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ECOLOGICAL SUCCESSION IN TROPICAL FORESTS: THE ROLE OF EDAPHIC  
FACTORS, INITIAL CONDITIONS AND COMPETITION

by

Sergio Estrada Villegas, B.Sc., M.Sc.

A Dissertation submitted to the Faculty of the Graduate School,  
Marquette University,  
in Partial Fulfillment of the Requirements for  
the Degree of Doctor of Philosophy

Milwaukee, Wisconsin

May 2019

## ABSTRACT

### ECOLOGICAL SUCCESSION IN TROPICAL FORESTS: THE ROLE OF EDAPHIC FACTORS, INITIAL CONDITIONS AND COMPETITION

Sergio Estrada Villegas, B.Sc., M.Sc.

Marquette University, 2019

Succession is a fundamental process in ecology in which ecosystems recover after disturbances. The goal of the study of ecological succession is to understand the mechanisms responsible for changes in species' density, diversity, and ecosystem processes. Understanding the mechanisms that determine how young tropical forests change during succession is crucial because approximately half of the world's tropical forests are regenerating after farmland abandonment, and successional forests are now expected to supply the vast majority of ecosystems services that were provided by old growth forests (e.g. carbon sequestration). Edaphic factors, initial conditions, and competition have been proposed to be key drivers that influence tropical forest succession; however, how these drivers alter succession remains poorly understood. For my doctoral dissertation research, I used census data from a young tropical dry forest, and a large-scale field experiment in a tropical moist forest to examine the combined effects of edaphic factors and initial conditions on forest succession, as well as the effect of lianas on trees, an intense form of plant competition, on forest succession.

In the dry forest, edaphic factors and initial conditions were strong determinants of succession. Soil fertility accelerated tree biomass accretion. Topography made liana composition more similar over time. Initial conditions decreased sapling recruitment and biomass accretion, probably due to lower light levels when there is more basal area early in succession. The accumulation of tree species was slowed while tree composition similarity increased with more basal area early in succession. Competition for space may have delayed tree recruitment in the canopy and homogenized composition. In the moist forest, liana competition significantly influenced succession. Lianas contributed 20% of the foliage to the forest canopy, and thus significantly reduced light level and tree biomass accumulation. Lianas reduced tree biomass accumulation even when trees received full sunlight and their canopies were intact. Finally, using a comprehensive literature review on liana removal experiments, I report that lianas decrease tree establishment, growth, biomass accumulation and reproduction across the world's tropical forests. In summary, liana competition, edaphic factors, and initial conditions all influence the rate and direction of succession in young tropical forests.

## ACKNOWLEDGMENTS

Sergio Estrada Villegas, B.Sc., M.Sc.

I would like to thank the funding sources that made this research possible. I have been supported by a fellowship from the Departamento Administrativo de Ciencia, Tecnología e Innovación COLCIENCIAS, and received support from my advisor Stefan A. Schnitzer through his grants from the US National Science Foundation (NSF DEB-1019436, DEB-1258070, IOS-1558093), University of Wisconsin-Milwaukee and Marquette University. The first chapter of this dissertation was partially financed by The Grantham Foundation for the Protection of the Environment. I am grateful to the private landowners who allowed me to work on their properties. Edwina von Gal and Vernon Scholey provided useful background information and support throughout the study in Playa Venao and surrounding areas. I am very grateful to the staff of the Achotines Laboratory of the Inter-American Tropical Tuna Commission (IATCC) and Eco Venao for their generosity during field visits. The datasets I used could not have been completed without the dedication and hard work by numerous individuals participating in field work. I am particularly grateful to Andres Hernandez, Carlos Diaz, Johana Balbuena, Anabel Rivas, Guillermo Fernandez, Miguel Nunez, Edwin Garcia, and Cristina Barber. I thank Jenny Calvo, Julia Gonzales, Fernando Garcia, Yuriza Guerrero and others for data collection and processing and the Turner lab at STRI for soil analyses. I thank Michiel van Breugel, Jefferson Hall, Trevor Caughlin and Benjamin Turner for allowing me to use their datasets for my first chapter. I also thank Federico Davies and Estrella Yanguas for logistical support, Milton Solano for GIS support, and Mario Bailon, Rolando Perez and Salomon Aguilar for help in classifying tree species.

The second chapter of this dissertation was financed with grants from University of Wisconsin-Milwaukee and the US National Science Foundation granted to Stefan A. Schnitzer, and with grants received by the Smithsonian Tropical Research Institute (STRI) and by Jefferson Hall. The research for the second chapter was conducted at the Agua Salud Project, an amazing endeavor made possible by the contributions of the Smithsonian Tropical Research Institute (STRI), the Panama Canal Authority (ACP), and the National Environmental Authority of Panama (ANAM) and part of the Smithsonian Institution Forest Global Earth Observatory (ForestGEO). For this portion of my dissertation I am incredibly grateful to those who helped me cut lianas, measure trees and take LAI measurements. I thank Guillermo Fernandez, Oldemar Valdes, Boris Bernal, Avelino Valdes, Erick Díaz, Jeremy La-Che, Megan Walentowski, William Walker, Kenneth Contreras, Silfredo Tascon, Eric Valdes and Edwin Peres. A special thanks to Rigoberto Rivera Camaña who took over the sampling campaign of 2016 after my motorcycle accident. Evelyn Sánchez provided logistical support at the onset of this project. I also want to thank Federico Davis for the wise proverb “El dolor es inevitable, el sufrimiento es opcional”. KC Cushman, M. Elizabeth Rodríguez-R, Geertje van der Heijden and Katie Barry helped me with data analysis, and shared many of their ideas about ecology and lianas. David Deffilipis and Felipe Mello were instrumental at my time in Stefan’s lab at Marquette University.

A very special thank you to Katherine Sinacore. I appreciate all your help throughout this dissertation, and thank you for many valuable lessons about life. Thank you Carrupi! I am also very grateful to my family in Panama; Eugenio Estrada Villegas, Cristina Gutiérrez Gutiérrez, Daniel Estrada Gutiérrez and Sofia Estrada Gutiérrez. All my friends in Gamboa, Agua Salud and BCI over these years made my time as PhD student incredibly enjoyable.

I am in debt to my Milwaukee family! Thank you Sarah Oszuscik, Joe Oszuscik, Jane Glodoski, Kate McSorley, Kevin McSorley, Leo Oszuscik and Adelaide Oszuscik. Your constant moral support, love and care made this dissertation possible, and made my time in MKE unforgettable.

Finally, I am indebted to Stefan A. Schnitzer for guidance and helping me polish my ideas and writing style. I also want to thank my graduate committee Jim Maki, Tony Gamble, Jeff Hall and Natalia Norden for very insightful discussions and help throughout this process.

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## I. INTRODUCTION

### Succession, Trajectories and Drivers

Succession is a central theory in community ecology and it seeks to understand how and why species' abundances change after a severe disturbance (Begon et al. 2006, Scheiner and Willig 2008). Successional theory is key in ecology because it provides the principles that explain community assembly after the removal of vegetation and soil structure (i.e. primary succession), or after the removal of most of the vegetation but not soil structure (i.e. secondary succession) (Walker and Del Moral 2003). The study of secondary succession has changed dramatically since it became a core subject in ecology; succession was perceived as an ordered process with a predictable turnover of species, and a clear and predetermined endpoint (Clements 1916, Odum 1969). Now ecological succession is understood as a complex interplay between predictable and unpredictable processes; while the changes of certain community properties are fairly predictable over time (i.e. biomass), other community properties do not change in a predictable fashion over time (i.e. species composition) (Gleason 1926, Cain 1947, Whittaker 1956, Pickett et al. 1987, Arroyo-Rodríguez et al. 2015b). Today, improving many aspects of successional theory is paramount because we need to understand the main drivers behind forest recovery in abandoned farmland that has been subjected to prolonged and intense disturbances. As more farmland is abandoned due to human migration into cities or mechanization of agriculture, regenerating forests in abandoned farmland have the potential to sequester large quantities of carbon dioxide and help mitigate climate change (Chazdon et al. 2016). However, we do not fully understand how several drivers affect

the regeneration of early secondary tropical forests, and the consequences of such affectations on tropical forest community assembly.

Successional theory has three main tools to study how succession takes place; the description of successional stages, the description and prediction of successional trajectories, and the evaluation of the drivers responsible for changes within and among successional trajectories (Walker and Del Moral 2003, Prach and Walker 2011). While describing successional stages is an important endeavor, forest recovery after severe disturbances in tropical agricultural landscapes is a patchy and an idiosyncratic phenomenon among forest stands across the landscape (Anderson 1986, Chazdon et al. 2007). Such idiosyncrasies are reflected in the variability of the rates of change that different community properties experience over time after a severe disturbance. For example, several forest stands can show parallel trajectories of increasing forest biomass over time, however those same stands can show parallel but steady trajectories in terms of species richness for that same time period (Norden et al. 2015). Understanding the variability of successional trajectories is vital because it helps us identify causal relationships between biotic or abiotic variables and trajectory variability, and can shed light into which drivers and mechanisms might be responsible for the observed trajectories (Walker and Del Moral 2003, Walker et al. 2010). Ultimately, experiments can be the best way to identify the mechanisms that can cause the observed changes in community properties within or among trajectories over time (Prach and Walker 2011).

There are two crucial debates that have shaped the history of successional theory, one is the relative importance of deterministic versus stochastic drivers during succession, and the other is how competition shapes community properties during

succession (Webb et al. 1972, McIntosh 1986). In the first debate, drivers can be considered deterministic if their effect on ecological communities are highly predictable (Chazdon 2011). For example, life history strategies among species can have a predictable effect on forest succession; species with high photosynthetic capacity and fast growth rates tend to dominate plant communities early in succession (Bazzaz and Pickett 1980, Noble and Slatyer 1980, Craven et al. 2015). Likewise, environmental variables, such as soil fertility, can have a deterministic effect on succession; young successional forests growing on soils with low nutrient content have lower canopy height and basal area (total cross-sectional area at breast height of all stems in forest plot) compared to successional forests growing on soils with higher nutrient content (Tucker et al. 1998, Guariguata and Ostertag 2001).

The opposing side of that debate gives more importance to stochastic drivers than deterministic drivers. Drivers are considered stochastic if they are produced by random events. Even if the effects of the drivers can be predictable, the random occurrence of the drivers makes it stochastic. For example, seed dispersal can be considered a stochastic driver because the probability of dispersal into a particular microsite is random with respect to species identity, if dispersal happens at all (Vellend et al. 2014). In other words, it is highly likely (i.e. high predictability) that a seedling can establish if a seed is dispersed into a suitable microsite, but the probability of a seed being dispersed at that particular microsite is random in itself, and random with respect to the identity of the species that will be dispersed. Another example of a stochastic driver are the initial conditions among sites that are undergoing or will undergo succession (Pickett et al. 2001, Gill et al. 2017). Initial conditions represent the presence and distribution of

vegetation across sites at the onset of succession or during the first decades of succession. Initial conditions can be considered stochastic because their occurrence (i.e. presence/absence or relative abundance of the initial condition) can be random with respect to nearby sites also undergoing succession (Parker and Pickett 1998, Fukami 2010). Even though the debate between deterministic versus stochastic drivers is not over (Chazdon 2011), it is evident that both deterministic and stochastic drivers are playing key roles in how plant communities undergo succession. Finding the relative importance of deterministic and stochastic drivers is an important undertaking in successional theory, not only because it helps us create more accurate models of how large tracts of tropical areas may undergo forest regeneration (Norden et al. 2015), but because it can guide management practitioners interested in forest restoration during the anthropocene (Chazdon 2008).

The second debate in successional theory is how competition shapes community properties during succession. The importance of competition during succession is unquestionable (Meiners et al. 2015b), but how intense competition can be, and how it is able to steer the trajectories of different community properties throughout forest succession is still under scrutiny (Pulsford et al. 2016). Connell and Slatyer (1977) proposed that tolerance, together with inhibition and facilitation, were the main drivers of succession. Tolerance is in fact a competitive mechanism because the only species able to persist as succession progresses are those able to withstand low resource levels and outcompete other species (Connell and Slatyer 1977). As time goes on during succession, competition intensifies because resources become scarcer (Huston and Smith 1987, Lohbeck et al. 2015). Competition occurs simultaneously with inhibition and facilitation,

as well as other drivers (e.g. soil mutualisms, allelopathy), but theoretical expectations and field data have settled part of the debate and have concluded that the intensity of competition increases during early stages of succession, peaks later on, and decreases over time (Christensen and Peet 1984, Walker and Chapin 1987, Tilman 1990).

How exactly competition intensity can steer succession? The strength by which competition can direct forest succession depends on how plants allocate biomass to maximize resource acquisition. Very early in forest succession, plants rapidly allocate biomass to leaves and roots so as to capture as much light and water as possible (Grime and Hodgson 1987). But as plants quickly shade one another, competition for light quickly intensifies, and biomass allocation is mostly devoted to vertical growth and to the deployment of leaves at the top of the canopy (Uhl and Jordan 1984, Aerts et al. 1990). Therefore, stem growth can be very rapid and biomass allocation maximized to produce leaves during the first decades of forest succession. For example, mid age successional forests allocate up to 15% to leaf biomass while old growth forests allocate roughly 2.8% (Williams-Linera 1983, Feldpausch et al. 2004, Kenzo et al. 2010). Likewise, most of the leaf biomass and leaf area in young and mid aged successional forests is allotted to the top few meters of the canopy (Rodríguez-Ronderos et al. 2016, Cattanio 2017). Therefore, species that are able to spatially arrange their leaves on the top layers of the canopy maximize light interception and have a competitive advantage early in succession (Aerts 1999).

