 2016; Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). If logging and drought increase liana abundance, then the negative effects of lianas on trees are potentially increasing in logged forests, threatening forest recovery. On the other hand, if drought and logging severely decrease the tree canopy, liana cover in logged forests may promote tree seedling establishment and growth through amelioration of temperatures and water loss (Campanello et al., 2007), especially during El Niño induced drought when growing conditions become hotter and drier (Holmgren, Gómez-Aparicio, Quero, & Valladares, 2012; Holmgren & Scheffer, 2010).

Liana cutting (termed ‘climber cutting’ in some regions) is suggested as a management technique in some tropical forest regions with the intention of releasing seedling and adult trees from their competitive effects (Alvira, Putz, & Fredericksen, 2004; Grauel & Putz, 2004). There is strong empirical support that the silvicultural practice of liana cutting prior to felling reduces logging damage and improves forest recovery (Alvira et al., 2004; Lussetti, Axelsson, Ilstedt, Falck, & Karlsson, 2016; F. Putz, 1991). In addition, recent studies have shown positive effects of liana cutting in logged forests (i.e. after felling) for seedling, sapling and tree growth (Campanello et al., 2007; Estrada-Villegas & Schnitzer, 2018; Grauel & Putz, 2004). However, empirical evidence supporting post-felling liana cutting practices in Asia remains limited with most studies on lianas in tropical Asia focusing on liana community structure and diversity (Campbell & Newbery, 1993; DeWalt, Ickes, Nilus, Harms, & Burslem, 2006; Magrach et al., 2016; F. E. Putz & Chai, 1987) and pre-felling cutting (Lussetti et al., 2016; F. Putz, 1991).

We used experimental enrichment planted plots in a logged area of aseasonal lowland dipterocarp forest to test the effects of liana cutting on tree demographic rates. We removed all lianas twice (2011 and 2014) or once (2014) in 4-ha plots of the Sabah Biodiversity Experiment (SBE) and compared seedling, sapling and tree growth and survival in these treatments to rates in controls with lianas removed along seedling planting lines (but not in the areas between the lines). The control plots with standard enrichment line planting represent a common management practice to improve growth and survival of planted seedlings in Malaysian Borneo. We hypothesized that complete liana cutting would improve tree demographic rates by alleviating competition for water and nutrients and by increasing the understorey light availability.

Materials and methods

Site description

We established the experiment in Malua Forest nearby to the Malua Field Station (N05º05’20’’ E117º38’32’’; 102 MASL) within the Sabah Biodiversity Experiment (Hector et al., 2011; Tuck et al., 2016), which is approximately 22 km north of Danum Valley. This forest is located in eastern Sabah, has an aseasonal climate, an average monthly rainfall (se) of 240 mm (33) and an average yearly total of 2900 mm (90), as recorded at Danum Valley Field Centre over the last 25 years.

The primary forest in surrounding areas is dominated by dipterocarps, which have been the main target of the logging industry (Kettle, Maycock, & Burslem, 2012). Malua Forest was logged more than two decades ago and, except for the Sabah Biodiversity Experiment, was re-logged between 2004 and 2006 (Reynolds et al., 2011). The remaining forest consists primarily of fast-growing early successional species (e.g. *Macaranga* spp.) and lianas with dense patches of climbing bamboo and rattans. Remnant dipterocarps larger than 30 cm diameter at breast height are still present, estimated to be approximately 18 trees ha^{-1} (Berry, Phillips, Ong, & Hamer, 2008), and the vegetation composition and structure is heterogeneous due to variability in the topography and historical logging intensity.

Experimental design

The Sabah Biodiversity Experiment was designed in 2000/2001 and is described in detail in Hector et al. (2011). The experiment follows a randomized block design (2 blocks) in which 124 plots of 200 × 200 m were planted (starting 2002) with seedlings of either 1, 4 or 16 species of dipterocarp (32 replicates of each diversity level: 96 plots) or left unplanted (natural regeneration: 12 plots). In the enrichment planted plots, seedlings were planted every 3 m along cleared lines that were spaced 10 m apart (cleared lines were 1 – 2 m wide for a total of 20 lines). Species were selected from a pool of 16 that had seedlings available in adequate numbers. An additional 16 replicates of the 16-species plots were included to study the impacts of complete liana cutting after the experiment was fully established. Replicates of all treatments are divided equally between the two blocks with the exception (due to logistical site constraints) of the complete liana cutting where 10 plots are in the southern block and 6 in the northern.

The liana cutting sub-experiment uses 22 plots planted with the 16-species mixture, comparing measurements of survival and growth taken in 16 plots subjected to complete liana cutting (either one or two rounds of cutting) with those from 6 plots subject to standard enrichment line planting (complete cutting is used to distinguish the treatment from the line cutting control treatment). The size of the experimental plots and other logistical constraints meant that the complete liana cutting treatment was applied in two phases. In July 2011, we cut all lianas from 10 plots in the Southern Block of the SBE (every liana at least 10 cm in height was cut at base). Six standard enrichment planting plots were selected as controls which were identical except that liana cutting occurred solely in the seedling planting lines while retaining lianas between lines — i.e. 1 – 2 m of liana cutting and ~9 m of retained lianas (Dzulkifli, 2014). This standard enrichment line planting control represents a common management practice in Malaysia, and because the SBE is designed to test management practices, it provides the baseline treatment typically carried out in forest restoration. In June 2014, we performed a first complete liana cutting treatment for an additional 6 plots in the northern block. At the same time, we also performed a second round of complete liana cutting for the initial 10 plots in the Southern Block. Therefore, all lianas were cut twice (2011 and 2014) from 10 plots in the Southern Block and once (2014) from 6 plots in the Northern Block. There were six control plots, located only in the Southern Block.

