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A Comprehensive Synthesis of Liana Removal Experiments in Tropical Forests

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Abstract

Lianas are a quintessential feature of tropical forests and are often perceived as being poorly studied. However, liana removal studies may be one of the most common experimental manipulations in tropical forest ecology. In this review, we synthesize data from 64 tropical liana removal experiments conducted over the past 90 yr. We explore the direction and magnitude of the effects of lianas on tree establishment, growth, survival, reproduction, biomass accretion, and plant and animal diversity in ecological and forestry studies. We discuss the geographical biases of liana removal studies and compare the various methods used to manipulate lianas. Overall, we found that lianas have a clear negative effect on trees, and trees benefitted from removing lianas in

nearly every study across all forest types. Liana cutting significantly increased light and water availability, and trees responded with vastly greater reproduction, growth, survival, and biomass accumulation compared to controls where lianas were present. Removing lianas during logging significantly reduced damage of future merchantable trees and improved timber production. Our review demonstrates that lianas have an unequivocally detrimental effect on every metric of tree performance measured, regardless of forest type, forest age, or geographic location. However, lianas also appear to have a positive contribution to overall forest plant diversity and to different animal groups. Therefore, managing lianas reduces logging damage and improves timber production; however, the removal lianas may also have a negative effect on the faunal community, which could ultimately harm the plant community.

Lianas are a ubiquitous and characteristic component of tropical forests. The presence of lianas, perhaps more than any other physiognomic feature, is often considered to be the single most distinguishing characteristic of tropical forests compared to temperate forests (Schnitzer & Bongers **2002**). Lianas are woody vines that are rooted in the ground and typically use trees to ascend to the forest canopy. They are a diverse, polyphyletic guild that can be found in nearly one-quarter of the world's plant families (Gianoli **2015**). Lianas commonly contribute 25% of the woody stems in lowland tropical forests (Schnitzer & Bongers **2002**, Schnitzer *et al*. **2012**, **2015a**, Wyka *et al*. **2013**). In terms of diversity, lianas can contribute up to 35% of the woody species, which is far higher than would be predicted by stem number alone (Schnitzer *et al*. **2012**, **2015b**). Lianas also provide food sources to insects, birds and mammals, particularly when trees are not flowering or fruiting (Morellato & Leitao-Filho **1996**). By linking treecrowns, lianas provide aerial pathways that are utilized by many animal species (Yanoviak & Schnitzer **2013**).

Lianas compete intensely with trees in tropical forests. Lianas climb their tree hosts and deploy their foliage in the high-light environment at and near the top of the forest canopy, thus competing intensely for light (Putz **1984b**, Toledo-Aceves **2015**, Rodríguez-Ronderos *et al*. **2016**). Lianas also compete with trees for belowground resources (Dillenburg *et al*. **1995**, Schnitzer *et al*. **2005**, Álvarez-Cansino *et al*. **2015**). Lianas have been shown to reduce tree survival (van Der Heijden & Phillips **2009**, Ingwell *et al*. **2010**), fecundity (Kainer *et al*. **2014**, García León *et al*. **2018**), recruitment (Schnitzer & Carson **2010**), and the growth of tree seedlings, saplings, and adults (Pérez-Salicrup **2001**, Schnitzer *et al*. **2005**, Álvarez-Cansino *et al*. **2015**, Martínez-Izquierdo *et al*. **2016**).

Lianas also appear to reduce several important emergent properties of communities and ecosystems, such as tree diversity and forest-level biomass uptake (Schnitzer & Carson **2010**, van der Heijden *et al*. **2013**, **2015**, Schnitzer *et al*. **2014**, Schnitzer **2015**, Ledo *et al*. **2016**). Given that lianas commonly infest up to 75% of the trees in tropical forests (van der Heijden *et al*. **2008**, **2015**, Ingwell *et al*. **2010**), they likely compete with the vast majority of trees in tropical forests. Thus, determining the ecology of lianas and their effects on trees is essential to fully understand the structure, diversity, and dynamics of tropical forests (Schnitzer *et al*. **2015a**).

Most observational studies in tropical forest ecology have ignored lianas and instead have focused on trees. For example, of the 46 large-scale sampling plots in the Center for Tropical Forest Science plot network, only four have sampled lianas (Makana *et al*. **2004**, Carson & Schnitzer **2008**, Schnitzer *et al*. **2012**, **2015a**, Bongers & Ewango **2015**, Thomas *et al*. **2015**), only one plot sampled lianas across the entire 50 hectares (Schnitzer *et al*. **2012**, **2015a**), and in all cases, liana censuses were initiated many years after the tree censuses were completed (but see Laurance *et al*. **2001**). Moreover, very few large-scale studies in tropical forest ecology have quantified liana abundance or liana infestation levels of trees. Quantifying the effects of lianas on trees appears to be especially important in explaining tree growth and survival, as well as the accumulation of biomass over long time periods (Ledo *et al*. **2016**, Visser *et al*. **2018**). Additionally, many of the large-scale and influential studies on lianas have examined only very large lianas (*e.g.*, Phillips *et al*. **2002**, Chave *et al*. **2008**), which are not particularly common (Schnitzer *et al*. **2012**, **2015a**). However, this latter trend is beginning to change and more studies now include much smaller lianas (*e.g*., DeWalt *et al*. **2015**). With the recent recognition that lianas alter many important forests processes, there has been a burst of large-scale experimental studies on lianas (Kainer *et al*. **2014**, Álvarez-Cansino *et al*. **2015**, van der Heijden *et al*. **2015**, Reid *et al*. **2015**, César *et al*. **2016**, Lussetti *et al*. **2016**, García León *et al*. **2018**).