Competition can steer succession because those species able to maximize biomass allocation at the top of the canopy can become dominants for many years and even delay species turnover. There are clear examples from tropical successional forests. Native or



introduced grasses on abandoned pastures can reach very high densities, dominate the plant canopy for years, and preclude tree establishment and growth (Holl et al. 2000). For example, Hooper et al. (2005) showed that the introduced grass *Saccharum spontaneum* delayed tree establishment for years in Panama, but some tree species were able to establish and facilitate forest succession if fires were avoided. Ferns can also outcompete with trees and persist many years. For example, Slocum et al. (2006) showed that the native fern *Dicranopteris pectinate* could also delay forest succession for more than 25 years in Dominican Republic, and its fast growth after farmland abandonment would create monodominant canopies 3 m tall. Even if early successional forests are not furthered disturbed, life forms other than trees can be extremely competitive early in succession and persist in the canopy for decades (Aide et al. 1995). In sum, competition can be very intense early in succession, especially because plants maximize biomass allocation to intercept light. Plants able to recruit abundantly during the first years of succession and dominate the canopy can modulate the trajectories of different community properties for decades. This is especially prevalent in early successional tropical forests where life forms other than trees are able to allocate more biomass on leafs and less on diametric stem growth.

In sum, evaluating the relative importance of deterministic, stochastic, and competitive drivers is one of the most effective ways to understand how and why community properties change during forest succession (Arroyo-Rodríguez et al. 2015b, Pulsford et al. 2016). To assess how different drivers might affect succession, both observational and experimental approaches should be employed (Prach and Walker 2011). However, few studies on ecological succession in the tropics have evaluated two

drivers simultaneously (Guariguata and Ostertag 2001, Martínez-Ramos et al. 2016), and even fewer studies have employed field experiments to assess how strong is the effect of a driver across early tropical successional forests.

### Edaphic Variability, Initial Conditions and Competition as Drivers of Forest Succession

In the debate between stochastic and deterministic drivers, two of the most overlooked yet crucial drivers that affect tropical successional forests are edaphic variability and initial conditions (Inouye and Tilman 1988, Lockett and Goodwin 1999, Phillips 2004, Fukami 2015, Meiners et al. 2015a). The variability of edaphic factors (soil texture, soil chemistry and topography) within forest stands and across the landscape is expected to have a significant and deterministic effect on species composition in early tropical successional forests (Walker and Wardle 2014, Powers and Marín-Spiotta 2017). Edaphic factors are known to affect old growth forests (ter Steege et al. 1993, Hall et al. 2004, Baldeck et al. 2013, Condit et al. 2013, Turner et al. 2018), but the information available from early tropical successional forests is sparse, so the strength of the effect of edaphic factors on early successional forests is still being studied. From a theoretical perspective, gradients of soil nutrients (controlled by soil texture and soil chemistry) can determine species composition because some species are better adapted to extract different ratios of soil nutrients compared to other species. As the ratios of soil resources change through time during succession, species composition changes as well (Tilman 1985).

Observational and experimental data indicates that variability in edaphic factors, particularly soil texture and chemistry, affect species composition and other community

properties during forest succession. For example, Réjou-Méchain et al. (2014) found that soil texture (sandy or clayey) affected species composition early in succession. But as succession progressed, species composition converged probably because soils became more similar as forests aged. Early successional forests growing on soils with more clay and with more N, Ca, Mg have taller trees, more basal area, and higher relative biomass accumulation compared to forests growing in sandy soils with less nutrients and higher concentrations of Al (Tucker et al. 1998, Moran et al. 2000, Lu et al. 2002). Variation in soil chemistry and texture explained a substantial portion of species' occurrences (Powers et al. 2009) and distribution (Werden et al. 2018) across successional dry forests in Costa Rica. Nutrient addition experiments on early tropical successional forests have shown that trees grow more with nitrogen addition, suggesting that soils after farmland abandonment are nitrogen limited (Ceccon et al. 2003, Davidson et al. 2004, Siddique et al. 2010). However, other experiments on less fertile soils have shown that the effect of fertilization on stem growth was not homogeneous across forest age and across species, which indicates that not all species are nutrient limited during succession (Davies and Semui 2005, Campo et al. 2012). These studies show that the effect of soil chemistry on early successional forests is still unresolved.

Edaphic variability in terms of topography is also expected to exert a significant effect on succession, but the effect of topographic variability on early tropical successional forests has not been thoroughly evaluated. Soil sciences have shown that ridges hold less moisture and erode quicker, which can lead to more nutritious and wetter soils in troughs, but sometimes with lower pH (Jenny 1994). Moreover, steeper slopes erode faster and expose parental material more often than shallower slopes (Jenny 1994),

so variations in slope, which influences soil depth, should affect which species will assemble in the community during early succession (Scatena and Lugo 1995, Arroyo-Rodríguez et al. 2015b). Examples from early successional tropical forests seem to support these expectations. Herrera and Finegan (1997) found that steeper slopes in a 30-year-old successional forests were dominated by *Vochysia ferruginea* whereas gentler slopes were dominated by *Cordia alliodora*. The regenerating forests on the steeper slopes also tended to be less species rich compared to the successional forest on the gentler slopes (Finegan and Delgado 2000). Slope also affects tree growth. For example, Yang et al. (2013) and Scholten et al. (2017) found that trees on steeper slopes on more convex terrains grew less in an experimental plantation. However, in plantations that experience higher precipitation, trees grew more and accumulated more biomass on steeper slopes, probably because waterlogging in troughs increased tree mortality (Healy et al. 2008). Most of the relationships between topography and tropical forests have been studied in old growth forests (Lescure and Boulet 1985, Basnet 1992, Oliveira-Filho et al. 1994, Clark et al. 1995) or in plantations (Healy et al. 2008), so we currently do not have a good assessment on how topography may affect the successional trajectories of different community properties. Even though there are clear predictions on how edaphic variability would mechanistically affect early successional forests, we do not fully understand how different edaphic factors affect the successional trajectories of many community properties.

Initial conditions among sites undergoing succession are also expected to affect the rates at which community properties change over time (Myer and Pickett 1990). Succession is a highly heterogeneous process across the landscape; a large area at early

stages of succession is bound to have sites where vegetation has started to change in composition and abundance, whereas other sites are still covered by abandoned pastures or crops (Pickett et al. 2001). Spatial heterogeneity of community properties (e.g. composition or biomass) across an area undergoing succession is usually due to variability in the time of agricultural abandonment; sites that were recently abandoned usually have high tree density, low basal area and low richness, whereas sites that were abandoned long ago usually have lower tree density, but higher basal area and higher richness (Walker et al. 2010). In other words, community properties are spatially heterogeneous because different areas across abandoned fields were ceased to be used at different times. Under this type of spatial heterogeneity, the rates of change of community properties can be more or less predictable if several early successional forests only differ in the time of abandonment.

However, succession is also spatially heterogeneous independent of time of abandonment. The amount of vegetation among sites can highly heterogeneous, either in terms of stem density or basal area, even if sites have very similar ages (Pickett et al. 2001, Donato et al. 2012). For example, Kennard (2002) and Lebrija-Trejos et al. (2010a) showed that young successional forests (5-20 years old) can vary up to three-fold in basal area and stem density across patches that were the same age. Likewise, Guariguata and Ostertag (2001) reviewed six different data sets and showed that basal area varied about 440% on sites of the same age. These differences in basal area or stem density across contemporary sites can be linked to management practices, but the differences are not necessarily equally distributed or predictable across space. Areas abandoned by farmers are rarely covered by a single species and they usually have legacies from how the land

was disturbed and managed (Tarbox et al. 2018). Legacies can be either isolated trees or riparian forests that were spared by farmers after deforestation (Griscom and Ashton 2011), or trees that were planted and tended after agriculture began (Manning et al. 2006). While the location of forest fragments around troughs is fairly predictable due to shared management practices between farms, the location and abundance of other legacies, especially spared trees, is not necessarily predictable. Therefore, biological legacies increase the spatial heterogeneity of succession across contemporary sites, but the spatial location of some of these legacies are not necessarily predictable.

Initial conditions are expected to affect the rates at which succession progresses, especially across pastures that were abandoned at the same time. Variability in initial conditions across abandoned pastures can be evidenced not only in terms of basal area or forest cover, but also in the variability of microclimatic variables such as sunlight exposure, water vapor pressure deficit or soil water content (Bazzaz 1979). Sites with more basal area can ameliorate microclimatic conditions that can enhance seedling survival, and can allow seedlings of different species to establish and contribute to community turnover (Turnbull et al. 2000). In comparison to patches with lower basal area or stem density, areas with more plant cover can also speed up succession because reproducing plants can disperse seeds nearby and increase the probability of seedling establishment within and outside the patch (Maza-Villalobos et al. 2011). Biological legacies can also serve as perches for birds and bats and promote seed dispersal, which will also increase the probabilities of seedling establishment and species turnover (Medellin and Gaona 1999). Additionally, the rates at which biomass is accumulated among patches with different initial conditions can differ many fold because patches with

higher basal area will accumulate more biomass than patches with lower levels of basal area (i.e. lower number of legacies) (Lockett and Goodwin 1999).

However, initial conditions in a particular site may not necessarily accelerate changes in community properties early in succession. For example, sites with an established canopy and more basal area may start to face competition for space for seedling establishment, or competition for light as canopy closes (van Breugel et al. 2012). In other cases, very few species that are able to withstand harsh conditions on abandoned farm fields (e.g. high dissection or low nutrient availability) may establish in great numbers and comprise the largest portion of the basal area (Connell and Lowman 1989). If these few species are the only ones able to tolerate such conditions, and successfully recruit under their canopies, then high basal area or stem density among contemporary sites might not translate into higher rates of change in community properties (i.e. richness) as succession progresses (Connell and Lowman 1989). Under this scenario, sites with more basal area are not necessarily going to show higher rates of change in community properties compared to patches with lower basal area and lower stem density.

Overall, it is clear that some community properties are predicted to increase over time as succession progresses. For example biomass accumulation is expected to plateau after 80 to 100 years after farmland abandonment (Martin et al. 2013, Poorter et al. 2016), and species richness is expected to increase steadily as succession progresses during the first six decades after abandonment (Uhl et al. 1988, Van Breugel et al. 2007, Lebrija-Trejos et al. 2008, Mora et al. 2015). Never the less, variability in the rates of change of community properties across young successional forests (5-20 years) can be

driven by the varying levels of initial conditions (e.g. basal area or forest cover), and can make trajectories idiosyncratic and highly variable among sites but predictable within every site (Lockett and Goodwin 1999, Norden et al. 2015, Gill et al. 2017).

Contrary to edaphic factors and initial conditions, competition is the mechanism most often invoked as the driver of succession, and many aspects of competition drive species turnover during succession (van Breugel et al. 2012, Pulsford et al. 2016, Uriarte et al. 2016). First, species that are able to establish at the very onset of succession preempt space, and by doing so they will have a competitive advantage compared to species that arrive later in succession. For example, space preemption by grasses (Holl et al. 2000), ferns (Aide et al. 1995), and especially lianas (Barry et al. 2015), is one of the reasons why tree establishment can be difficult very early in succession. Aside from space preemption, plant species able to colonize early in succession with high photosynthetic capacity, soft wood and fast growth can effectively compete for light and space, transient resources but in high supply during the first years of succession (Lebrija-Trejos et al. 2010b). As the supply of light and space decrease, and as initial colonists fail to replenish their own populations because resources are too low for their seedlings to grow, species with slow growth and high persistence begin to have a competitive advantage as succession progresses. As shade-intolerant species begin to die, shade-tolerant species with hard wood take over (Poorter et al. 2010). Parallel to species turnover with different life history strategies, competition slowly becomes highly asymmetric during succession. Plants that establish first or grow fast will usually take a greater share of the available resources, cast larger shades, and will speed up density dependence mortality (i.e. self-thinning) of neighboring plants (Uhl and Jordan 1984,



Weiner 1990). In sum, strong competition for resources during succession helps to drive changes in stem abundance and species turnover. However, most of what is known about competition in early tropical successional forests comes from studies that have evaluated tree-tree competition, and little is known about how intense competition is between trees and other plant life forms, and how such intensity may affect successional trajectories.

### Competition Between Trees and Lianas as a Driver of Forest Succession

Lianas (i.e. woody vines) are a quintessential life form in tropical forests but their competitive effect on early successional forests is poorly understood. Observational data suggests that liana-tree competition can be detrimental to early successional forests (Schnitzer et al. 2000, Visser et al. 2018) but we lack conclusive experimental data. Lianas might affect successional forests because lianas are able to recruit in very high densities early in forest succession and preempt space (Letcher and Chazdon 2009, Yuan et al. 2009). For example, Barry et al. (2015) found that liana densities in ten-year-old forests had a density that was 60% greater than a near-by old growth forest. Moreover, many liana species are wind dispersed or have very small seeds with arils that are bird dispersed (Letcher and Chazdon 2012). Small seed size is highly correlated with fast growth rates (Bazzaz and Pickett 1980, Swanborough and Westoby 1996). Thus, high dispersal and fast growth can partially explain high liana densities in early successional forests.