Seedling measurements

Seedlings were measured in two lines, out of the twenty, within each of the SBE plots. To get the most precise estimates possible for as many of the 16 species as we could, the two lines in each plot with the most living seedlings were selected to maximize sample size (see Table S1 in the Supporting Information for seedling information). All seedlings within these lines were measured for height and diameter at 10 cm above the soil with calipers. Only diameter was used as the growth metric because height was not measured after seedlings reached ~4 m. We characterized the light environment based on canopy cover by taking hemispherical densiometer measurements in the four cardinal directions above the seedling (or around them in the case of tall seedlings). The first measurement was made in May 2011 (Dzulkifli, 2014) prior to the first liana cutting (n = 153 seedlings in control plots and n = 251 in complete-cutting plots). Measurements were made again in July and November of 2011 and in July 2012. Seedlings were then measured in May 2014 prior to the next complete-cutting and in July 2014 immediately after the treatment (n = 207 seedlings in control plots, n = 261 in complete-cutting plots twice-cut and n = 356 in complete-cutting plots once-cut). After the measurement in July 2014, seedlings were measured approximately every 3 to 6 months until May 2017.

Tree and liana measurements

Naturally-occurring saplings and trees were not monitored before May 2014, but prior to the 2014 complete-cutting, subplots of approximately 10 × 10 m were placed between the seedling planting lines to measure naturally-occurring saplings and trees in addition to the enrichment-planted seedlings. Subplots were selected by making a grid of 400 subplots within each 200 × 200 m plot and randomly selecting 10 subplots. Within each subplot 5 trees with a diameter at breast height (DBH; 1.3 m) of less than 4.95 cm and 5 trees of greater than 9.95 cm DBH were randomly selected, tagged and measured for DBH (see Table S2 in the Supporting Information for sapling and tree information). At three points along the diagonal of the subplot, a hemispherical densiometer reading was taken in four cardinal directions to characterize canopy cover in the subplot, and all lianas (i.e. rattans, climbing bamboo and lianas) above and below 5 cm diameter at base were counted (including young sprouts and seedlings at least 10 cm in height). If a liana had multiple stems that split before 10 cm of stem length, then each was treated as a separate individual. Therefore, our assessment of liana abundance was stem number (ramets) not number of rooted individuals (genets), which meant abundance was high relative to other studies (Addo-Fordjour, Rahmad, & Shahrul, 2012; Appanah, Gentry, & Lafrankie, 1993; DeWalt et al., 2006; F. E. Putz & Chai, 1987), especially when climbing bamboo was present (the most common species present in the plots) which tends to produce many sprouts from a single culm. Tree measurements and liana counts were done at the same time as the seedling measurements.

Drought estimation

We assessed drought (i.e. soil water deficit) from the rainfall data collected at Danum Field Centre from January 2011 to June 2017 using the model described by Daws, Mullins, Burslem, Paton, & Dalling (2002). Soil water deficit was assumed to be amount of rainfall required to return soil to field capacity. We assumed the soil profile is at field capacity following heavy rain (i.e. positive deficit values after extensive rain were set to 0 mm) and that soils are freely draining (Daws et al., 2002). We set daily evapotranspiration to 4 mm (Kumagai et al., 2005; Kume et al., 2011) and ignored declining evapotranspiration with decreasing water availability. From daily soil water deficit, we calculated the 30-day moving average of soil water deficit. This simple model allowed us to assess periods of severe soil water deficit through time, the onset of drought and the return of typical water availability.

Statistical analysis

We analyzed seedling growth separately for the first (2011) and second (2014) complete-cutting periods. The first assessment includes 5 measurements of seedling growth between May 2011 and May 2014 and analyzes seedling growth in the first once-cut treatment (2011) and the standard enrichment planting control. The second assessment includes 9 measurements of seedling growth between May 2014 to May 2017 and analyzes seedling growth in the second once-cut treatment (2014), the twice-cut treatment (2011 and 2014) and the control. Saplings, trees and liana recovery (i.e. re-sprouting of ramets and growth of new individuals) were only measured following the second complete-cutting in 2014, and therefore, these data are only assessed from May 2014 to May 2017. All analyses were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R statistical software (version 3.3.2; http://r-project.org).

Analysis of liana and canopy recovery

We used a mixed-effects model approach to analyse recovery of lianas and canopy openness after the second cut as a function of census (a factor with 9 levels), treatment (3 levels; control, once-cut and twice-cut) and their interaction with a Gaussian distribution. Number of lianas and percent canopy openness were log-transformed to meet assumptions of linearity. Random effects were used for plot (22 levels) and subplot nested in plot (220 levels). We used an *a priori* contrast to compare the two- and three-level versions of the cutting treatment (see Supplementary Table S3 for the Wald statistics).