Although lianas have been largely ignored in observational studies, experimental work on lianas, mainly liana cutting manipulations, have a long history in ecology and forestry. Indeed, the effects of lianas on trees may be one of the most experimentally manipulated plant-plant interaction in tropical forest ecology. Over the past 90 yr, there have been 64 liana removal studies in tropical forests. These experiments range from a focus on a single tree species spanning a time range of 5 mo to 10 yr (Pérez-Salicrup & Barker **2000**, Kainer *et al*. **2014**), to studies on multiple tree species that spanned 28 yr (Okali & Ola-Adams **1987**). Experimental studies have been conducted in many tropical areas, ranging from the Solomon Islands to Malaysia, to Nigeria, Cameroon, Bolivia and Surinam (Neil **1984**, Okali & Ola-Adams **1987**, Parren & Bongers **2001**, Dekker & de Graaf **2003**, Forshed *et al*. **2008**, Villegas *et al*. **2009**). The wealth of information that has been learned from liana removal experiments includes how lianas reduce tree recruitment, growth, survival, reproduction, biomass uptake and allocation, and community-level species diversity and carbon dynamics.

There have been a number of important reviews of the liana literature (Schnitzer & Bongers **2002**, Isnard & Silk **2009**, Paul & Yavitt **2011**, Wyka *et al*. **2013**, Schnitzer *et al*. **2015a**) and a recent study reviewed and quantified part of the literature on the effect of lianas (and liana cutting) on annualized tree growth and biomass (Marshall *et al*. **2017**). However, no review has comprehensively summarized the full liana removal experiment literature and synthesized their results. In this review, we examine the extensive literature on liana removal experiments and summarize the evidence on the effects of lianas on tree establishment, growth, survival, and reproduction in tropical forests across the globe. We categorize studies by their focal area, either ecology or forestry, and whether the liana manipulation was paired with other manipulations such as tree removal and canopy thinning. In each focal area, we address the following questions: (1) are the effects of lianas on tree establishment, survival, growth, biomass, reproduction, forest diversity and forest fauna in tropical forests positive or negative? (2) Are the effects of lianas on tree mortality and gap formation during logging positive or negative? (3) Where are liana manipulation studies carried out, and do the effects observed differ by global region? (4) What are the most common methods used in liana manipulation experiments, and do they differ in efficacy? In this review, we examine the extensive literature on liana removal experiments and summarize the evidence on the effects of lianas on tree establishment, growth, survival, and reproduction in tropical forests across the globe. We categorize studies by their focal area, either ecology or forestry, and whether the liana manipulation was alone or paired with another manipulation, such as tree removal and canopy thinning. In each focal area, we examine the extent and magnitude of the effects that lianas have on tree establishment, growth, survival, and reproduction, which provides a clear picture of the effects of lianas on tropical forest trees and on community and ecosystem processes. We also review the limited literature on the positive contributions of lianas to tropical forest processes, particularly their positive contribution on forest animals. We identify the geographic locations and forest types where liana manipulations have been conducted, as well as where they are poorly studied. We discuss the methods that have been used in liana manipulation experiments and the efficacy of different methods. Finally, we identify major gaps in liana experimentation, and provide suggestions for future experiments that will ultimately provide a more comprehensive understanding of the role of lianas in forests worldwide.

Compiling and Summarizing the Results of Liana Removal Experiments

We found a total of 64 published studies spanning the past 90 yr that used liana removals to explore the role of lianas in tropical and subtropical forest ecosystems (Table **1** and Table **S1**). To amass the liana experimental literature, we first searched the public comprehensive liana data base that is maintained by the LianaEcologyProject.com. To ensure that we did not omit any relevant studies, we then searched Web of Science on March 17, 2014, with the words 'liana' and 'experiment' or 'removal'. We selected studies performed *in situ* in tropical ecosystems and excluded studies that were conducted exclusively in greenhouses. We also checked the references of the liana removal studies, which often lead to additional older experiments. We included studies published after 2014 as they became available online and we ended our search in October of 2017.

Table 1. Number of publications, time range of publications, and time for a liana removal to have an effect on trees

	Effect of liana cutting on trees	**Liana cutting as silvicultural treatment**	**Liana cutting and tree elimination/harvesting as silvicultural treatments**
Total number of publications	20	21	23
Time range of publications	1987–2017	1960–2016	1927–2013
Data papers	20	18	20
Review papers	0	3	3
Rainfall precipitation range (papers that report it)	1450–2600 (18)	1200–3050 (14)	1050–4000 (17)
Duration of study	3 d to 10 yr	2 mo to 18 yr	2 mo to 28 yr

We begin our review by summarizing experimental studies on liana-tree competition, emphasizing on more recent studies, and then show how lianas affect plant growth, biomass accumulation, reproduction, tree forest diversity and forest fauna. All the studies, with one exception, reported that lianas reduced the performance of adult tree, saplings, or seedlings (Table **1** and Table **S1**).

Results of Liana Removal Experiments

Competition with trees

Lianas compete with trees for both light and soil resources, and the use of these resource by lianas contributes to the reduction in performance of adult trees, saplings and seedlings. A recent review by Toledo-Aceves (**2015**) summarized how lianas and trees compete above and belowground. We use that review, together with liana removal literature, to elucidate the complexity of tree- liana competitive interaction.