Competition between lianas and trees can also be intense early in succession because lianas thrive on the high sunlit environments of abandoned farmland. In relation to trees, lianas have higher maximum photosynthetic rates (Cai et al. 2009), higher leaf

respiration rates (Santiago et al. 2015), higher concentrations of elements for growth such as N and P (Asner and Martin 2012) and higher concentrations of elements for metabolism such as Ca and K (Asner and Martin 2012). In terms of leaf traits related to metabolism and growth, lianas seem to have a head start in succession compared to trees early, especially in areas that are hotter and drier such as very early successional tropical forests (Asner and Martin 2012).

Finally, the majority of liana species that establish in early successional forests twine or use tendrils and hooks to climb at the top of the canopy (Yuan et al. 2009, Letcher and Chazdon 2012). Therefore, lianas depend on trees for structural support for vertical growth. When lianas reach the top of the canopy they deploy their foliage either on top or in close proximity to tree's foliage, and by doing so, lianas use up the light that would have been otherwise available for trees (Putz 1984b, Clark et al. 2008, Rodríguez-Ronderos et al. 2016). In sum, many liana species that recruit in high numbers early in succession are adapted to take advantage of the resources that are available after farmland abandoned, and have climbing mechanisms to reach the top of the canopy and compete for light.

Lianas decrease tree growth, biomass accumulation and survival, but we ignore if the competitive effect of lianas in early successional forests is as high as in old growth forests. For example, several liana removal experiments in old growth forests or in mid age forests have shown that tree growth increased between 25% and 372% after liana cutting (Grauel and Putz 2004, Campanello et al. 2007, Grogan and Landis 2009, Schnitzer and Carson 2010, Álvarez-Cansino et al. 2015). Likewise, experimental evidence has shown that trees accumulated between 52% and 436% more biomass where

lianas have been removed compared to control plots where lianas were not removed (Schnitzer et al. 2014, van der Heijden et al. 2015b, César et al. 2016). Lianas also decrease tree survival; high percent of liana coverage (i.e. liana infestation) decreases tree survival. For example, Ingwell et al. (2010) found that trees with liana infestation lower than 75% had a 20% mortality in a ten-year lapse. Mortality doubled when trees had more than 75% liana infestation. If lianas decrease growth, biomass accumulation and survival in early successional forests as much as they do in older forests, then it is likely that lianas stagnate forest regeneration and redirect succession of early secondary forests from a tall canopy, high carbon state towards a low canopy, low carbon forest dominated by pioneers and lianas (Schnitzer et al. 2000, Chave et al. 2001). If early secondary forests fail to regenerate as it has been predicted due to strong liana-tree competition, then early secondary forests might not play a significant role in reduction of atmospheric carbon dioxide and climate change mitigation.

Even though the study of lianas has increased over the last decades (Schnitzer et al. 2015a), most of the studies on tropical forest ecology have been observational and do not reflect the importance of lianas in tropical forests. Lianas can contribute up to 25% of the woody stems, and up to 35% of the woody species in lowland tropical forests (Schnitzer et al. 2012). Therefore, lianas make a considerable contribution to forest structure and diversity, but with respect to trees, lianas have been understudied. For example, the number of studies specifically about lianas is four orders of magnitude lower than the number of studies in ecology (Schnitzer et al. 2015c). In fact, a considerable portion of the studies that have found that lianas have a detrimental effect on tree growth and biomass accumulation are observational (Toledo-Aceves 2015). Despite

all this crucial information on tropical forest ecology, there has not been a systematic review of the studies that have used liana removal experiments to determine the intensity of liana competition on trees. Without a systematic and thorough review on experimental manipulations of liana abundance, it will be difficult to disentangle the effect of tree-tree competition from liana-tree competition. Moreover, lianas can be used as a model group to study plant-plant interactions via liana removal experiments (Schnitzer 2018), but there hasn't been a structured and methodological synthesis that has compiled and compared the available information on liana removal experiments to determine how intense liana competition can be.

#### Questions, Hypotheses and Predictions.

The main goal of this dissertation is to understand three key drivers that affect early successional tropical forests after severe anthropogenic disturbances, and to provide the most updated literature review on liana removal experiments throughout the tropics. Specifically, in my first chapter I ask whether variation in edaphic factors and initial conditions are significant drivers of change in the successional trajectories of forest structure, richness, biomass and composition of young regenerating tropical dry forests of very similar age. I hypothesize that edaphic factors will have a significant and positive effect on successional trajectories because sites with higher nutrient availability and gentler slopes should enhance plant growth, and therefore experience faster changes in species richness, biomass, and community composition. However, initial conditions may blur the effects of edaphic factors. Even if sites were abandoned at the same time (i.e. contemporary) and had high soil fertility on gentle slopes, sites with lower basal area and

lower forest cover may undergo faster rates of change in structure, richness, biomass and composition because there is more space available for new species to recruit, which in turn accumulate more species and plant biomass. Alternatively, I also hypothesize that even if sites were contemporary and had high soil fertility with gentle slopes, higher levels of basal area and forest cover may help sites to experience higher rates of change in structure, richness, biomass and composition because initial conditions can enhance tree recruitment via dispersal or via facilitation. Edaphic factors and initial conditions can have a synergistic effect on successional trajectories on contemporary young successional forests, or initial conditions can confuse the effects of edaphic factors on successional trajectories.

In the second chapter I ask how intense is the competitive effect of lianas on trees in early successional forests. Specifically, I want to assess how lianas affect biomass uptake in early secondary forest. I hypothesized that lianas may have the strongest effect on tree biomass uptake in the youngest forests because liana proliferation can stall tree growth and regeneration. As the forest matures, trees may shed lianas, thus reducing the negative effects of lianas on larger trees. Alternatively, I also hypothesize that lianas may have the strongest effect on trees in older successional forests if the effect of lianas is commensurate with their density, which increases dramatically in the first decades of forest regeneration.

In the last chapter I ask how intense is the competitive effect of lianas on trees across the liana removal experiments available in the literature. Specifically, I asked (1) if the effects of lianas on tree establishment, survival, growth, biomass, reproduction, forest diversity and forest fauna in tropical forests are positive or negative; if (2) the effects of

lianas on tree mortality and gap formation during logging operations are positive or negative; and (3) if liana removal effects differ by the global region where studies have been conducted. I hypothesize that lianas have had a strong negative effect on tree establishment, survival, growth, biomass, reproduction and forest diversity, but a positive effect on forest fauna across the reviewed studies. I also hypothesize that lianas increase gap sizes and tree mortality during logging operations, and that the effect of liana removal will be positive and strong regardless of the global region where studies have been conducted.

## II. EDAPHIC FACTORS AND INITIAL CONDITIONS INFLUENCE SUCCESSIONAL TRAJECTORIES OF EARLY REGENERATING TROPICAL DRY FORESTS.

One of the main goals in forest ecology is to understand that main drivers that shape successional trajectories (Meiners et al. 2015a). Edaphic factors, which include soil chemistry, soil texture and topography, may have a strong and deterministic effects on community composition. Availability of different levels of soil resources can filter out species as communities assemble throughout succession, creating predictable changes in forest composition (Powers and Marín-Spiotta 2017). Initial conditions represent the amount of vegetation present across sites during early stages of forest succession (Parker and Pickett 1998, Phillips 2004, Donato et al. 2012). Initial conditions across sites can influence succession in a contrasting way than edaphic conditions, especially if sites are abandoned at similar times. For example, initial conditions such as vegetation remnants can speed of community recovery via seed dispersal or facilitation regardless of the edaphic conditions across sites (Moran et al. 2000, Pickett et al. 2001). Given that both edaphic factors and initial conditions may be important drivers in the successional dynamics of secondary forests, incorporating both of these factors into models of forest succession is critical to accurately predict how rates of forest recovery vary across secondary forests (Norden et al. 2015). Understanding how forests recover after anthropogenic disturbance is especially urgent as half of all tropical forests are undergoing early or intermediate stages of succession after human alterations (Chazdon et al. 2016).

A wide range of data indicates that edaphic factors exert a deterministic effect on plant communities early in forest succession (Powers and Marín-Spiotta 2017). For

example, nutrient addition experiments indicate that edaphic factors influence tree communities in successional forests; addition of N and P increased plant growth (Davidson et al. 2004), seedling richness and survival (Ceccon et al. 2003), and can shift species composition by favoring a subset of species (Siddique et al. 2010). However, observational studies show that the effects of soil nutrients depend on which community properties and which nutrients are analyzed. For example, Ayala-Orozco et al. (2017) showed that total N and P did not affect changes in basal area or species richness in an early successional tropical dry forest in Mexico, but that richness was positively related to ammonium and nitrate concentrations. Lu et al. (2002) showed that higher available N concentrations on Alfisols positively affected forest biomass accumulation in early successional forests in Brazil, but that this effect was not present on Oxisols and Ultisols. In successional dry forests in Costa Rica variation in soil chemistry and texture explained a substantial portion of species' occurrences and distribution (Powers et al. 2009, Werden et al. 2018), but the relationship between soil properties and above ground biomass was weak (Becknell and Powers 2014). At a regional scale, above ground biomass of secondary forests across the Neotropics does not seem to be related to soil cation exchange capacity (Poorter et al. 2016). Therefore, the direction and magnitude of the effects of edaphic factors depend on how sites differ in soil chemistry, which community property is studied, and the spatial scale of the study.

Topography is also expected to have a predictable effect in structuring forests undergoing succession (Scatena and Lugo 1995). In old growth forests, topography affects soil formation, soil water content and nutrient concentration (Jenny 1994), which in turn determines the abundance of about 30 species in a tropical lowland community



(Clark et al. 1999). A similar relationships has been found on early successional forests, where topography affects nutrient concentrations (e.g. P and Mg), which then affect community composition between upslope plots versus downslope plots (van Breugel et al. 2019). Other aspects of young successional forests seem affected by topography. For example, stands located in valleys or troughs appear to regenerate rapidly, presumably because they have higher soil moisture and higher soil nutrients compared to slopes and ridges (Griscom and Ashton 2011). Ridges have better drained soils and nutrients leach from the ridges and may accumulate in the valleys (Jenny 1994, Scatena and Lugo 1995), thus increasing tree growth in the valleys (Scholten et al. 2017). As soil conditions differ along slopes, different species colonize at different rates according to the grade of the slope. For example, Herrera and Finegan (1997) found that *Vochysia ferruginea* was more abundant in steeper slopes whereas *Cordia alliodora* was more abundant in gentler slopes across 36 successional forests in Costa Rica. Additionally, regenerating forests on the steeper slopes also tended to be less species rich compared to the successional forest on the gentler slopes (Finegan and Delgado 2000). Topography not only covaries with soil chemistry, it can also covary with initial conditions. For example, intermediate or steep slopes can harbor older patches of forests because they tend to be less easily farmed (Crk et al. 2009). Also, farmers may also protect forest cover along riparian corridors in the valleys, thus providing a rich propagule source for forest regeneration (Griscom et al. 2009). In sum, both soil nutrients and topography can affect the structure and trajectories of successional communities, but their covariation and their effects on young successional forests remains poorly understood (Griscom and Ashton 2011).

Initial conditions can differ greatly across sites of similar age, and they are expected to affect the speed at which forest structure and composition change during regeneration (Phillips 2004, Donato et al. 2012). Initial conditions vary many fold in young successional forests. For example, Guariguata and Ostertag (2001) reviewed six different data sets of young successional tropical forests (< 20 years) and showed that basal area varied about 440% across contemporary sites. Such variation can be due to differential growth rates among sites, but also due to drastic variation in initial conditions as a result of tree sparing by farmers, or due to the presence of narrow forest strips at the bottom of troughs also spared by farmers (Manning et al. 2006, Griscom and Ashton 2011, Tarbox et al. 2018). Sites with different levels of initial conditions should also undergo succession at different rates (Watt 1947, Pickett and Cadenasso 2005, Martínez-Ramos and García-Orth 2007). For example, young sites with higher stem density or basal area tend to accumulate biomass at a faster rate compared to sites of similar age but with lower stem density or basal area (Lockett and Goodwin 1999, Babst et al. 2014). Moreover, initial conditions in terms of forest cover (i.e. isolated trees or riparian forests) across contemporary young successional sites may affect successional trajectories because forest cover increases propagule availability and may speed up species turnover (Thomlinson et al. 1996, Griscom et al. 2009, but see Holl et al. 2017). For example, the presence of spared tree species that fruit abundantly can accelerate succession because they attract a variety of seed dispersers (Medellin and Gaona 1999), and the community recruiting underneath their canopy tends to be more rich than nearby sites away the canopy (Sandor and Chazdon 2014). Therefore, initial conditions can have a pivotal role

on how regenerating forests change in structure, species richness, composition and biomass during regeneration (Norden et al. 2015).