Analysis of seedling growth

We used a two-stage analysis of growth in which we first estimate a growth rate for each individual seedling and then analyze these growth rates in relation to the experimental treatments. To estimate relative growth rate (RGR) for each seedling, diameter at base was log transformed and analyzed as a function of time (a continuous variable in months) in a linear mixed-effects model with random intercepts and slopes for individual seedlings. These RGRs where then analyzed using mixed-effects models that included the effects of all treatment and design variables (O'Brien, Ong, & Reynolds, 2017; O'Brien, Reynolds, Ong, & Hector, 2017). For the assessment of the first cutting, the relative growth rates were calculated from the initial pre-cutting measurement in May 2011 to the initial pre-cutting measurement before the second treatment in May 2014 (5 measurements). These relative growth rate values were analyzed as a function of climber treatment (a fixed factor with 2 levels; control and complete-cutting). Random effects were used for species (a factor with 16 levels), plot (16 levels), line nested in plot (32 levels) and species nested in plot (256 levels). A covariate for initial seedling diameter (a continuous variable in mm) was used to account for initial size differences among seedlings. See Supplementary Table S4 for the ANOVA table of Wald statistics and variance components.

For the assessment of the second complete liana cutting treatment, the relative growth rates were calculated from the pre-cutting measurement before the second cut in May 2014 to the final measurement in May 2017 (9 measurements in total). These relative growth rate values were analyzed as a function cutting treatment (a fixed factor with 3 levels; control, once-cut and twice-cut). We also used an *a priori* contrast to test whether control and complete-cutting treatments explained more variation than the number of complete-cutting treatments. Random effects were used for species (16 levels), plot (22 levels), line nested in plot (44 levels) and species nested in plot (352 levels). A covariate for initial seedling diameter (a continuous variable in mm) was used to account for initial size differences among seedlings. See Supplementary Table S4 for the ANOVA table of Wald statistics and variance components.

Analysis of sapling and tree growth

Because naturally-occurring saplings and trees were only measured after the second cutting, we only assessed their growth from May 2014 to May 2017 (9 measurements in total). We used the same method to estimated relative growth rate as described for the seedlings. These relative growth rate values were analyzed as a function of climber treatment (a fixed factor with 3 levels; control, complete-cutting once and complete-cutting twice). Random effects were used for plot (a random term with 22 levels) and subplot nested in plot (220 levels). A covariate for initial diameter (a continuous variable in mm) was used to account for initial size differences. We used an *a priori* contrast (a fixed factor with 2 levels: control vs. complete-cutting) in which the two complete-cutting treatments were combined to test for differences in response to whether lianas had been removed once or twice. See Supplementary Table S5 for the ANOVA table of Wald statistics and variance components.

Analysis of mortality

Seedling mortality after the first cut was low (<5% in control and <8% in complete-cutting treatments died between 2011 and 2014). In addition, tree and sapling mortality was low (<5% for trees and <8% for saplings averaged across all treatments died between 2014 and 2017). Therefore, there was not sufficient data for survival analysis of these groups. After the second liana cutting in 2014, seedling mortality increased, which allowed analysis of seedling survival from May 2014 to May 2017. Seedling survival as a binomial response (1 = alive and 0 = dead) was analyzed as a function of time (a continuous variable in months), treatment (a factor with 3 levels; control, once-cut and twice-cut) and their interaction with a binomial distribution and complimentary log-log link function. Random effects were used for species (16 levels), plot (22 levels), line nested in plot (44 levels) and line nested in plot nested in census (352 levels). As for growth, we used an *a priori* contrast to compare models with the two- and three-level versions of the cutting treatment (see Supplementary Table S6 for the Wald statistics).

Results

Liana and canopy recovery

Prior to liana cutting in 2014, plots without any previous cutting had liana densities similar to the control treatments having 4820 lianas ha^{-1} (95% CI: 3136 – 7408) and the previously uncut plots having 5239 lianas ha^{-1} (95% CI: 3409 – 8052). In contrast, the plots previously cut in 2011 had half the density due to resprouting climber bamboo culms and new seedlings (2165 lianas ha^{-1}, 95% CI: 1597 – 2935). Lianas greater than or equal to 5 cm diameter comprised 2% of the abundance in control plots, 1.2% in the previously uncut plots and 0.9% in the previously cut plots. Three years after the second cut, the liana density was fewer than 700 lianas ha^{-1} in the twice-cut treatment (Fig. 1a, b, c). The once-cut treatment after 3 years had slightly, but significantly, higher density with about 1200 lianas ha^{-1}. Liana density in the control treatment remained significantly higher than the complete-cutting treatments for the 3 years. By 2017, lianas greater than or equal to 5 cm diameter were mostly absent from the liana cutting treatments (see Supplementary Table S7 for liana densities by size class).