Five studies found that lianas have a measurable effect on light penetration into the interior of tropical forests. For example, in a large liana removal experiment in a moist forest in Panama, Rodríguez-Ronderos *et al*. (**2016**) found that lianas attenuated approximately 20% of the light that arrived at the forest canopy. That is, they found that light increased 20% 1-yr following the removal of lianas in eight 80 × 80 m plots (with eight additional same-sized plots serving as controls). Light penetration remained high in the eight liana removal plots compared to the eight controls for the first 2 yr. Four years after the initial liana removal, however, trees appeared to have fully compensated for the loss of liana leaves, and light penetration did not differ between liana removal and control treatments (Rodríguez-Ronderos *et al*. **2016**). Also in Panama, in 17 natural treefall gaps, Schnitzer and Carson (**2010**) found that lianas blocked a significant proportion of light by comparing the leaf area index before and after removal. Such changes in the light regime allowed shade-tolerant species to increase their relative growth rate by 56%, whereas growth rates of shade-intolerant species were invariant to the increase in light availability (Schnitzer & Carson **2010**). In dry forests in Bolivia and Brazil, canopy openness and light penetration in the understory were 4–12% higher in liana removal than control plots (Pérez-Salicrup **2001**, César *et al*. **2016**), which allowed seedlings to increase twofold in height and fivefold in biomass. In an Amazonian dry forest, canopy light transmission doubled from pre-cutting to post-cutting, and this difference remained for 2 yr following liana removal (Gerwing **2001**). In sum, lianas decrease light availability for trees, which affects tree growth and survival is due, in part, to competition for light (see Growth and Biomass subsections below).

Lianas may also decrease soil moisture, and removing lianas may result in higher soil moisture availability for trees. Using a large-scale liana cutting experiment in a moist forest in Panama, Reid *et al*. (**2015**) showed that the removal of lianas increased surface water availability (10 cm depth) 5 mo after liana cutting, and increased water availability in deeper soil layers after 3 yr. Two processes may explain the results of Reid *et al*. (**2015**). Removing lianas results in fewer roots that are competing for water, which increases soil moisture. In the long run, higher evapotranspiration due to higher irradiance following liana removal can dry the topsoil layer, while deeper layers remain moist. In fact, lianas are thought to transpire more water than similar sized trees, and lianas may also absorb water from deeper soil layers (Restom & Nepstad **2001**, **2004**, Andrade *et al*. **2005**). However, not all studies were able to detect an effect of lianas on soil moisture. A study in Bolivia reported that a reduction in liana abundance did not affect soil water moisture on the topsoil layer and at 1 m depth (Pérez-Salicrup **2001**). Detecting higher soil moisture following liana removal is difficult because upon liana cutting trees immediately begin to use available soil moisture (Tobin *et al*. **2012**, Álvarez-Cansino *et al*. **2015**), reducing soil moisture to low levels. Nonetheless, the experimental results from Reid *et al*. (**2015**), and the correlative physiological studies that compare tree and liana rooting depths, indicate that lianas reduce soil water moisture.

Lianas can alter the water balance of trees, presumably via competition for water during seasonal drought (Toledo-Aceves **2015**). Three studies have shown that removing lianas increased the water status of trees, which, in turn, enhanced tree growth. In a seasonal moist forest in Panama, Álvarez-Cansino *et al*. (**2015**) showed that liana removal significantly increased sap velocity on 53 canopy trees of six species. The increase in sap flow was correlated with a positive effect on diametric growth (Álvarez-Cansino *et al*. **2015**). Most importantly, these effects were more pronounced during the dry season, when soil moisture is at its lowest, and disappeared during the wet season, when soil moisture was not limited (Álvarez-Cansino *et al*. **2015**). Working in the same forest, Tobin *et al*. (**2012**) removed lianas from four canopy trees of different species and found that tree sap velocity increased by 8% compared to the four control trees. They also removed a comparable amount of tree and liana biomass from canopy trees and found that sap velocity did not change following tree removal compared to the control trees, demonstrating that liana-tree competition has a much larger negative effect on canopy trees than does tree-tree competition when controlling for biomass (Tobin *et al*. **2012**). Similarly, in a highly seasonal dry forest in Boliva, Pérez-Salicrup and Barker (**2000**) removed lianas from 10 trees of *Senna multijuga* (Caelsalpinioideae) and reported that leaf water potential increased immediately after removing lianas and remained higher than controls for the 5-mo study period. Furthermore, trees without lianas grew twice as much as controls over this same period (Pérez-Salicrup & Barker **2000**). In a companion study, however, Barker and Pérez-Salicrup (**2000**) showed no noticeable effects of removing lianas on the stomatal conductance and leaf water potential of four trees of *Swietenia macrophylla* (Meliaceae), indicating that lianas do not have the same negative effect on the water status on all species. Finally, in a dry forest in Côte d'Ivoire, Schnitzer *et al*. (**2005**) reported that competition from lianas on tree saplings appeared to be for belowground resources, and was likely for water (see also Dillenburg *et al*. **1993**, **1995**). Similarly, in a moist forest in Panama, Wright *et al*. (**2015**) showed that tree seedlings compete strongly with lianas when rainfall (and thus soil moisture) is scarcer, whereas tree seedlings compete with other understory vegetation for light when rainfall is high. In sum, liana removal experiments show that lianas compete intensely with trees for soil moisture, particularly during the dry season, and for light at the top of the canopy.