We tested whether edaphic factors and initial conditions could explain the variation in forest dynamics of early secondary forests in a human-modified landscape. We conducted the study in a series of tropical dry forests of similar ages. Tropical dry forests are one of the most threatened ecosystems worldwide due to high rates of historic deforestation (Banda-R et al. 2016). While old growth dry forests are still being deforested (Aide et al. 2013), large areas of farmland in former dry forests are being abandoned in some areas across the Neotropics, and are undergoing early stages of succession (Rudel 2012, Caughlin et al. 2016). Determining whether edaphic factors and initial conditions influence the trajectories of young successional dry forests can help refine which specific drivers accelerate or suppress forest regeneration. Moreover, assessing the relative importance of edaphic factors initial conditions may support land-use management policies, forest restoration practices and conservation planning in heavily human modified landscapes.

In this study, we first describe the trajectories of change of forest structure, richness, biomass and composition during six lapse years of succession in 22 young regenerating dry forests plots that range from 12 to 20 years after abandonment. We then describe the trajectories of species composition as these forests age. Second, we test whether edaphic factors and initial conditions are significant drivers of change in forest structure, species richness, biomass and composition.

We predicted that both edaphic factors and initial conditions would alter forest succession, but in different ways. Forest stands with more available nutrients and gentler

slopes should experience faster increases in species richness and plant biomass, as well as faster changes in community composition, because gentler slopes accumulate more nutrients and retain more soil moisture (Jenny 1994). Gentler slopes and more nutrients should enhance the establishment of species unable to tolerate even dryer conditions on ridges, or infertile conditions on steeper slopes. Additionally, young stands with higher initial conditions should show faster increases in species richness and plant biomass because sites with more basal area or forest cover may facilitate establishment of new species and favor community turnover (Lebrija-Trejos et al. 2010b, Lohbeck et al. 2013). However, stands with lower initial conditions (i.e. lower basal area) can undergo even faster rates of change in structure, richness, biomass and composition compared to sites with high initial conditions because lower basal area and lower forest cover can indicate more free space for recruitment, less competition for space in the canopy, which can lead to more biomass accumulation.

## Materials and Methods

### Study Site

Our study was conducted in the municipality of Pedasi, province of Los Santos, Panama ( $7^{\circ}25'30''\text{N}$ ;  $80^{\circ}10'30''\text{W}$ ). The forests in this region are classified as tropical dry (Holdridge 1964). The mean annual precipitation in this area is 1,706 mm (Empresa de Transmisión Eléctrica S.A., Cañas Station, 1976–2017). The dry season is typically from December until May. Mean annual temperature of this area is  $25^{\circ}\text{C}$  (Griscom et al. 2011). The landscape ranges in elevation from 10 to 100 m. The land was cleared in the 1940s

and 1950s for cattle ranching, and conversion of forest to ranching accelerated in 1978 (Griscom et al. 2009). However, cattle farming was reduced from 2000 to 2010, leading to ~4% net forest gain in the region during this decade (Caughlin et al. 2016). Cattle pastures are the dominant land use across the province, but parcels are also used for small-scale tourism and environmental restoration initiatives.

### Plot Selection and Data Collection

We chose three areas that had the same land use type before and after pasture abandonment. The areas were logged in the 1960s and 1970s, underwent prescribed burnings for cattle farming (Heckadom-Moreno 1984), and were abandoned between 2004 and 2007. In one area, pastures were abandoned in 1999. As in other dry forests in Central America, a few large trees (e.g. *Enterolobium cyclocarpum*) were spared in the pastures to provide shade for cattle (Griscom et al. 2011). The 11 sites we chose in all three areas are representative of young forests regenerating on abandoned pastures. From our interviews with land owners, the sites were left unmanaged after the years of abandonment, and there have not been disturbed (e.g. fires) since.

We sampled the forest at each site with two plots ( $50 \times 20\text{m}$ ) that were located perpendicular to the slope. This sampling scheme allowed us to account for the effect of topography and land use in forest structure (van Breugel et al. 2013). In each plot, we tagged, measured, and identified to species all trees and shrubs  $\geq 5$  cm diameter at breast height (DBH), and lianas  $\geq 1$  cm diameter of. We measured tree DBH at 1.3 meters from the ground for trees, while lianas were measured 1.3 m from the roots, following the protocols suggested by (Schnitzer et al. 2008). We also tagged, measured, and identified

all trees and shrubs with a DBH between 1–5 cm in one half of each plot. For convenience, we refer to these smaller trees and shrubs as ‘saplings’ and trees with DBH >5 cm as ‘trees’. We refer to all woody climbing plants as ‘lianas’, and refer to ‘small lianas’ as those with a diameter 1-3 cm and ‘large lianas’ as those with a diameter >3 cm. We used these thresholds because lianas larger than 3 cm in diameter usually have already reached the forest canopy, whereas those smaller than 3 cm usually have not managed to reach the forest canopy (Kurzel et al. 2006). We conducted full forest inventories (seven) on every plot once per year from 2010 to 2016. Across all plots, we measured 3512 saplings, 1787 trees, 2100 small lianas, and 464 large lianas during the seven years of sampling. We identified > 98% of individuals to species. Finally, in each plot we bulked three soil samples at 15 cm depth per plot and extracted base cations (Al, B, Ca, Cu, Fe, K, Mg, Mn, Zn, Table 1) and P using Mehlich-III solution (Mehlich 1984), with detection by inductively-coupled plasma optical emission spectrometry (ICP–OES) on an Optima 7300 DV (Perkin Elmer, Inc, Shelton, CT, USA).

## Data Analysis

### Description of successional trajectories.

We first assessed changes abundance, species richness, composition, and biomass as basal area increases during our sampling period. We calculated these changes separately for saplings, trees, small lianas, and large lianas. We calculated basal area per hectare, diversity as species richness (i.e. Hill number 0), and changes in species composition between censuses with the Horn index. Even though tree basal area and tree biomass are usually correlated because DBH is used to calculate both, we opted to use

forest basal area to compare among plots, life forms and size classes because basal area is a reliable indicator of stand performance in terms of tree growth, recruitment and mortality (van Breugel et al. 2006). Moreover, basal area has been recently used to compare dry forest stands (Lebrija-Trejos et al. 2010b, Lohbeck et al. 2013) and is expected to have a differential effect on saplings and lianas because sapling density declines whereas liana densities can remain high as succession unfolds (Barry et al. 2015). We calculated the Horn index for effective number of species (Jost et al. 2011) as implemented in the package “vegetarian” for R (Charney and Record 2009). Finally, we calculated biomass per stem for saplings and trees with a global multispecies allometric equation that accounts for bioclimatic stress (Chave et al. 2014), which we calculated with local climatological data. We calculated biomass for small and large lianas using regional multispecies allometric equation (Schnitzer et al. 2006).

#### Changes in species composition over time

We first tested whether trajectories of species composition showed significant changes over time, and whether changes in composition showed directionality. Assessing directionality quantitatively helped us elucidate how composition changed before testing whether edaphic factors and initial conditions affected composition. We first calculated Horn similarity indices for all plots between each census for saplings, trees, small lianas and large lianas, and then calculated ordinations using non-metric multidimensional scaling (NMDS). To test whether composition across plots changed significantly from 2010 to 2016, we used a Procrustes analysis, calculated with Gower’s statistic  $m^2$ , and tested the significance of  $m^2$  with a permutation test (Jackson 1995). The Procrustes

analysis looks for the best fit between two matrices (NMDS of 2010 and 2016) by transforming one matrix with respect to the other. Smaller  $m^2$  means that two matrices are highly similar, and p values  $<0.05$  indicate that high similarity is greater than expected by chance (Lisboa et al. 2014). To detect directionality, we plotted the trajectories for each forest plot with two NMDS axes to visualize how species composition changed through the first years of succession (Feeley et al. 2011). If there were directional changes in species composition, we expected a non-random direction of change from census to census per transect. Thus, we calculated the mean direction of change between censuses for each NMDS axis and used bootstrapping (10000 resamples) to calculate 95%CI around the mean direction of change in composition; if the 95%CI did not overlap with zero, species composition would show directionality (Feeley et al. 2011). To calculate ordinations, we used the function “metaMDS” implemented in the package “vegan” for R, with Wisconsin standardization and square root transformation of the Horn dissimilarity data (Oksanen et al. 2011). To perform the Procrustes analysis, we used PROTEST (Jackson 1995) implemented in “vegan”. To calculate bootstraps, we used the package “boot” (Canty and Ripley 2016).

To visualize which species showed the greatest changes in abundance, we plotted the natural logarithm of species abundances in the initial census versus the natural logarithm of species abundances in the last census. We also plotted the percent change from the initial to the last census for species with an abundance greater than 35 individuals for saplings and small lianas, and species with more than 20 individuals for trees and larger lianas (Appendix 1). We tested whether abundance between the first and last census across plots were significantly different with a paired t-test.



Effect of edaphic factors and initial conditions on successional trajectories.

We used linear mixed effects models (LMM) to determine whether edaphic factors and initial conditions explained the trajectories of change in forest structure, richness, biomass and composition. For edaphic factors, we used one topographic variable and two axes of soil inorganic nutrients. To select one topographic variable for our models, we first estimated elevation, slope, aspect, Terrain Roughness Index (TRI) and Topographic Position Index (TPI) for each plot using a digital elevation model (Caughlin et al. 2016). TRI is the sum change in elevation between a grid cell and eight cells around it, with 0 m being minimum roughness. TPI measures the relative topographic position of a cell as the difference between the elevation of that cell and the mean elevation of a predetermined neighborhood of cells (Riley et al. 1999, De Reu et al. 2013). We then preselected the topographic variable that best fitted our data by comparing Akaike Information Criterion values from LMM using all the initial condition variables (see below) for each response variables (e.g. abundance) per life form and size class, but tested one topographic variable at a time. To do so we used the function “lme” implemented in the package “nlme” (Pinheiro et al. 2018). For random factors, we nested plots within sites, accounted the temporal autocorrelation of our data. Fixed factors were standardized by dividing each variable by twice its standard deviations (Gelman 2008). The two axes of soil inorganic nutrients were calculated from measurements of Al, B, C, Ca, Cu, Fe, K, Mg, Mn, N, P, and Zn with a NMDS (Table 1, and Appendix 1 to see variability of soil nutrients across sites).

Table 1. Mean soil nutrient concentration for 22 forest plots of early successional dry forests in Panama, and Pearson correlations between soil nutrients and two soil fertility axes calculated using Nonmetric Multidimensional Scaling. Units for cations and P are in mg kg<sup>-1</sup>; C and N %. SE=Standard Error.

Nutrient	Mean	SE	NMDS 1	NMDS 2
C	3.11	0.0789	-0.062	0.04
N	0.244	0.00606	-0.038	-0.001
P	2.42	0.231	-0.662	-0.215
Al	918	13.9	0.474	-0.219
B	0.23	0.0268	-0.021	0.044
Ca	5386	111	-0.999	-0.007
Cu	5.96	0.348	-0.079	-0.484
Fe	129	3.3	-0.289	0.316
K	57.9	5.58	0.17	0.048
Mg	1315	32.1	-0.071	0.997
Mn	68.9	4.66	-0.063	-0.055
Zn	1.18	0.0818	-0.083	-0.334

We used two explanatory variables to quantify initial conditions; initial plot basal area (basal area in the first census), and forest cover in 1998. Basal area was the sum of the basal area of all woody stems (lianas and trees) expressed on a per ha basis. Forest cover was calculated as the average tree cover within and around each plot across five radiuses (30 m, 50 m, 75 m, 100 m, 300 m) from the edge of the plot. Initial basal area is a good proxy for initial conditions because it represents the spatial heterogeneity of forest structure across sites that were abandoned around the same time (Donato et al. 2012). More importantly, initial basal area is expected to significantly affect stem size distribution, biomass accumulation and competition intensity as succession progresses (Lockett and Goodwin 1999, Niklas et al. 2003, van Breugel et al. 2006). By incorporating initial basal area in our analysis, we are in fact accounting for some of the conditions experienced by the stands as they have undergone succession (i.e. high basal area today is probably related to high basal area in the past), and it serves as a proxy for future stand performance (Niklas et al. 2003, Babst et al. 2014). Our measure of forest

cover is a good proxy for the initial conditions around the stands at the onset of succession because it includes isolated trees on pastures, small strips of riparian forests and life fences in 1998. Isolated trees, riparian forests and life fences are very stable over time (4.25%) in this area of Panama (Tarbox et al. 2018), so we are confident that our measure of forest cover is a good representation of the initial conditions experienced by the plots when they were abandoned. To calculate forest cover, we manually digitized tree cover in high resolution aerial photographs taken in 1998 and obtained from the Tommy Guardia National Geographic Institute of the Republic of Panama. To select the forest cover radius that best fitted our data, we ran LMMs with initial basal area for each response variable per life form and size class, tested one radius of forest cover at a time, and selected the model with the lowest AIC. We also used the number of censuses (1-7) as an explanatory variable because we also expected that community properties would change from year to year throughout our study and as succession progressed.