Prior to the second cut in 2014 (Fig. 1d, e, f), canopy openness was similar between the once-cut (8.8% canopy openness, 95% CI: 8.1 – 9.6), the control (8.1% canopy openness, 95% CI: 7.7 – 8.7) and the plots not previously cut (7.8% canopy openness, 95% CI: 7.3 – 8.2). Immediately after the second cut in 2014, canopy openness remained similar in the control (7.8% canopy openness, 95% CI: 7.2 – 8.4) but increased in the once-cut (10.5% canopy openness, 95% CI: 9.7 – 11.4) and twice-cut (8.9% canopy openness, 95% CI: 8.3 – 9.4) treatments. The only slight increase in canopy openness after the second cutting suggests the trees had filled the canopy after the first cutting, and lianas were less prominent in the canopy. Furthermore, the canopy openness returned to about 8% within 300 days after the second cutting (similar to the control levels). In contrast, the canopy in the once-cut treatment took longer to recover, remaining more open than the other two treatments until between 17 and 23 months after the cut.

Growth

Seedling relative growth rate for the three years after the first cut in 2011 was significantly faster in the once-cut treatment than in the standard enrichment planting control (difference in growth = 0.0007 mm mm^{-1} month^{-1}, 95% CI: 0.0002 – 0.001; Fig. 2a), which equates to about 12 mm of additional diameter growth per year. After the second complete-cutting in 2014, a significant effect of the cutting number was found (Fig. 2b) whereby seedlings in the once-cut treatment grew significantly slower than seedlings in the control (difference in growth = -0.003 mm mm^{-1} month^{-1}, 95% CI: -0.004 to -0.001), which equates to about 12 mm less diameter growth per year. Seedling growth was statistically indistinguishable between control and the twice-cut treatments (difference in growth = 0.001

mm mm^{-1} month^{-1}, 95% CI: -0.001 – 0.002), but twice-cut grew significantly faster than once-cut (difference in growth = 0.003 mm mm^{-1} month^{-1}, 95% CI: 0.002 – 0.005).

After the complete-cutting in 2014, saplings followed a similar growth pattern as seedlings (Fig. 2c). Saplings in the once-cut treatment grew significantly slower (0.002 mm mm^{-1} month^{-1}, 95% CI: 0.001– 0.003) and saplings in the twice-cut treatment significantly faster (0.004 mm mm^{-1} month^{-1}, 95% CI: 0.0035 – 0.0047) than saplings in the control (0.003 mm mm^{-1} month^{-1}, 95% CI: 0.0024 – 0.0038). However, trees were unaffected by the number of cuts (Fig. 2d), but instead, showed significantly slower growth in both of the complete-cutting treatments (once-cut = 0.0002 mm mm^{-1} month^{-1}, 95% CI: -0.001 – 0.002 and twice-cut = 0.002 mm mm^{-1} month^{-1}, 95% CI: 0.001 – 0.003) than in control (0.005 mm mm^{-1} month^{-1}, 95% CI: 0.003 – 0.006) regardless of the number of cuts.

Survival and drought

Seedling survival showed a significant interactive effect (see Table S6 for Wald statistics) between treatments and time since complete-cutting in 2014 (Fig. 3a) where the probability of survival in control treatments did not significantly decrease through time (change in probability of survival per month = -0.004, 95% CI: -0.012 – 0.004) while the probability of survival in complete-cutting treatments did (-0.013, 95% CI: -0.02 to -0.005). Therefore, the probability of seedling survival per month was statistically indistinguishable between control and complete-cutting treatments for the first 10 months, but by 25 months, complete-cutting treatments had significantly lower probability of survival and continued to decrease. During this 15-month period two severe El Niño induced droughts occurred whereby soil water deficit was as low as -126 mm and achieved levels below -50 mm three times within 2 years of the cutting (Fig. 3b).

Discussion

We first summarize the main results of our experiment before exploring them in greater detail below. First and foremost, our results are mostly consistent with the widely-reported beneficial effects of liana cutting for the growth and survival of trees — at least under typical climatic conditions experienced in years with regular precipitation patterns. However, they also caution that these positive effects could be temporarily reduced during El Niño events in logged forests of SE Asia that have been recently subjected to liana cutting — although areas that have had lianas previously removed (a few years earlier) do not show this loss of beneficial effects. Below we argue that the most parsimonious explanation for the reduction of the beneficial effects in newly liana-cut areas is El Niño induced drought which is likely more intense in the understorey of cut areas relative to controls due to the more open canopy that results in the year following liana cutting. This mediation of drought impacts by canopy openness would also explain why the benefits of liana cutting were maintained in the twice-cut plots during the El Niño event since our data show that in these areas, canopies were less open following compensatory growth by tree crowns after the first round of liana cutting. However, our results to date are based on a single event and require further testing over longer time periods and in other forest types (e.g. secondary, primary and seasonal forests) to establish their generality.