Tree growth

Lianas reduce tree growth. For example, following liana removal, relative annualized growth rates of large trees (≥10 cm diam.) increased between 25% to 372% (Grauel & Putz **2004**, Campanello *et al*. **2007**, Grogan & Landis **2009**, Schnitzer & Carson **2010**, Álvarez-Cansino *et al*. **2015**). Lianas had a similar negative effect on tree seedlings and saplings. In an Amazonian dry forest, mean tree diameter growth doubled over a 2-yr period in liana removal plots for trees larger than 5 cm diameter and nearly tripled for trees 2–5 cm diameter (Gerwing **2001**). In a Panamanian forest, tree seedlings of 14 different species grew 300% taller over a 2-yr period in liana removal plots compared to the control treatments (Martínez-Izquierdo *et al*. **2016**). In a moist forest in Tanzania, in small plots where lianas were 'touching or obstructing all "sapling" trees stems', seedlings on removal plots grew 119% more in diameter over a five-period year compared to control plots (Marshall *et al*. **2017**). In studies in Neotropical forests, many sapling species in the forest understory grew between 54% to 213% more in removal plots versus control plots (Gerwing **2001**, Pérez-Salicrup **2001**, Grauel & Putz **2004**, Wright *et al*. **2015**). In an analysis of published studies, Marshall *et al*. (**2017**) found the same direction and similar magnitudes for experimental and observational studies using weighted quantitative comparisons for growth rates. In sum, eleven liana removal experiments unequivocally demonstrate that lianas reduce the growth of tree seedlings, saplings and adults.

Forest biomass

Lianas reduce tree and ecosystem biomass accumulation, but liana biomass uptake does not compensate for the biomass that they displace in trees. Schnitzer *et al*. (**2014**) removed lianas from treefall gaps in a seasonal tropical moist forest in Panama and found that, after 8 yr of removal, trees without lianas accumulated 180% more biomass than trees in control gaps where lianas were present. In this study, forest biomass accumulation in the absence of lianas was mainly due to a large increase in tree growth and a minor decrease in tree mortality compared to the control gaps (Schnitzer *et al*. **2014**). Lianas themselves, however, could not account for the biomass that they displaced in trees (Schnitzer *et al*. **2014**). In a large-scale liana removal study in 16 80 × 80 m plots (eight liana removal and eight control plots) in Panama, van der Heijden *et al*. (**2015**) examined the effects of lianas over a 3-yr period and determined that lianas reduced tree biomass uptake by 76% annually. Moreover, they found that lianas altered forest-level biomass allocation. In areas where lianas were removed, 44% of forest biomass productivity was in the form of woody tissues and 33% in leaves. In forests where lianas were present (*i.e*., control plots), only 29% of the forest biomass productivity was in the form of woody tissues and 53% in leaves (van der Heijden *et al*. **2015**). Thus, because lianas invest more biomass in leaves than stems, the presence of lianas appears to alter the forest-level allocation of carbon into leaves, which are rapidly recycled, thus increasing forest carbon turnover.

Experimental studies outside of Panama showed a similar trend in tree biomass gain following liana removal. In a subtropical moist forest in Brazil, César *et al*. (**2016**) reported that tree sapling biomass increased 52% after 1 yr of liana removal compared to control plots. In an experiment in a tropical dry forest in Côte d'Ivoire, Schnitzer *et al*. (**2005**) showed that planted tree saplings accumulated 436% more biomass after 2 yr in plots where lianas were removed compared to control plots where lianas were present. Likewise, in Tanzanian moist forest, Marshall *et al*. (**2017**) reported that sapling tree biomass increased 109% after 5 yr of liana removal compared to control plots. In summary, five studies have shown that lianas are able to reduce tree growth and survival, which results in lower biomass accumulation in tropical forests.

Tree reproduction

Five liana removal experiments show that lianas reduce tree reproduction at both the population and community levels. Two years after removing lianas from five adult *Bursera simarouba* trees in Costa Rica, fruit production increased by 148%, compared to the mean annual fruit production over the previous 5 yr

(Stevens **1987**). In an Amazonian moist forest in Brazil, Kainer *et al*. (**2006**) removed lianas from 78 Brazil nut trees (*Bertholletia excels,* Lecythidaceae) and found that, after 4 yr, fruit production increased threefold compared to 60 control trees. Kainer and colleagues followed these same trees for six more years and reported that, after 10 yr, fruit production was 77% higher in the liana removal treatment compared to control treatment (Kainer *et al*. **2014**). In a degraded fragment in Brazil, César *et al*. (**2017**) showed that the total number of seeds produced increased fivefold 1 yr after liana removal compared to controls. In a large-scale liana removal study in Panama, the number of tree individuals and species that were fruiting was substantially higher in plots where lianas had been removed compared to control plots where lianas were present. Specifically, García León *et al*. (**2018**) examined the reproductive output of 576 canopy trees comprising nearly 60 species and found that 5 yr after cutting lianas, the number of trees bearing fruit was 150% higher in liana removal plots than in control plots. They also found that the number of canopy tree species with fruits was 109% higher in liana removal plots than in control plots. Collectively, these findings show that lianas have a strong detrimental effect on tree reproduction.