Our response variables were the changes abundance, species richness, biomass and composition between consecutive censuses. The changes between consecutive censuses per plot characterize the direction and magnitude of forest succession between censuses. We also calculated changes in species composition using the Horn index. Before performing LMMs between response and explanatory variables, we performed two preliminary analyzes. The first allowed us to discard explanatory variables that were highly collinear ( $>0.75$ ) and determine whether initial conditions reflected the differences in forest age (Appendix 2). Given that initial basal area was correlated with forest age, we retained initial basal area as an explanatory variable for the rest of the analysis. The second preliminary analysis allowed us to explore the relationships between explanatory

and response variables as static data by averaging the changes in community properties across censuses. By plotting the average changes of all response variables against initial basal area and forest cover, we had a better understanding of our dataset before analyzing the dynamic data (i.e. rates of change between consecutive censuses) (Appendix 3 and 4).

Finally, we determined how much of the variation in the change abundance, richness, biomass and composition could be explained by edaphic factors and initial conditions by calculating LMMs with all explanatory variables plus censuses (1-7) as fixed effects, and time and plots nested within sites as random effects. We calculated the variances explained by each model (one per response variable per life form and size class) using marginal and conditional coefficients of determination for generalized mixed-effect models with the function `r.squaredGLMM`, implemented in the package “MuMIn” (Bartoń 2013). We standardized each variable (Gelman 2008) to compare the magnitude of the effects of significant fixed factors to the response variables. To determine whether a fixed variable in the model had a significant effect on abundance, species richness, composition and biomass for each life form and size class, we plotted the estimated coefficient from the LMM and their 95%CI.

## Results

### Successional Trajectories

The observed trajectories indicate that while abundance, richness and biomass of large trees increased, the abundance and richness of saplings tended to decrease while their biomass remained fairly constant (Figure 1A, B, E, F, I, J). By contrast, abundance

and biomass of both large and small lianas increased or stayed the same over the course of succession (Figure 1C, D, G, H, K, L). The abundance and biomass of saplings and large lianas appeared to diverge during succession, indicating an increase in variation across plots (Figure 1A, D). Community composition showed some variation among plots, especially for trees and large lianas, but similarity was overall high across all sites for all life forms and size classes (Figure 1M, N, O, P).

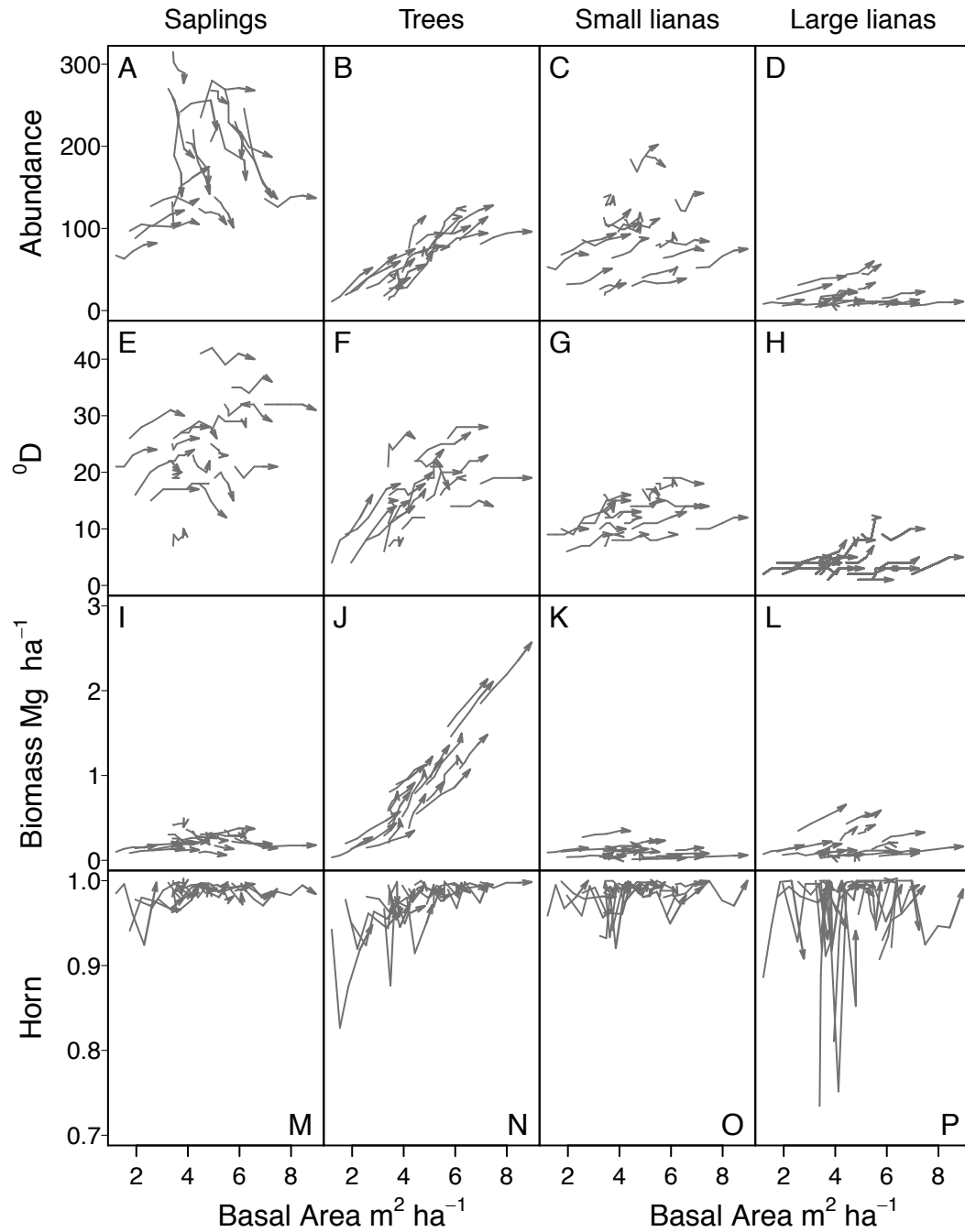


Figure 1. Trajectories of early forest succession for saplings (1-5cm DBH), trees (>5cm DBH), small lianas (1-3cm DBH) and large lianas (>3cm DBH) in a dry forest in Panama. Abundance (A-D), species richness (i.e.  $^{\circ}D$ ) (E-H), biomass (I-L) and changes in species composition (M-P) between censuses (Horn index) are plotted against forest basal area.

## Species Composition

Changes in composition were not directional; bootstrapping analyses showed that mean rate of change among the NMDS axes of species composition between consecutive censuses was not significantly different from zero for all life forms and size classes (Appendix 5). Consequently, composition across plots did not change in a directional manner in seven years, a short time lapse in forest succession. Compositional similarities were statistically significant for all life forms and size classes (saplings:  $m^2=0.212$ ,  $p=0.001$ ; trees:  $m^2=0.487$ ,  $p=0.001$ ; small lianas:  $m^2=0.464$ ,  $p=0.001$ ; large lianas:  $m^2=0.806$ ;  $p=0.024$ ).

At the species level, the saplings with the greatest increase in abundance from 2010 and 2016 were *Cedrela odorata* ( $t=-2.472$ ,  $p=0.022$ ), *Bursera simaruba* and *Astronium graveolans*. The species with the greatest decrease were *Lippia americana* ( $t=2.553$ ,  $p=0.018$ ) and *Casearia corymbosa* ( $t=2.698$ ,  $p=0.013$ ) (Figure 2, Appendix 6). For trees, *Bauhinia ungulata*, *Bursera simaruba* and *Genipa americana* showed the greatest increases. *L. americana* was the only tree species that showed a reduction in abundance across succession ( $t=2.553$ ,  $p=0.018$ ) (Appendix 7). The small liana *Macrosepis hirsuta* showed a marked reduction in abundance, and *Bauhinia glabra*, *Machaerium microphyllum*, *Chomelia spinosa* and *Combretum fruticosum* increased both as small lianas and as large lianas (Figure 2, Appendices 8 and 9). Neither small nor large lianas showed a significant net change in abundance between 2010 and 2016.

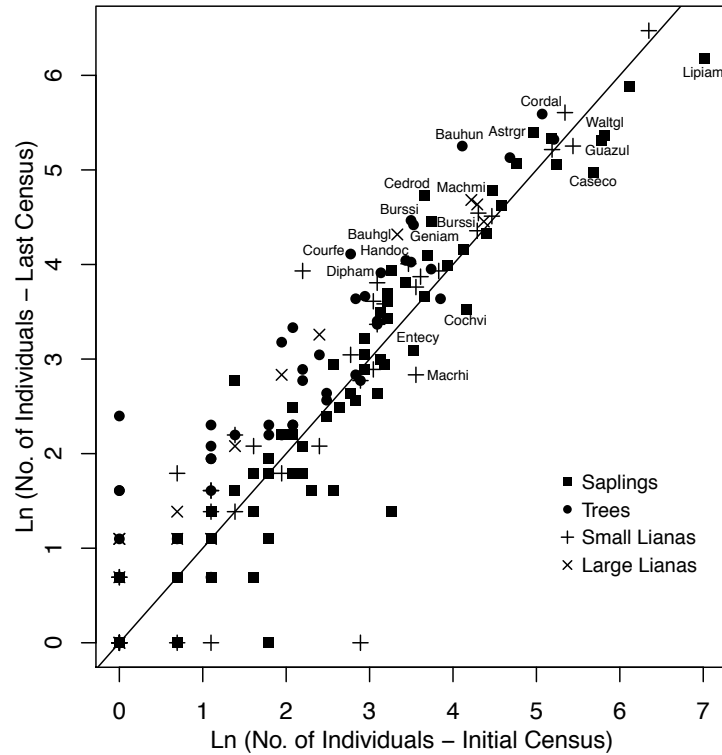


Figure 2. Changes in species abundances of saplings, trees, small lianas and large lianas after six years of early succession in a tropical dry forest in Panama. Species further away from the 1:1 line had the greatest changes in abundance from the initial to the last census. Ln stands for natural logarithm. Labels correspond to species with an abundance greater than 35 individuals for saplings and small lianas, and species with more than 20 individuals for trees and larger lianas. Saplings: Astrgr = *Astronium graveolans*, Burssi = *Bursera simaruba*, Caseco = *Casearia corymbosa*, Cedrod = *Cedrela odorata*, Cordal = *Cordia alliodora*, Cochvi = *Cochlospermum vitifolium*, Entecy = *Enterolobium cyclocarpum*, Guazul = *Guazuma ulmifolia*, Lipiam = *Lippia americana*, Waltgl = *Waltheria glomerata*. Trees: Bauhun = *Bauhinia unguolata*, Burssi = *Bursera simaruba*, Courfe = *Coursertia ferruginea*, Dipham = *Diphyssa Americana*, Geniam = *Genipa americana*, Handoc = *Handroanthus ochraceus*. Small lianas: Macrhi = *Macrosepsis hirsuta*. Large lianas: Bauhgl = *Bauhinia glabra*, Machmi = *Machaerium microphyllum*.

### Edaphic Factors and Initial Conditions

A combination of edaphic factors and initial conditions explained up to 44.7% of the variance in community properties (Table 2). Edaphic factors and initial conditions (marginal coefficients) explained more of the variation in the changes in abundance,



richness, and biomass of saplings and trees than for small and large lianas (Table 2).

Likewise, changes in composition (Horn) of saplings and trees were better explained by edaphic factors and initial conditions than for small lianas and large lianas (Table 2).

Table 2. Effects of edaphic factors and initial conditions rates of change in four community properties for saplings, trees, small lianas and large lianas in an early successional dry forest in Panama.  $R(m)^2$  stands for marginal coefficient, which represents the variance explained by the fixed factors.  $R(c)^2$  stands for conditional coefficient represents the variance explained by fixed and random factors.  $\Delta$  = Rates of change.  $^0D$  = Hill number zero.

Life form	Response variable	$R(m)^2$ (%)	$R(c)^2$ (%)
Saplings	Structure ( $\Delta$ Abundance)	30.6	55
	Richness ( $\Delta$ $^0D$ )	18.1	21.9
	$\Delta$ Biomass	25.9	50.8
	Composition (Horn)	23	27.7
Trees	Structure ( $\Delta$ Abundance)	7.9	9.4
	Richness ( $\Delta$ $^0D$ )	20.7	27.2
	$\Delta$ Biomass	36.7	57.2
	Composition (Horn)	44.7	58.7
Small lianas	Structure ( $\Delta$ Abundance)	10.8	10.8
	Richness ( $\Delta$ $^0D$ )	6.4	10.9
	$\Delta$ Biomass	11.3	21.3
	Composition (Horn)	5.9	19.7
Large lianas	Structure ( $\Delta$ Abundance)	10.9	26.6
	Richness ( $\Delta$ $^0D$ )	6.3	6.3
	$\Delta$ Biomass	7.5	61.9
	Composition (Horn)	15.7	19.3

Initial basal area had a strong and significant negative effect on changes in sapling abundance and tree richness (Figure 3, Appendix 3). Initial basal area had a strong significant negative effect on tree composition, and a positive strong effect on tree biomass although marginally significant. Forest cover had a strong positive effect in the abundance of saplings although marginally significant (Figure 3, Appendix 4). Edaphic factors, in terms of Soil Axis 1 had a significant positive effect on tree biomass, and Soil

Axis 2 had a strong but marginal effect sapling abundance (Figure 3). Topography, in terms of TPI, had a significant positive effect in the composition of large lianas. The effect of census was significant for structure, richness and biomass of saplings, and for biomass of large lianas (Figure 3).