Liana recovery and canopy dynamics

The results suggest that complete-cutting did significantly reduce liana density, indicating that liana resprouting was hindered and that removing lianas twice reduces re-sprouting. Twice-cut treatments had lower liana densities both before and after the second complete-cutting in 2014 and both once and twice-cut treatments had significantly lower liana densities than control plots in 2017. However, the lack of differences in canopy openness between treatments in 2014 indicates that despite lower liana densities after one complete-cutting the canopy recovered to levels similar to the control. The rapid recovery of canopy cover in the twice-cut treatment after the second complete-cutting in 2014 suggests that lianas comprised a much lower proportion of leaf area in the canopy. In contrast, the once-cut treatment had significantly slower recovery of canopy cover, remaining open for 2 years, which supports previous findings on canopy openness following liana cutting (Perez-Salicrup, 2001; Rodríguez-Ronderos, Bohrer, Sanchez-Azofeifa, Powers, & Schnitzer, 2016). Overall, these dynamics suggest that liana cutting after one complete-cutting increased canopy openness while the impacts on the overstory of twice-cutting treatments was marginal, potentially suggesting one cut is sufficient to reduce the proportion of lianas in the canopy and allow compensatory regrowth of tree canopies.

Seedling growth after one complete liana cutting in 2011

For the 3 years following the first complete liana cutting in 2011, growth of planted seedlings significantly increased, although it was relatively small (a 5% increase in growth rate). For example, a single species in a logged forest in Panama had as much as a 66% increase in growth within the first 2 years of liana cutting in severely infested areas (Grauel & Putz, 2004). Another study in late-secondary forest in Panama (~60 year old forest) showed seedlings grew nearly three times faster with liana cutting, although the effect of liana cutting on growth was no longer present after 18 months (Martínez-Izquierdo, García, Powers, & Schnitzer, 2016). Our data are not able to identify the cause of the small growth increases relative to other studies, but we can suggest three potential hypotheses for the differences. First, our study site is aseasonal with rainfall distributed evenly throughout the year compared with other studies in seasonal forests that experience a dry season of 3 to 5 months (Grauel & Putz, 2004; Martínez-Izquierdo et al., 2016; Perez-Salicrup, 2001). Dry seasons may promote resistance to the increased temperatures (Campanello et al., 2007) and light associated with liana cutting (Perez-Salicrup, 2001; Rodríguez-Ronderos et al., 2016). Second, the liana abundance at our site was high (due to the inclusion of climbing bamboo, rattans and seedlings in our counts) relative to other estimates in Borneo (DeWalt et al., 2006; F. E. Putz & Chai, 1987). Therefore, the difference in the understorey environment before and after cutting would be greater relative to other studies, which may have resulted in initial stress following liana cutting that delayed a growth response even with an improved light environment. Finally, our control had liana cutting in the lines where seedlings were planted (standard enrichment planting technique in Sabah and the region) whereas other studies used controls with no liana cutting at all (Grauel & Putz, 2004; Martínez-Izquierdo et al., 2016). Our control with liana cutting in lines may be sufficient to increase seedling growth without removing all lianas. Therefore, our controls were likely growing faster than closed-canopy controls in other studies (Martínez-Izquierdo et al., 2016). In addition, this effect indicates that complete liana cutting may not be necessary to stimulate seedling growth. Further studies assessing a gradient of liana cutting (i.e. 25, 75 and 100% cutting) under different levels of liana densities (i.e. high and low) on seedling growth would provide valuable insights into more accurate liana cutting prescriptions.

Seedling growth and survival after complete liana cutting in 2014

Seedlings in plots with the first complete cutting of lianas in 2014 had significantly slower growth for the 3 years following liana cutting. We argue that this contrasting response between seedlings with liana cutting in 2011 and 2014 was due to differences in the climate for the years following the 2011 and 2014 liana cuttings. After 2011, the 30-day running average of water deficit remained above -50 mm, indicating consistent precipitation with few dry periods. In contrast, after 2014, there was two periods of severe drought within two years of the liana cutting (the first beginning within 8 months before canopy openness had recovered). The combined effects of increased canopy openness and understorey light due to liana cutting (Campanello et al., 2007) and decreased precipitation, humidity and cloud cover due to drought may have promoted increased understorey temperatures, higher vapour pressure deficits and greater evaporative demand on seedlings. Therefore, the drought may have had a more pronounced negative effects on seedlings without liana cover than those with partial liana cover. Lianas may provide a facilitative effect to understorey seedlings during drought, even in this aseasonal system (Holmgren et al., 2012; Holmgren & Scheffer, 2010; A. Wright, Schnitzer, & Reich, 2015), by buffering seedlings from poor growing conditions — i.e. increased temperatures and evapotranspiration rates (Campanello et al., 2007). Although previous studies have not found pronounced negative effects of liana cutting on soil moisture (Campanello et al., 2007; Perez-Salicrup, 2001; Reid, Schnitzer, & Powers, 2015), these studies also did not experience precipitation patterns outside the normal cycles of the system (i.e. no droughts) whereas our study period had 2 periods of severe drought. Regardless of decreased soil moisture, higher vapour pressure deficit and solar radiation alone, could cause water and temperature stress on seedlings in liana cut areas.