Tree species diversity

Four studies have used liana removal manipulations to examine the effects of lianas on tree species diversity. For example, in naturally occurring gaps in a moist forest in Panama, Schnitzer and Carson (**2010**) found that tree species richness increased significantly for both shade-tolerant and intolerant species after 8 yr of liana removal. However, community composition of all species between control and removal plots did not differ (Schnitzer & Carson **2010**). In a dry forest in Brazil, Gerwing (**2001**) found that the sapling (>25 cm tall and <2 cm diameter) composition of the most abundant tree species was significantly different in liana removal plots than in control plots. However, tree species composition was not determined prior to the experiment, so there is no way to determine whether these differences were not present prior to the manipulation. Finally, two long-term studies (>20 yr), one in a dry forest in Nigeria and the other in a moist forest in Surinam, suggested that liana removal did not have a long-term effect on forest composition (Okali & Ola-Adams **1987**, Dekker & de Graaf **2003**). However, these results are contentious because the effect of liana removal was confounded with the effects of silvicultural practices such as tree girdling (Dekker & de Graaf **2003**) or prescribed burnings (Okali & Ola-Adams **1987**). Girdling and burning could have masked the effect of liana removal because the structural damage and the elimination of seedlings and saplings could have had more lasting consequences than did the liana removal alone (Gerwing **2001**). In sum, lianas may reduce species richness and alter the composition of abundant species, but additional studies are still necessary to determine the extent of these effects.

Forest fauna

Only one published study, as far as we are aware, has experimentally assessed the effects of lianas on forest fauna. In a tropical moist forest in Venezuela, Mason (**1996**) found that liana cutting increased bird richness and evenness, perhaps due to an increase in species that benefit from disturbance without eliminating the species that depend on old growth forests. Additional information on the effects of lianas on animal communities comes from correlative (observational) studies, and it shows that lianas are key food sources and essential for animal movement throughout the forest canopy in tropical forests (Arroyo-Rodríguez *et al*. **2015**, Michel *et al*. **2015**, Yanoviak **2015**). For example, howler monkeys and muriquies consume lianas when other food sources are in short supply (Martins **2006**, Dunn *et al*. **2012**). Lianas are also a vital food source for pollinators because trees and lianas often flower asynchronously (Morellato & Leitao-Filho **1996**). Lianas facilitate animal movement between tree's canopies. For example, sloths use lianas to move from crown to crown (Chiarello *et al*. **2004**), and ant community structure is affected by the presence of lianas by connecting treecrowns and allowing the persistence of solitary foraging ants (Adams *et al*. **2017**).

In conclusion, the experimental evidence shows that lianas have consistent negative effect on trees, including tree recruitment, growth, reproduction, and survival. Lianas also decrease tree sap flow, which correlates strongly with tree growth, and thus supports the hypothesis that lianas decrease water availability. The liana-induced reduction in tree growth likely has important implications in limiting tree reproductive output, which will have consequences on forest tree demography and community composition. By reducing tree growth, lianas limit whole-forest biomass accumulation (Schnitzer *et al*. **2014**, van der Heijden *et al*. **2015**). However, lianas have a positive effect on increasing forest-level plant diversity (Gianoli **2015**) and lianas provide important resources and connectivity for forest animals.

Results of Removing Lianas in Forestry Experiments

Although forestry-related studies are sometimes overlooked by ecologists, foresters have experimented extensively with removing lianas and trees to maximize timber production. Of the 64 liana removal experiments that we found, 44 were conducted in a silvicultural context. A subset of these experiments (23) used liana removal in conjunction with tree elimination (thinning) or tree harvesting as silvicultural treatments (Table **1**). All the forestry-related studies concluded that lianas negatively affect trees.

Fifteen forestry experiments concluded that lianas had a detrimental effect on tree growth and seedling regeneration. For instance, in a wet tropical forest in Belize, liana cutting and tree girdling increased the number of seedlings of mahogany trees (*Swietenia macrophylla*) up to 389% over a 17-mo period (Stevenson **1927**). In wet and dry forests in both Neotropical and paleotropical sites, liana cutting and tree girdling increased the basal area and growth of adult trees of several different commercial species by 20% to 72% compared to control plots where lianas were present (Barnard **1955**, Baidoe **1970**, Lowe & Walker **1977**, Putz *et al*. **1984**, Okali & Ola-Adams **1987**, Schwartz *et al*. **2013**, Venturoli *et al*. **2015**). In a Costa Rican wet forest, Guariguata (**1999**) found that four timber species grew significantly more after both adjacent trees and lianas were eliminated, presumably because the timber trees received more resources such as sunlight and nutrients. In two dry forests in Bolivia, Peña-Claros *et al*. (**2008b**) and Villegas *et al*. (**2009**) reported that girdling smaller trees (<10 cm dbh) and cutting lianas increased tree diameter growth by 33% to 50%, respectively. Contrary to these results, Duncan and Chapman (**2003**) found that vegetation removal (including lianas and shrubs) had a positive response on some species after 1 yr of removal, but the effect disappeared in the second year. They concluded that the poor response of trees was due to the high-light availability at their plots, making the competitor removal manipulation inconsequential.