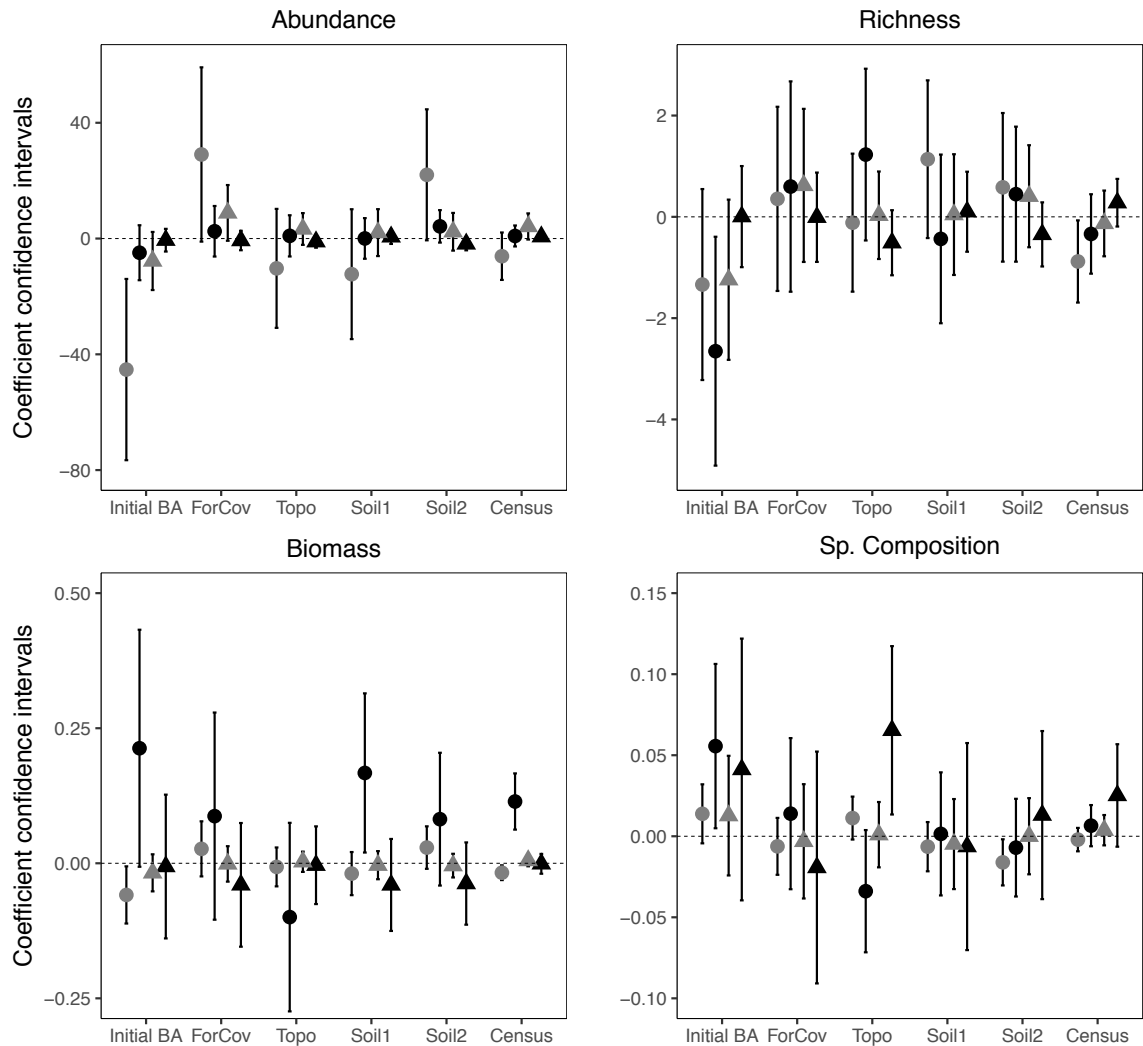


Figure 3. 95% confidence intervals of regression coefficients estimated with linear mixed models using two initial conditions, three edaphic factors and census intervals to explain the change in abundance, richness, biomass and composition across early tropical successional forests in Panama. Saplings = gray circles, trees = black circles, small lianas = gray triangles, and large lianas = black triangles. Initial BA = Initial Basal Area, ForCov = Forest Cover inside around plots. The radius of forest cover was selected for each data set using linear mixed models (50 m for saplings, 30 m for trees, 75m for small lianas and 50m for large lianas). Topo = Topographic inside

and around the plots (Elevation for saplings, slope for trees, aspect for small lianas, and TPI (Topographic Position Index) for large lianas).

## Discussion

As far as we are aware, our study is the first to assess how trajectories of early successional tropical dry forests are simultaneously affected by edaphic factors and initial conditions for both trees and lianas. We found that edaphic factors and initial conditions predicted almost half of the variation in the trajectories of some community properties of young successional tropical dry forests. Specifically, variation in the abundance tree biomass was correlated to soil nutrients, and the variation in the composition of large lianas was correlated to TPI. The variation in the abundance and biomass of saplings, and the variation of richness and composition of trees was correlated to initial basal area. While the trajectories of saplings and trees seemed to reflect community thinning, the trajectories of small and large lianas seemed to stay the same or diverge as succession progressed.

## Edaphic Factors

Soil fertility had a significant effect on tree biomass accumulation, and a marginal effect on changes in sapling abundance. In old growth forests, soil nutrients have been found to determine species distributions (Hall et al. 2004), to determine community structure at local scales (Baldeck et al. 2013), to affect growth of both saplings and trees (Turner et al. 2018), and to determine the distribution of tree species at regional scales (Condit et al. 2013). In young secondary forests, soil fertility in terms of N and P can

have significant effects on plant performance (Lawrence 2003, Ayala-Orozco et al. 2017, Powers and Marín-Spiotta 2017, van Breugel et al. 2019). For example, Werden et al. (2018) found that soil chemistry, including P, determined the distribution of 82 species across 84 successional dry forest plots in Costa Rica. Likewise, Davidson et al. (2004) showed that experimental addition of N significantly increased tree biomass in a young successional moist forests in Brazil. Aside from N and P, other nutrients seem to play a role in tree biomass accumulation; Santiago-García et al. (2019) found that K and Cu were associated with the variability of tree biomass in young wet regenerating forests in Costa Rica. Our results indicate that Soil Axis 1 represents a gradient of soil nutrients that ranges from high to low P, and from Al to Ca (Table 1). Phosphorus availability affects leaf photosynthetic rates (Reich et al. 2009), Ca availability affects cellular respiration and stomatal control (McLaughlin and Wimmer 1999), and Al can increase soil pH and preclude plants to absorb nutrients (Lüttge and Clarkson 1992). Our results are comparable to what Moran et al. (2000) found in young successional forests in Brazil, where differences in Al and Ca significantly affected changes in tree height across forest plots. Phosphorus and Ca are also key for fine root growth in successional dry forests in Costa Rica (Powers and Pérez-Aviles 2013), and root growth directly impacts biomass accumulation (Cairns et al. 1997). In sum, the variability across studies on which soil nutrients affect successional forests, plus the lack of correlations between our soil fertility axes and other community properties, highlights the difficulty in studying the role of soil nutrients in successional trajectories. Nevertheless, the significant correlation we found indicates a role for soil nutrients in tree biomass accumulation in young tropical dry forests.

Topographic variables explained the changes in species composition of large lianas. The positive correlation between community similarity and Topographic Position Index (TPI) indicate that temporal species turnover of large lianas is low on slopes and ridges (TPI values  $\geq 0$ ), whereas turnover is higher in valleys and troughs (TPI values  $< 0$ ). The positive correlation between TPI and community similarity may be related to species' specific associations to slopes and ridges. In a moist old growth forest in Panama, Dalling et al. (2012) found that 44% of all liana species showed habitat preferences, with 26 species showing significant associations with slopes and the drier upper plateau. If species are associated with a specific habitat, low temporal turnover could be expected because species tend to recruit, establish and remain in areas (i.e. preferred habitats) where their performance is higher (Feeley et al. 2011, Kanagaraj et al. 2011). If that is the case, species turnover of large lianas may be more stable on slopes and ridges in early regenerating dry forests.

Compositional similarity of lianas can also remain high over time if topographic position is related to tree fall gaps. Forest gaps are responsible for the maintenance of liana diversity (Ledo and Schnitzer 2014), so if gaps form more often on slopes, as it has been reported by Poorter et al. (2009), gap formation via topography could also explain why liana composition was consistently high on slopes and ridges over time. However, if gap formation was associated with topography, changes in the abundance of saplings or small liana should have also been correlated with topography because an influx of resources due to gap formation increases the abundance of saplings and small lianas (Schnitzer and Carson 2001). The association joint effect of topography and gap formation on the changes in community properties for other life forms merit further

study. Overall, topography has been shown to affect forest succession (Scatena and Lugo 1995, Scholten et al. 2017), but variation in topography only seems to be meaningful for large lianas across our young successional plots.

### Initial Conditions

Initial conditions denote two related drivers across plots undergoing succession. One is the variation in forest cover across contemporary plots at the onset of forest succession, and the other is the variation in the amount of area covered by woody plants across plots during succession (Meiners et al. 2015b). Both drivers are key to understand forest succession because the first (i.e. forest cover) is linked to abandonment conditions, agricultural history, propagule source and landscape connectivity (Parker and Pickett 1998). The second driver (i.e. initial basal area) is linked to competition, stem growth and mortality during or after the formation of a canopy (Chazdon et al. 2007). Therefore, assessing initial conditions in terms of forest cover and initial basal area is vital to determine how drivers at the onset of succession or during succession affect the rates at which early successional forests accumulate biomass and gain species (Phillips 2004, Donato et al. 2012).

Our results showed that forest cover at the onset of succession had a positive effect on seedling establishment, although marginally significant. Our results support other studies that have shown that forest cover enhances plant recruitment, perhaps via facilitation or by increasing seed dispersal (Lebrija-Trejos et al. 2010a, Griscom and Ashton 2011, Maza-Villalobos et al. 2011, Avila-Cabadilla et al. 2012, Lohbeck et al. 2013, Derroire et al. 2016b). Higher forest cover might have increased the abundance of

the species already present in the riparian corridors around our plots. For example, wind dispersed species, such as *Astronium graveolans*, *Cedrela odorata* and *Cordia alliodora*, are abundant in the riparian forests in our field sites (Griscom et al. 2011) and increased in abundance throughout our study. It is possible that forest cover at the onset of succession might contribute to the increase in saplings as succession progresses.

Our results support the prediction that stands with lower initial basal area experience faster changes in plant abundance, richness and biomass, as evidenced by the decreasing rates of change in sapling abundance and biomass, and in tree richness (Figure 3, Appendix 2). Basal area can be an indicator of competition intensity early in succession because low initial basal area can reflect space availability for recruitment and growth. Conversely, high initial basal area can produce high mortality of saplings due to less light available in the understory, and less free space in the canopy to support tree growth (Chazdon et al. 2007). Fast and decreasing rates of change in abundance, richness and biomass in areas with low initial basal area can indicate high plant recruitment, fast growth and low mortality. Our results resemble what van Breugel et al. (2006) found in a successional forest in Mexico, where mortality via self-thinning was higher than recruitment along a gradient from high initial basal area to low initial basal area. van Breugel et al. (2006) also found that as stands gained recruits and stems increased in size, basal area also increased, but mortality via self-thinning also increased. This gradient in local initial basal area may help explain our results; the decrease in saplings abundance and biomass over time can be due to mortality via self-thinning, whereas the decrease in tree richness over time can be due to competition for resources and space preemption.

Our results also support the prediction that stands with lower initial basal area can undergo fast rates of change in species composition and biomass accumulation. We found that community similarity increased as initial basal area increased across plots, which is mirrored by the decrease in tree richness (Figure 3, Appendix 2). As self-thinning reduces sapling abundance and richness, and as competition delays sapling growth into the next size class, tree species composition becomes more homogeneous. In other words, as initial basal increases, space in the canopy becomes more crowded and competition intensifies, making it harder for saplings from different species to grow, reach a space in the forest canopy and increase tree species richness. Given that our plots are young, it might take decades for the stem exclusion phase of succession to end and gaps begin to form (Chazdon 2014) so saplings of new species are able to grow and join the forest canopy. The positive marginal effect of high initial basal area on tree biomass accumulation can be explained by the fact that larger trees are able to accumulate biomass at a faster rate than smaller trees (Lockett and Goodwin 1999, Stephenson et al. 2014). Contemporary plots that have more initial basal are expected to show higher rates of biomass accumulation because larger trees (i.e. higher initial basal) have higher leaf mass and leaf area, which allows them to sequester more carbon per unit of diametric growth (Stephenson et al. 2014).