Seedling growth of the twice-cut treatment after 2014 was unaffected by the drought, which may be due to faster tree canopy closure than in the once-cut treatment as lianas had reduced abundance due to the previous cutting in 2011 — i.e. lianas comprised a lower proportion of the canopy and a second cut had limited impact on canopy openness (Rodríguez-Ronderos et al., 2016). Therefore, the effect of liana cutting on canopy openness in the twice-cut treatment was minimal, and the twice-cut treatment likely experienced less extreme shifts in the understorey conditions relative to the once-cut treatment. Overall, seedling growth was slower in the period following the complete-cutting in 2014, but the magnitude of the reduction was dependent on the number of complete-cuttings with the twice-cut treatment being less sensitive to the climatic conditions than the once-cut treatment. These contrasting sensitivities between once- and twice-cut treatment support the importance of sufficient recovery time between liana cutting and drought (more than 12 months) to allow seedlings to adjust to the new environment or for compensatory growth of the tree canopy to fill open space and restore cover (~17 months). Prediction of El Niño induced drought remains challenging, but scientists continue to improve their models, which are extending prediction horizons to more than a year (L'Heureux et al., 2017; Ludescher et al., 2014; Park, Kug, Li, & Behera, 2018) thereby reducing the difference between the onset of El Niño and planning liana cutting. Therefore, incorporating our results into a temporal management plan around El Niño cycles still requires technological advancements in climate and atmospheric sciences before accurate and temporally relevant predictions of El Niño can be made for managers in the field.

Probability of seedling survival decreased significantly through time in complete liana cutting treatments but not in the control treatment with partial liana cutting. Although the percentage difference in risk on a per month basis is 6%, this results in a doubling of seedling mortality levels over a year. This result further supports the reduction in growth that was found and suggests that the increased canopy openness combined with the El Niño induced droughts negatively impacted seedlings while the line cutting controls were potentially buffered by the maintenance of canopy cover between lines (Holmgren et al., 2012; Holmgren & Scheffer, 2010).

Growth of naturally-occurring saplings and trees

Saplings followed a similar pattern as seedlings after the 2014 cutting with the twice-cut treatment having increased and the once-cut treatment having decreased growth relative to controls, further supporting the negative effects of severe drought following liana cutting and the benefits of multiple liana cuttings for reducing those effects. Surprisingly, trees responded with reduced growth relative to controls regardless of the number of complete-cuttings. However, reduced diameter growth may be due to a shift in allocation to height, leaf production or reproductive success and may not be indicative of a negative effect (Stevens, 1987). Furthermore, the differences in these relative growth rates for large diameter trees are biologically small (i.e. 0.5 mm difference in 12-month incremental growth between the control and once-cut treatments). Alternatively, reduced relative growth rates could indicate water limiting growth or shifts in the timing of growth due to the drought (O’Brien, Ong, et al., 2017). Regardless of the cause, slightly reduced diameter growth rates did not lead to high mortality, and therefore, the response does not directly equate to an overall negative effect of liana cutting on trees, at least in the short-term. Instead, these results indicate a potentially plastic response in resource allocation and growth of trees in response to liana cutting and highlights the need for more holistic measurements of tree responses to liana cutting.

Conclusions

Although tropical studies of lianas in the Americas and Africa have commonly shown positive effects of liana cutting on seedling and sapling growth and survival, our results show a more complex dynamic whereby climate can alter the direction and magnitude of the effects of liana cutting on seedlings and saplings in logged everwet forests of Southeast Asia. The more open canopies of plots that have had lianas recently removed may have led to increased temperatures and vapour pressure deficit during the severe El Niño induced drought of 2015/16 causing growth to become inhibited and probability of survival to decrease. Our results suggest that the management practice of removing lianas to encourage seedling regeneration is effective under typical climatic conditions (i.e. consistent high rainfall). However, with increased drought under climate change, liana cutting may come with a risk of reduced growth and increased mortality in logged forest of SE Asia. These results need further support from studies encompassing multiple droughts and across other forest types including seasonal and secondary forests.

Authors’ contributions

The 2011 liana cutting project was conceived and designed by AH and GR with advice from RO (the local collaborator on the project 2011 - 2018). DD, CDP, JS and MOB implemented the initial measurements and treatments. MOB managed the experiment beginning in 2014 with the addition of the tree, sapling and liana recovery measurements. MOB analyzed the data and wrote the manuscript with revisions from AH and GR and input from all authors.

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Data accessibility

'Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.2sq2d (O’Brien et al., 2018)

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Supporting information

Table S1: Summary of seedling abundance and size in each treatment in 2014.
Table S2: Summary of sapling and tree abundance and size in each treatment in 2014.
Table S3: ANOVA of liana density and canopy openness.
Table S4: ANOVA of seedling RGR for first and second cut.
Table S5: ANOVA of saplings and trees RGR.
Table S6: ANOVA of seedling survival after second cutting.
Table S7: Summary of liana densities per hectare.