The combination of liana and tree removal also increases tree growth and biomass. For example, 28 yr after silvicultural treatment in a dry forest in Nigeria, Okali and Ola-Adams (**1987**) showed that tree biomass in liana/tree removal plots increased by 70% compared to control plots. In a dry forest in Bolivia, Peña-Claros *et al*. (**2008a**) found that after 4 yr of removing both lianas and trees, tree growth increased by 60% after timber extraction compared to areas where lianas and trees were not removed. These authors used Reduced-Impact Logging (RIL) practices (*e.g*., selective logging, liana cutting prior to felling, skid row planning), which reduce damage to the forest during logging operations (Pinard *et al*. **1995**). In a recent study in a wet forest in Malaysia, Lussetti *et al*. (**2016**) demonstrated that cutting lianas followed by selective logging doubled tree biomass at the stand level in a forest that had been logged 18 yr earlier, and increased dipterocarp tree biomass by approximately 81% over the 18-year study. In sum, the experimental data from forestry studies indicate clearly that lianas have a strong detrimental effect on tree production and forest-level biomass accretion.

Tree mortality during logging

One of the goals of foresters is to determine whether cutting lianas will reduce post-felling tree damage during logging. Lianas can bind trees together, resulting in multiple trees being pulled down with the target tree. The loss of multiple trees is undesirable because it kills future merchantable trees, and can also be extremely dangerous for foresters during tree-felling operations. Thus, the reduction in logging damage after liana cutting is a desired outcome of forestry liana removal experiments. Indeed, eight studies reported that liana cutting reduced total tree damage by ~25% and decreased the number of trees that are killed when felling merchantable trees (Fox **1968**, Pinard & Putz **1996**, Sist *et al*. **1998**). In a wet forest in Indonesia, Fox (**1968**) was the first to show that removing lianas before logging lowered the number of nearby trees that were damaged. He found that 44% of the trees snapped during logging in liana removal plots compared to 62% in same-sized control plots. Also in Indonesia, Appanah and Putz (**1984**) demonstrated that liana removal reduced by half the number and the size of damaged trees after logging.

The simultaneous contribution of liana cutting and tree girdling reduced tree damage and mortality. For example, using RIL protocols in Indonesia, tree mortality dropped from 37% to 13%, and 56% less plant biomass was lost when RIL practices were used (Pinard *et al*. **1995**, Pinard & Putz **1996**). Similarly, in both Indonesian and Brazilian forests, RIL protocols resulted in 25–50% less overall damage to the forest (*i.e*., trees that were uprooted, crushed, or snapped-off below crown) (D'Oliveira & Braz **1995**, Johns *et al*. **1996**, Pinard & Putz **1996**, Sist *et al*. **2003**). In summary, cutting lianas, alone or in combination with tree girdling, results in less damage to the surround trees during logging, and it enables foresters to increase the yield of marketable timber.

By contrast, in a Mexican dry forest, Garrido-Pérez *et al*. (**2008**) reported that liana cutting could either increase and decrease treefalls during strong disturbance, depending on forest age. They found that cutting lianas reduced the number treefalls during a hurricane in older (>55 yr) secondary forest, but increased treefalls in young (10–18 yr) forest. Thus, lianas may increase treefalls during large storm events in older forests by pulling down multiple trees, or stabilize trees and reduce treefalls in younger forest by binding canopy trees together and preventing treefalls.

Treefall gap size during logging

Liana removal and tree girdling may reduce the size of treefall gaps that are formed during logging. Foresters desire smaller treefall gaps because smaller gaps are an indication of less damage to, and less loss of, future merchantable trees. Tree felling after liana removal in a dry forest in Brazil reduced the mean gap size by 47% (Johns *et al*. **1996**). Gap sizes were significantly smaller when RIL practices were used; median gap area decreased by 62% from the industrial standards when RIL was utilized in Indonesia and Brazil (Gerwing & Uhl **2002**, Sist *et al*. **2003**). Nevertheless, when logging intensities were high, RIL practices did not reduce treefall gap sizes more than and conventional logging (Sist *et al*. **2003**), and both methods produced gaps that were significantly larger than natural treefall gaps (Felton *et al*. **2006**). Contrary to previous studies, Parren and Bongers (**2001**) showed that cutting lianas prior to felling in a moist forest Cameroon had no significant effect on resulting gap sizes, tree mortality, and damage levels. They suggested that liana cutting should be applied on a tree–by–tree basis, and contingent on the total amount of liana infestation per tree (Parren & Bongers **2001**, Schnitzer *et al*. **2004**). Similarly, in a moist forest in Venezuela, Mason (**1996**) showed that liana cutting during logging did not affect canopy height and openness. Despite the differences among experiments, four studies show that removing lianas tends to decrease the size of treefall gaps, which reduces damage to future merchantable trees in many forests.

Habitat and Geographic Distribution of Liana Removal Experiments

Liana removal experiments have been conducted in a wide variety of forest types, and across different successional stages throughout the tropics. The majority of liana removal studies (43 of the 64) were conducted in the Neotropics (Central and South America; Fig. **1**). Twenty studies were conducted in the paleotropics; nine in Africa, 10 in Asia, and one comparing liana removal experiments between Africa and Asia (Dawkins **1960**). Within the Neotropics, the majority have been conducted in Bolivia, followed by Panama and Brazil (Fig. **1**). Within the paleotropics, the majority have been conducted in Indonesia, Malaysia, and Nigeria (Fig. **1**). The bias of more studies in the Neotropics may reflect the general bias in terrestrial ecological studies across the tropics. For example, both Asia and Africa have disproportionately fewer ecological studies compared to Central and

South America (Martin *et al*. **2012**). Thus, the relative abundance of liana removal studies conducted in the Neotropics, as Marshall *et al*. (**2017**) has also pointed out, appears to follow the general trend in the primary ecological literature worldwide.