The amount of basal area early in succession can have crucial implications on successional trajectories because it can set the rate at which the structure, richness and biomass of saplings and trees change over time. Norden et al. (2015) provided an elegant and comprehensive model of tropical forest succession that incorporates the effect of basal area on the changes in structure and diversity. They found that initial basal area



very early in succession was associated with positive and increasing rates of change in stem density as succession progressed. Contrary to their model, our results show that high initial basal area early in succession decreased the rate of change at which saplings are recruited, sapling biomass is accumulated, and species are added to the forest. These apparently contradicting results may be explained by two concomitant processes; at the very onset of succession, initial basal area determines the magnitude of the rates of change at which forests will accumulate individuals, species and biomass. As succession proceeds, basal area will continue to increase but the rates of change, although positive, will decrease in magnitude over time just as Norden et al. (2015) and Lebrija-Trejos et al. (2010a) have found. As succession continues, basal area saturates, large trees begin to die (Denslow and Guzman 2000) and the rates of change of community properties stabilize just as biomass accumulation plateaus (Chazdon et al. 2007). Overall, our results show that the variability the initial conditions, as reflected by different initial basal areas across plots, may affect the rates of change of young successional tropical dry forests (van Breugel et al. 2006, Chazdon et al. 2007, Norden et al. 2015). As succession continues, processes such as competition or niche selective forces will probably override the effects that initial conditions had early in succession (Li et al. 2016).

### Species-specific Changes During Early Succession

The changes in the number of key tree and liana species seems to be consistent among neotropical dry forests. For example, *Astronium graveolans*, *Bursera simaruba*, *Cedrela odorata* and *Handroanthus ochraceus*, which increased in our plots, have also been found to increase in abundance early in succession in dry forests of Costa Rica

(Kalacska et al. 2004), Nicaragua (Marín et al. 2009), Brazil (Madeira et al. 2009) and Colombia (Castellanos-Castro and Newton 2015). Likewise, *Cordia alliodora* and *Bauhinia ungulata*, which also increased in abundance during our study, have been shown to increase during succession in dry forests in Nicaragua (Esquivel et al. 2008, Marín et al. 2009). Most of these species either have small seeds that are wind dispersed, show high specific leaf area, or are deciduous (Wright et al. 2010, Engemann et al. 2016). A combination of these traits typical of trees in young successional dry forests (Lohbeck et al. 2012). The species we found to decrease during our study have also been shown to decrease elsewhere. For example, *Lippia americana*, *Guazuma ulmifolia* and *Cochlospermum vitifolium* also decrease in abundance in successional dry forests in Colombia (Castellanos-Castro and Newton 2015) and Costa Rica (Kalacska et al. 2004, but see Powers et al. 2009). These three species are light demanding and become quickly outcompeted by surrounding taller vegetation (Griscom et al. 2011). The liana species *Machaerium microphyllum* and *Bauhinia glabra*, which increased during our study, also increased through succession in a Colombian dry forest (Castellanos-Castro and Newton 2015). Even though we did not find significant changes in composition during 7 years of succession across plots that span 20 years of regeneration, it comes to no surprise that species-specific responses during succession seem to be shared across other successional dry forests in Central and South America.

### Successional Trajectories

Determining the predictability of forest succession has been a heavily debated topic (Pickett et al. 2001, Meiners et al. 2015a, Norden et al. 2015, Li et al. 2016). Our

findings concur with studies that show that tree abundance, and especially tree biomass, increase in a predictable fashion during early succession (Kennard 2002, Lebrija-Trejos et al. 2010a, Dupuy et al. 2012, Derroire et al. 2016a). However, our results also show important spatial and temporal heterogeneity in successional trajectories among sites of similar age for saplings and for small and large lianas. Moreover, no other study, as far as we are aware, has tracked the trajectories of change for structure, richness, composition and biomass of lianas in early successional dry forests. Other studies in successional moist forests have shown that liana abundance, biomass and richness are high early in succession, but liana density declines after 50 to 70 years of succession while liana basal area remains high as forests age (Dewalt et al. 2000, Barry et al. 2015, Lai et al. 2017). In wetter forests, liana abundance decline, richness remains constant, and biomass increases during forest succession (Letcher and Chazdon 2009). In drier forests, liana abundance, richness and basal area appear to increase rapidly and then decline as forests age (Madeira et al. 2009). Our results from an early successional dry forest show that liana structure, composition and biomass are heterogeneous and seem less predictable than trajectories for trees. High variability in liana structure and biomass can be related to different degrees of canopy closure among plots; lianas tend to show less recruitment when light availability in the forest floor decreases, and only lianas that were able to reach the top of the canopy will continue to grow and accumulate biomass (Letcher 2015). Overall, the direction and magnitudes of the trajectories for trees seem predictable and are congruent with other studies, but more detailed studies will be needed to determine why large lianas show almost divergent trajectories among plots.

## Conclusions

We followed the fate of approximately 8,000 trees and lianas for seven years and concluded that the succession of trees, measured by their abundance, richness, and biomass follow a predictable trajectory in tropical dry forests. However, the successional trajectories of lianas in these forests seemed less predictable. More importantly, we found that edaphic factors and initial conditions explained some of the changes in early successional dry forest communities. Edaphic factors were correlated with tree biomass accumulation and with changes in species composition for large lianas. Initial conditions were good predictors of the changes in sapling structure and biomass, and trees richness and composition. Low basal area during the first years of succession may allow rapid plant recruitment because more light and space are available. In areas with high basal area early in succession, the rates of change of sapling abundance, richness, and biomass decreased, which suggests a reduction in the speed of establishment and recruitment as succession progresses. Never the less, as basal area increases over time, larger trees accumulate more biomass. We propose that initial conditions, although stochastic in nature, can determine the magnitude of the rates at which early successional dry forests will accumulate trees, species richness, and accrue biomass. As succession proceeds, the rates of change will continue to be positive but will drop in magnitude over time, and the strong initial effect of initial conditions will diminish over time.

The aforementioned results enlighten the larger discussion on the importance of determinism versus stochasticity in forest regeneration. Determinism and stochasticity have different scales of analysis. One scale deals with the debate between plant succession as a developmental program similar to an organism's ontogeny (Clements 1916) versus changes in species composition as a response to the individualistic requirements across environmental gradients (Gleason 1926, Whittaker 1956). At this scale of analysis, stochasticity is seen in terms of species composition in space over time, whereas determinism is seen on fixed endpoints in ecosystem function over time (i.e. biomass accumulation) (McIntosh 1986).

The other scale of analysis between determinism and stochasticity focuses on the drivers responsible for changes in species abundances during succession. Drivers can be considered deterministic or stochastic if their effects have predictable or unpredictable on plant succession, respectively. However, drivers can also be considered deterministic or stochastic if the events that trigger the driver are non-random or random events. A paradigmatic example of a deterministic driver is edaphic variability because areas with higher soil fertility, which are influenced by topography, are expected to have a predictable effect on plant growth and species turnover. Several theoretical and empirical studies support this assertion (Tilman 1985, Clark et al. 1999, Jakovac et al. 2016, Powers and Marín-Spiotta 2017, Werden et al. 2018, van Breugel et al. 2019). Other deterministic drivers are related to species specific traits (i.e. seed mass or maximum photosynthetic rate) which have a strong phylogenetic control (Swenson et al. 2012).

The paradigmatic example of a stochastic driver is seed dispersal because there is high uncertainty if seeds will be dispersed into abandoned farmland, and high uncertainty

with respect to the species that will be dispersed. Even though there are subsets of species known to have higher chances of establishment on abandoned fields (e.g. pioneers), it is uncertain which species will be dispersed, if dispersal happens at all. It could be argued that another example of stochasticity is the spatial variability of initial conditions in terms of plant cover and basal area on plant succession. Even though higher plant cover and basal area can have a deterministic effect on plant succession, the spatial distribution of the initial conditions might not be entirely predictable. Using Vellend et al. (2014) definition of stochasticity, the spatial distribution of initial conditions across an abandoned field is stochastic with respect to any area picked at random across an abandoned field. Even though the location of forest cover on riparian corridors can be highly predictable, the location of isolated trees on pastures might be due to so many interrelated causes that it might produce a random spatial distribution. Some studies seem to suggest that this assumption is feasible (Haase et al. 1997, Foster and Gross 1999). The idea of initial conditions as truly stochastic driver (i.e. isolated trees on abandoned farmland) needs to be developed further but it is testable, and such test would help substantiate that the spatial variability of initial conditions, even if they can have a determinist effect on succession, can have a stochastic foundation.

If initial conditions can be considered stochastic, the results showed in this chapter enlighten the debate between deterministic versus stochastic drivers during succession. Edaphic factors, a type of deterministic driver, had a predictable effect the changes in tree biomass, and in community turnover of large lianas. Initial conditions, a stochastic driver, had a predictable effect on sapling abundance and biomass, and on tree richness and composition.

Now that deterministic and stochastic drivers have been explored, let's turn our attention to the effect of competition on young successional forests. To see how intense competition can be and how it shapes succession, we use the tree-liana interaction to see how competition affects biomass accumulation early in forest succession.

### III. LIANAS AFFECT BIOMASS ACCUMULATION IN EARLY SUCCESSIONAL TROPICAL FORESTS

More than half of the world's old growth forests have been altered or destroyed by humans (FAO 2015). Concomitantly, however, we have gained large tracts of secondary forests; between 1990 and 2007, there was an increase of 66% in forest cover in the neotropics due to the expansion of secondary forests (Aide et al. 2013), and a 50% increase in the amount of carbon stored by secondary forests (Pan et al. 2013). These regenerating secondary forests are purported to provide the ecosystem services that old growth forests once provided (Chazdon 2014). That is, the rapid expansion of secondary forests is expected to be pivotal in compensating for the loss of old-growth forests in terms of CO<sub>2</sub> sequestration (Baccini et al. 2012, Chazdon et al. 2016). Current research shows that large quantities of biomass quickly accumulate in the first four decades of forest regeneration after farmland abandonment (Saldarriaga et al. 1988, Martin et al. 2013, Poorter et al. 2016). Biomass, carbon sequestration, and carbon storage are particularly rapid during the early stages of forest regeneration, when trees grow quickly in the high-light conditions. By contrast, the rate of biomass accumulation slows during the later stages of succession because tree growth decelerates as competition for light and space increase (Huston and Smith 1987, Pan et al. 2013, Poorter et al. 2016). Therefore, secondary forests are thought to compensate for the loss of biomass due to deforestation of old growth forests (Chazdon et al. 2016).

The idea that secondary forests will compensate for the loss of old-growth forests may be overly optimistic. Many secondary forests may fail to regenerate as predicted due to unaccounted effects of strong plant-plant interactions. Indeed, the traditional successional model may be disrupted during early neotropical forest regeneration because



high densities of lianas (woody vines). Lianas exert strong and detrimental effects on trees, which may redirect succession in secondary forests from a high carbon state to a low carbon forest (Schnitzer et al. 2000, Chave et al. 2008). Lianas may play a critical role in forest development and alter succession in tropical forests. Lianas compete intensely with trees, reducing growth and biomass accumulation (Estrada-Villegas and Schnitzer 2018, Visser et al. 2018). For example, in a secondary forest in Panama, Schnitzer et al. (2014) and Schnitzer and Carson (2010) demonstrated that tree biomass accumulation and growth was 180% and 55% higher, respectively, in liana removal plots in forest gaps. In an older successional forests in Panama (60 years old), van der Heijden et al. (2015b) found that lianas reduced biomass production by 76% per year for three years. Consequently, lianas have the capacity to reduce forest regeneration and, in extreme cases, arrest succession in secondary forests, thus limiting forest biomass accumulation.

Lianas recruit rapidly and in great numbers following pasture and agricultural land abandonment (Dewalt et al. 2000, Letcher 2015, César et al. 2017). For example, liana density was 38% and 47% higher in 20-year-old forests compared to old-growth forests in Côte d'Ivoire and Costa Rica, respectively (Kuzee and Bongers 2005, Letcher and Chazdon 2009). Even forests as young as 5-years-old can have liana densities that exceed nearby old-growth forests (Barry et al. 2015). One observational study found that the effect of lianas on tree biomass increased during succession from 19% on young forests to 32% after 30 of succession (Lai et al. 2017). Despite their high densities, lianas do not compensate for the amount of biomass uptake that they reduce in trees; liana displaced three-times more tree biomass compared to the fraction of biomass they

contributed (van der Heijden and Phillips 2009, Schnitzer et al. 2014). Thus, lianas can significantly reduce biomass accumulation in trees, while contributing little to overall forest biomass. If lianas recruit in high abundance and displace trees early in forest regeneration, then the capacity of secondary forests to accrue biomass could be greatly reduced.

The effects of lianas on tree biomass accumulation during tropical forest succession are poorly understood and may be more intense than previously thought (Dewalt et al. 2000). The influence of lianas on forest regeneration in tropical forests may be much stronger now than in previous decades because lianas are increasing in abundance and biomass in neotropical forests (Schnitzer 2015). There are now 15 studies demonstrating that liana density, productivity, and biomass are all increasing relative to trees in tropical forests (Schnitzer 2015, Pandian and Parthasarathy 2016, Ceballos and Malizia 2017, Hogan et al. 2017). Lianas have increased in forests in Argentina, Bolivia, Brazil, Costa Rica, French Guiana, and India. In a study across multiple forest types in Amazonia, lianas increased 3.27% annually with respect to trees in a five-year interval (Phillips et al. 2002), a pattern that has been mirrored by more recent studies in Costa Rica, Brazil and Panama (Ingwell et al. 2010, Enquist and Enquist 2011, Laurance et al. 2014). These results, together with the fact that lianas recruit in high densities in early secondary forests (Barry et al. 2015, Lai et al. 2017), indicate that lianas may reduce biomass accumulation in early successional forests (Schnitzer et al. 2011).