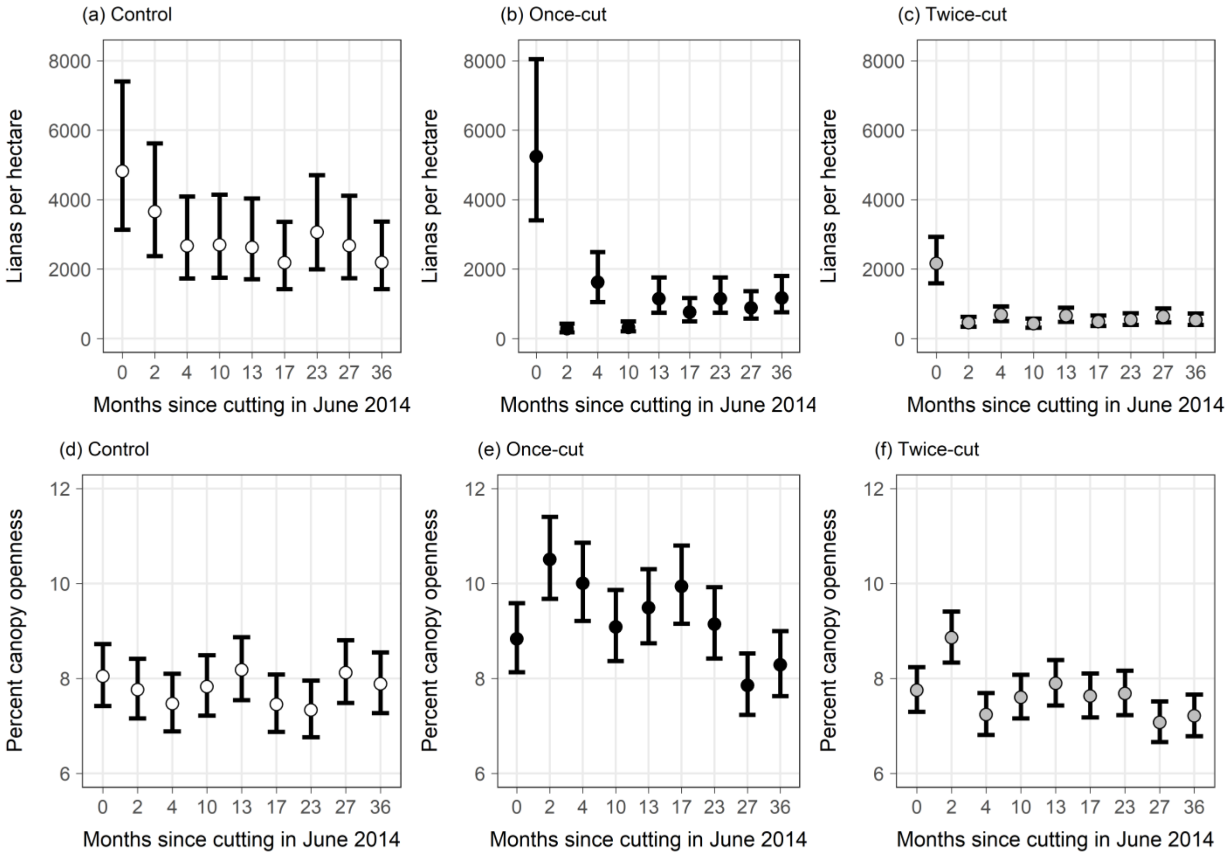

Fig 1. Liana and canopy openness dynamics. Number of lianas (95% CI) per hectare for in the a) control, b) once-cut (2014) and c) twice-cut (2011 and 2014) treatments over time since the complete-cutting in June 2014. Percent canopy openness (95% CI) in the d) control, e) once-cut and f) twice-cut treatments. Liana density after adding one and percent canopy openness were log-transformed to meet assumptions of linearity but were back transformed and presented on the normal scale.