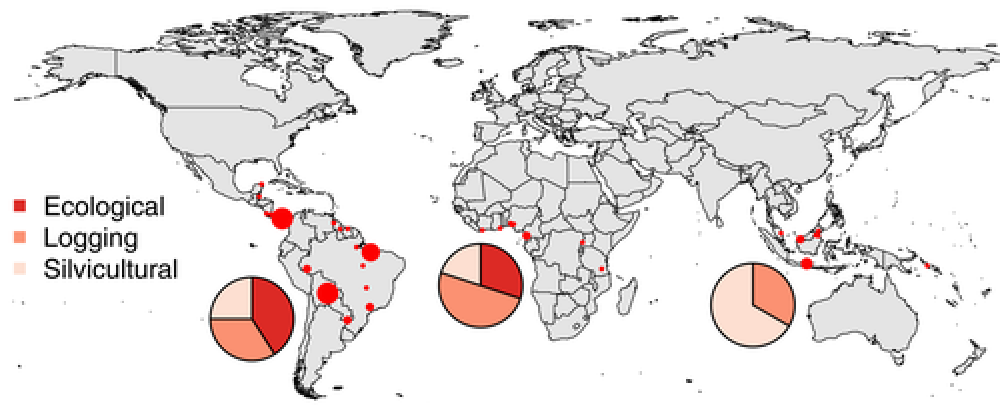

Figure 1
The pantropical distribution of liana removal studies (N = 64), including the locations where liana removal experiments have been conducted. The size of the points represents the relative number of studies conducted at each location. Geographical coordinates for each study were obtained from the publications or from the localities described in the methods section. Pie charts represent the distribution of publications by focal area of study per continent. Ecological = Effect of liana cutting on trees, Logging = Liana cutting and tree elimination/harvesting as silvicultural treatments, Silvicultural = Liana cutting as silvicultural treatment.

The number of liana removal studies is relatively balanced in terms of the major tropical forest types (Fig. **2**A). Of the 64 studies, 23 were conducted in tropical dry forests, 22 in tropical moist forests, 14 in tropical wet forest, and one comparing different forests, based on the Holdridge life zone classification system (Holdridge **1964**). Four studies were conducted in subtropical moist forests. Liana manipulations have been performed in forests that vary considerably in mean annual rainfall, from 1050 mm in Nigeria (Okali & Ola-Adams **1987**) to 4000 mm in Indonesia (Sist *et al*. **2003**). There is a geographical bias for the studies performed in tropical dry forests; 12 of the 23 studies in dry forests were conducted in Bolivia. The bias is less pronounced for other types of forests; 10 of 22 studies performed in tropical moist forests were conducted in Panama, whereas only three of 13 studies performed in tropical wet forest were conducted in Indonesia and Malaysia, respectively, with the rest of the studies distributed among different regions.

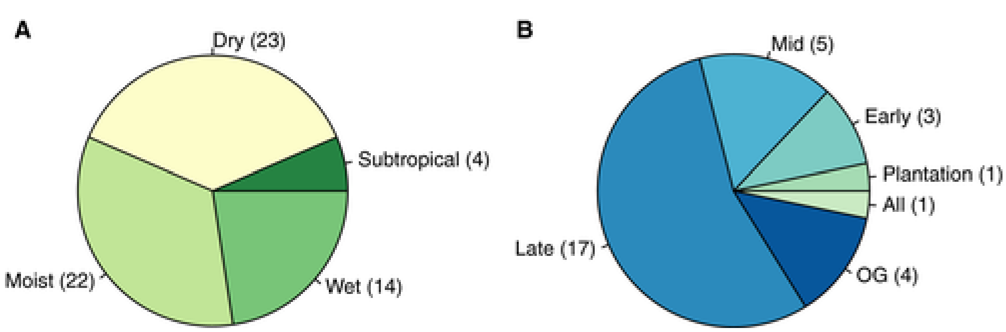

Figure 2
(A) The forest types studied in 64 liana removal studies using the Holdridge life zone classification. Dry = Tropical Dry Forests, Moist = Tropical Moist Forests, Wet = Tropical Wet Forests, Subtropical = Subtropical Moist Forests. One study compared different forest types. (B) The distribution of publications across forest successional stages (31 studies). OG = Old growth forest. All = Early, Mid and Late (1 study, Vidal *et al*. 1997). Number of studies per

category in parenthesis. The forest type and the successional stage (or age) for each study were obtained from the publications. Publications that lacked this information were not included in this figure.

Of the 31 studies that reported the age of the forest in which the liana removal experiment was conducted, 17 were in late secondary forests (>100 yr since abandonment), five in mid-secondary (20–60 yr since abandonment), four in old growth forests (>200 yr since abandonment or stated as old growth by the authors), and three studies in early secondary forests (0–20 yr since abandonment) (Fig. **2**B). From the 17 studies conducted in late-successional forests, 10 were in the moist forest of Barro Colorado Nature Monument in Panama. Although Vidal *et al*. (**1997**) assessed the cost of liana removal across forests of different ages, no study has conducted a systematic quantification of the effect of liana removal across forests of different ages. Regardless of geographical location, forest type, or forest age, results from liana removal studies consistently demonstrate that lianas have clear negative effects on tree growth, reproduction, and survival.

Variation in Methods of Liana Removal Experiments

Liana removal experiments have been conducted using a variety of methods to eliminate lianas, depending on the goals of the study. Most experiments designed to determine the effects of lianas on tree growth, survival, reproduction, and biomass accretion have used some form of liana cutting, often involving machetes (*e.g*., Pérez-Salicrup **2001**, César *et al*. **2016**). Forestry-based studies that are typically designed for optimizing tree production often use a combination of liana cutting and stem poisoning (*e.g*., Stevenson **1927**, Neil **1984**, Dekker & de Graaf **2003**). For example, 21 of the 33 studies that reported the exact removal methods used machetes to cut lianas and did not removed the lianas from the trees, with the justification that physically dislodging lianas would have damaged infested trees. Eleven studies added herbicide to the cut liana stem, in an effort to kill the liana and prevent regrowth from stored resources in the root system. There have been a variety of herbicides used to poison lianas, including application of sodium arsenite (Stevenson **1927**, Barnard **1955**, Fox **1968**), 2,4, 5-T butyl ester, and 2, 4-D, tricolpyr and glyphosate (Appanah & Putz **1984**, Neil **1984**). Additional liana removal methods include: fire, liana and vine uprooting, and the use of pole pruners and clippers (Stevens **1987**, Gerwing **2001**, Duncan & Chapman **2003**). The different methods used in liana removal experiments were distributed across different forest types and geographical area.

Even though several studies have compared the efficacy of different methods of liana removal, there is no consensus on the most effective technique. For example, Fredericksen (**2000**) compared the level of liana mortality from solely cutting with machete versus cutting and then applying herbicide and found that the use of herbicides was ultimately more effective, but was also more expensive due to product costs and the additional labor involved in applying the herbicide. Even liana cutting alone can be a costly endeavor (Pérez-Salicrup *et al*. **2001**), poisoning can be even more expensive and have undesired cascading effects when toxins seeping into the surrounding soils (Relyea **2005**). By contrast, Okali and Ola-Adams (**1987**) compared liana cutting and tree girdling versus liana cutting and prescribed burning and concluded that tree diversity increased when fire was not used because prescribed burnings had a detrimental effect on the survival on young trees. Gerwing (**2001**) showed that prescribed burning was not as effective as cutting to prevent liana recolonization after liana removal because fires increased tree mortality and made stands prone to additional fires (Gerwing **2001**). Burning may be a cheap initial option to remove lianas, but it might also reduce tree survival and regeneration in the longer term (Gerwing **2001**, Heuberger *et al*. **2002**).

The Future of Liana Removal Experiments: Where to Go Next

Liana removal experiments have increased our understanding of the role of lianas in tropical forests. Nevertheless, there are some important omissions in the liana experimentation literature. For example, we know relatively little about how lianas affect other lianas, and how lianas affect other type of life forms (*i.e*., palms, but see Putz **1984a**). We also know little about how the effect of lianas varies with resource gradients and forest age. Observational studies have described changes of liana abundance and diversity across gradients of rainfall (Schnitzer **2005**), disturbance (Letcher & Chazdon **2012**, Ledo & Schnitzer **2014**) and forest age (Barry *et al*. **2015**). However, there have not been any systematic experimental tests that carefully quantify how the effect of lianas varies with liana abundance and diversity, nor how lianas affect forests with different degrees of disturbance or across gradients of forest resources and age (but see Zagt *et al*. **2003** for logging effects on liana communities). Another omission is the lack of knowledge of how the effects of lianas on trees scales with liana size. If large lianas disproportionately affect forest trees, then an economical management recommendation may be to focus on the removal of large lianas while ignoring the smaller ones. This particular strategy would allow for managing the most detrimental aspects of liana infestation while saving time and effort, as well as without removing the remarkable diversity that lianas bring to tropical forests.

One of the stimulating areas for future studies of lianas will be to determine how increasing liana abundance will affect tropical forests (*e.g*., Schnitzer & Bongers **2011**, Schnitzer *et al*. **2015a**). Understanding the potential effects of increasing liana abundance may require more nuanced experimental approaches than cutting all lianas in a plot. Nearly all liana removal experiments have cut all lianas and compared this treatment with control plots where lianas were present. A nuanced approach, in which only a portion of the lianas are removed, may allow us to understand how increasing levels of liana abundance and can influence tree growth and survival. This type of experiment will give insights into whether an increase in liana density and basal area can have meaningful negative effects on trees. A liana addition treatment, in which lianas are planted next to and trellised onto a tree's canopy, while logistically difficult, would be of great value in predicting the effects of increasing lianas in tropical forests.

Conclusion

Liana removal experiments provide compelling evidence for the strong effect of lianas in tropical forests. To date, 64 studies have manipulated lianas in a variety of ecosystems throughout the tropics. These studies have consistently demonstrated that lianas reduce tree growth, biomass accumulation, survival and reproduction in tropical forests, regardless of forest type, successional stage, or geographic location. Lianas exert strong competitive effects on trees, which has emergent effects on community and ecosystem levels. In particular, lianas appear to reduce forest-level carbon uptake—an important ecosystem function of tropical forests. While most studies on plant–plant competition have focused on herbaceous communities (Gurevitch *et al*. **1992**), manipulating competition in forests has proven more challenging. Liana–tree competition proves a powerful approach to answer unexplored questions in plant competition and community ecology. Lianas also contribute positively to tropical forests, and studies are now beginning to document and quantify the positive effects of lianas on forest processes.

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