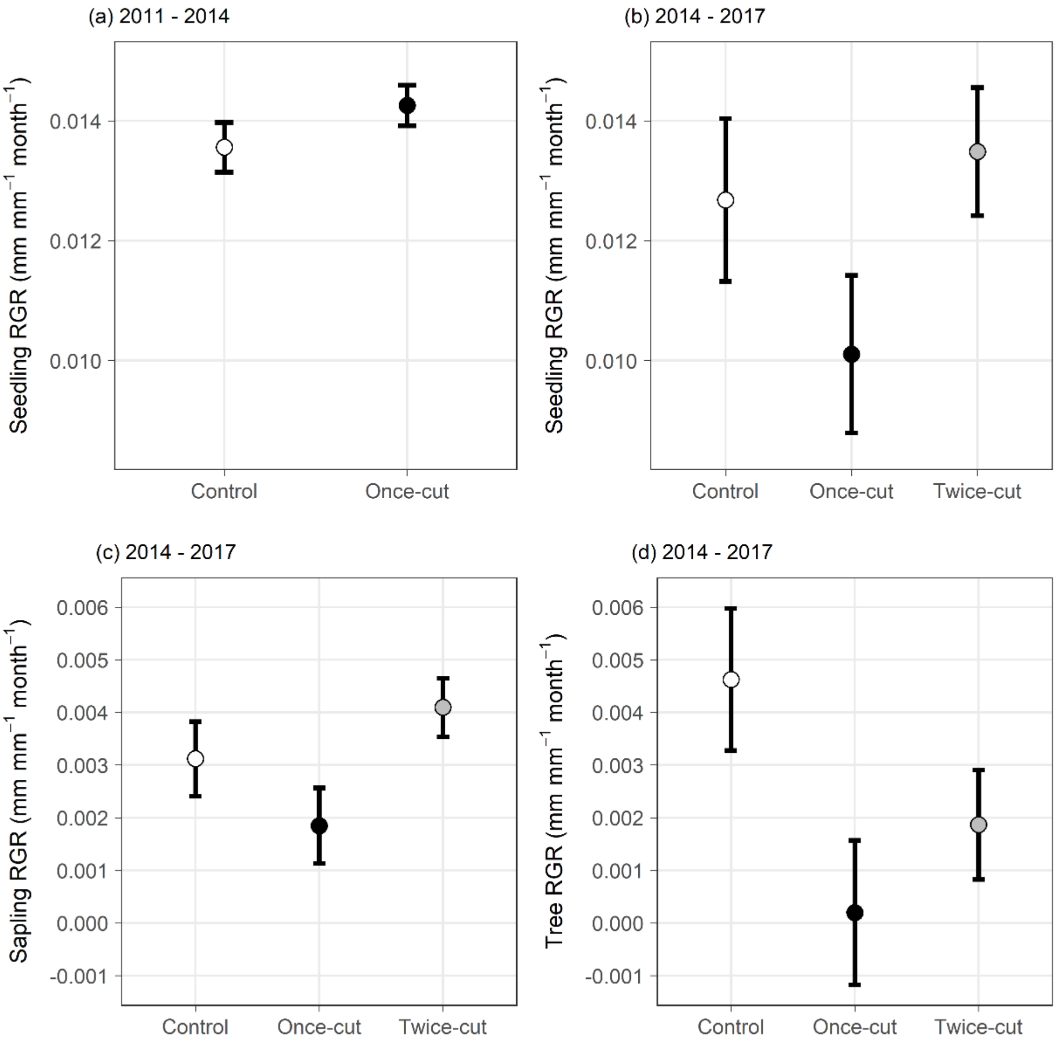

Fig 2. Relative growth rate of enrichment-planted seedlings and naturally-established saplings and trees. (a) Relative growth rate (95% CI) for seedlings grown in the control and complete-cutting treatments between May 2011 and May 2014 following the first cut. (b) Relative growth rates for seedlings grown in the control, once-cut and twice-cut treatments between May 2014 and May 2017 following the second cut. The once-cut treatment in 2011 became the twice-cut treatment after the 2014 complete-cutting. (c) Relative growth rate (95% CI) for saplings in the control, once-cut and twice-cut treatments. (d) Relative growth rates for trees in the control, once-cut and twice-cut treatments.

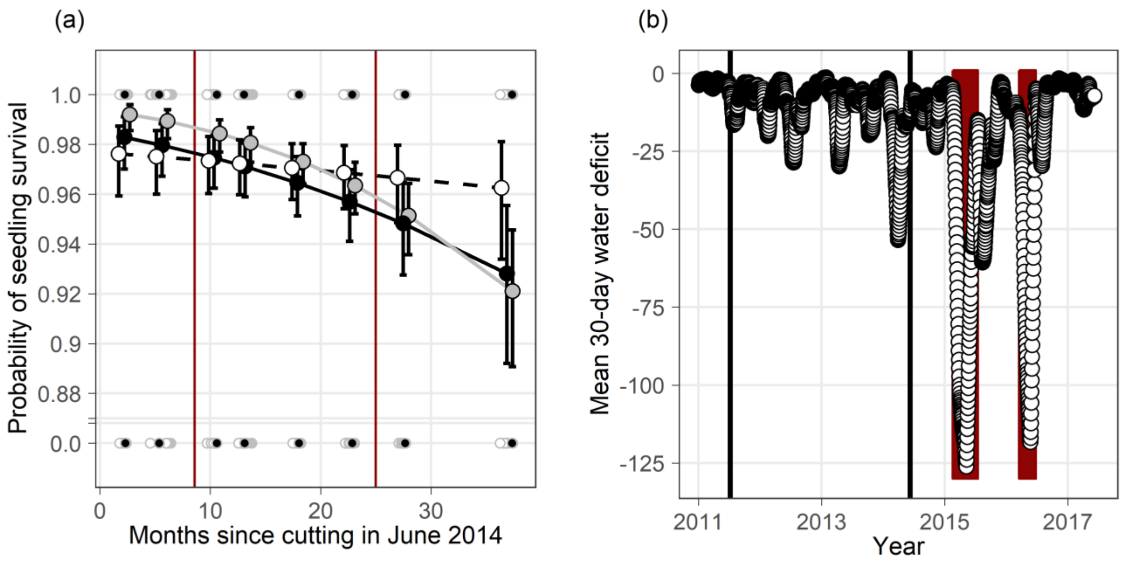

Fig 3. Seedling survival. (a) Probability of survival (95% CI) for seedling in the control (dashed-line and ○), once-cut (black line and ●) and twice-cut (grey line and ●) treatments since the complete-cutting in June 2014. The red lines represent the approximate onset of two drought periods in March 2015 and July 2016. The double line break is used to allow clear presentation of the data from a 0 to 1 scale. (b) The mean 30-day water deficit during the entire period (January 2011 to June 2017). The black vertical lines represent the onset of the two complete-cuttings and the solid red bars represent the severe El Niño induced drought following the 2014 complete-cutting, which are the red lines represented in (a).