We used a large-scale experimental approach in 30 secondary tropical forests to evaluate how lianas affect biomass uptake in early secondary forest. The forests ranged from 10 to 35 years in age and were located in the Agua Salud watershed in central

Panama. We hypothesized that lianas may have the strongest effect on tree biomass uptake in the youngest forests because liana proliferation can stall tree growth and regeneration. As the forest matures, trees may shed lianas, thus reducing the negative effects of lianas on larger trees. Alternatively, lianas may have the strongest effect on trees in older successional forests if the effect of lianas is commensurate with their density, which increases dramatically in the first 30 years of forest regeneration. Furthermore, we hypothesized that the detrimental effect of lianas on tree biomass accumulation would be evident even after accounting for differences in light availability and canopy health.

## Methods

### Study Site

We established a successional chronosequence of secondary forests in the Agua Salud watershed in central Panama (Figure 4). The 700 ha site where we conducted the study is composed of secondary forests in different stages of succession, cattle pastures, and timber plantations. Within the secondary forests, we established 30 20 m x 50 m plots in 30 forested sites that ranged from 10 years to 35 years-old (2 plots per forest). These sites fulfill the criteria of an appropriate space-for-time substitution in chronosequence studies (Johnson and Miyanishi 2008, Walker et al. 2010) because the sites differ in the time since last disturbance, and all have followed similar trajectories in forest development, they are located on homogenous parental material, have similar previous land use, and have been managed similarly since they were abandoned

(Neumann-Cosel et al. 2011, van Breugel et al. 2013). The mean annual precipitation at Agua Salud is 2700 mm, with a dry season from mid-December until mid-May (Ogden et al. 2013). Detailed information about the Agua Salud site can be found in Stallard et al. (2010), and van Breugel et al. (2013).

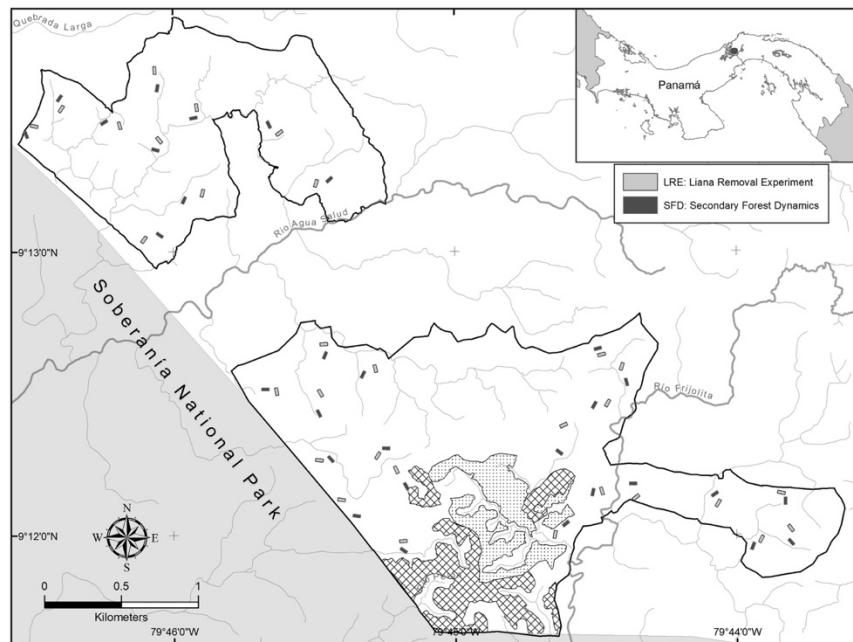


Figure 4. Map of the Agua Salud Project in Central Panama. Rectangles represent our 30 study sites composed of a liana removal plot (light gray), and a control plot (dark gray). Cross hatched areas represent a mixed-species reforestation experiment, dotted areas represent teak plantations.

### Sampling Methods

In 2011, we tagged, measured, and identified to species all trees  $\geq 5$  cm in diameter 1.3 m from the ground (DBH) in each plot (van Breugel et al. 2013). In the control plots, where lianas were present, we also tagged, measured, and identified to species all lianas  $\geq 1$  cm 1.3 m along the stem from the ground. The tree census followed

standardized protocols (van Breugel et al. 2013) and the liana census followed standardized protocols established by Gerwing et al. (2006) and Schnitzer et al. (2008).

To determine tree biomass accretion across the plots, we selected 24 species that were abundant across the chronosequence. We grouped them in three categories according to their wood density: light, medium and dense (Appendix 10). We obtained measurements of wood density from Barro Colorado Nature Monument, which is in the same region as Agua Salud, has similar soil characteristics (Neumann-Cosel et al. 2011) and receives comparable rainfall (Wright et al. 2010, Dylan Craven pers. com.). From each wood density category, we randomly selected three individuals from two different size classes; small (5-10cm DBH) and medium (10-20cm DBH) to include in the study. We selected three large individuals (>20cm DBH) from our species set regardless of their wood density. We also selected the largest three individuals in each plot regardless of wood density or species identities. The maximum number of total individuals per plot at the onset of the experiment was 24. Selecting individuals in this manner allowed us to replicate within species across the chronosequence, enabled us to assess the effect of liana removal across species with different sizes and wood densities, and allowed us to deliberately incorporate large trees because they disproportionately accumulate more biomass than smaller trees (Stephenson et al. 2014).

In 2013, we cut all lianas in each removal plot and in 5m buffers around each removal plot. We also cut all lianas that were rooted outside of the buffer but were growing into the plot. Lianas were cut at ground level and at shoulder level because some species (e.g. *Davilla nitida* or *Entada gigas*) are able of sprout roots from severed stems. We did not dislodge lianas from trees to avoid damaging the canopies (follows Schnitzer

and Carson 2010, Schnitzer et al. 2014). We revisited the plots once every year to cut the new stems produced by cut lianas as well as to cut all new lianas growing in the plots.

Before the liana cutting, and once every year after cutting, we calculated mean Leaf Area Index (LAI) for each plot by measuring LAI at 1.3 m above the soil surface on 24 fixed points along the 5m grid of the plot using a Li-Cor LAI-2000 (Li-Cor Biosciences, Lincoln, NE, USA). LAI was not measured in 2016. All measurements were taken at dawn, dusk or during continuous overcast. To calculate LAI, we compared the light measurements in the plots with those taken simultaneously with a second LAI-2000 located outside of the forest. We restricted light measurements to the northern portion of the sky by capping the south-facing half of each light sensor. Methods follow Schnitzer and Carson (2010) and Rodríguez-Ronderos et al. (2016).

We measured tree growth annually using a diametric tape on all stems selected in 2012. If a tree died between sampling years, we randomly selected another tree within the same wood density category and size class, and measured it throughout the study period. The total number of trees analyzed across all years was 1628. In 2015, we assessed light availability and canopy health by assessing canopy condition and illumination following standardized methods (Dawkins and Field 1978, Clark and Clark 1992). Canopy condition was scored from 1 to 4: trees with the highest score had 75-100% of the canopy intact, whereas trees with the lowest score had 0-25% of the canopy intact (most of the crown is gone). Crown illumination was scored from 1 to 5: trees with the highest score had canopies completely exposed to vertical light and to lateral light, whereas trees with the lowest score were not lit directly either vertically or laterally.

## Data Analysis

To determine how much foliage in the canopy was taken up by lianas before the onset of the experiment, and how trees' canopies responded to the removal of lianas, we took measurements on 24 points per plot, then calculated mean LAI per plot, and used the plot means to calculate mean LAI per treatment. To calculate above ground biomass uptake at the plot level, we first transformed growth measurements per stem were into above ground biomass (AGB) uptake using an allometric equation calculated for trees at the Agua Salud site (van Breugel et al. 2011). We then determined how much biomass each stem accumulated relative to the amount of biomass that it accumulated during the previous year. Thus, we calculated a biomass relative increment metric based on a relative growth rate equation:

$$\text{Biomass Relative Increment} = \frac{(\ln \text{AGB}_{\text{year } 1} - \ln \text{AGB}_{\text{year } 0})}{\text{year } 1 - \text{year } 0}$$

We calculated mean tree biomass relative increments per plot per year, and then tested for differences between treatments for each year of sampling. We used an ANCOVA to test whether liana removal and forest age increased biomass relative increment for every year of sampling for all size classes combined, and for each size class separately. At the individual tree level, we tested the direction and magnitude of the effect of liana removal, forest age, canopy condition, illumination and year of sampling on biomass relative accumulation using Linear Mixed Models (LMM; function `lme`, as implemented in the R package “nlme”; (Pinheiro et al. 2018)). We avoided

pseudoreplication and accounted for temporal autocorrelation by nesting trees within plots, plots within sites, and using repeated measures per tree over time. We defined treatment (liana removal vs control), forest age, canopy condition, canopy illumination, and sampling year as fixed factors, and plots within sites as a random factor. To compare the effects of each fixed factor on biomass relative increments, we standardized each fixed factor by twice its standard deviation (Gelman 2008), and plotted the estimated coefficient from the LMM and their 95%CI. We calculated the variances explained by the LMM using marginal and conditional coefficients of determination for generalized mixed-effect models with the function `r.squaredGLMM`, using the R package “MuMIn” (Bartoń 2013). Marginal coefficient represents the variance explained by the fixed factors, whereas conditional coefficient represents the variance explained by fixed and random factors (Bartoń 2013).

## Results

At the canopy level, lianas contributed 18% of the canopy foliage, as measured by the change in LAI one year after cutting lianas compared to the pre-liana-cutting differences (Figure 5). After the first year of the experiment, control plots showed significantly more foliage compared to removal plots ( $F_{1,56} = 20.44$ ,  $P = 3.239 \times 10^{-5}$ ), and this difference remained significant in 2015 ( $F_{1,56} = 6.356$ ,  $P = 0.016$ ). By 2017, however, four years following liana removal, tree canopies in the removal plots filled the space vacated by lianas, and differences in LAI between the sites were nearly identical to pre-liana-cutting differences. Thus, lianas took a significant portion of the forest canopy and,



four-years following liana cutting, tree's foliage captured the canopy area that had been covered by lianas.

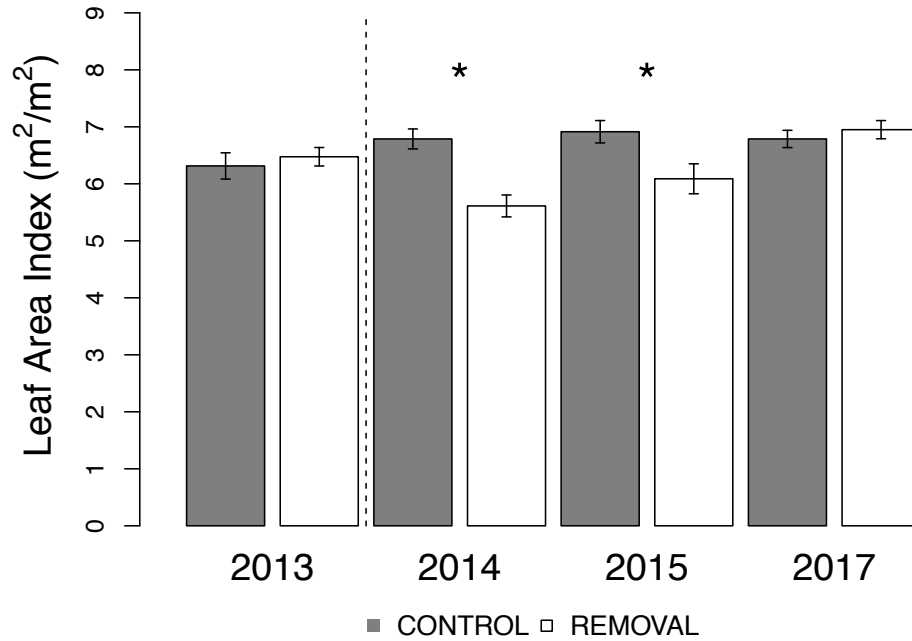


Figure 5. Mean Leaf Area Index for 30 control plots (gray bars) and 30 liana-removal plots (white bars) on Agua Salud Project, Central Panama. Data were collected using a LiCOR LAI-2000 optical system. Error bars represent one standard error.

\* $P < 0.05$ . Dotted line represents liana cutting.

Biomass relative increment in liana removal plots was consistently higher than in control plots throughout our experiment (Figure 6). Biomass relative increment in removal plots was 18.5% higher in 2015, and 21.9% higher in 2017 compared to control plots (2015:  $t = -2.096$ ,  $P = 0.045$ ; 2017:  $t = -1.863$ ,  $P = 0.073$ ). We did not detect significant differences between treatments in 2016, however the pattern was consistent with 2015 and 2017 – removal plots, on average, accumulated 12.9% more biomass than control plots ( $t = -1.458$ ,  $P = 0.156$ ) (Figure 3). Liana removal had a significantly positive effect on biomass relative increment for large trees throughout the chronosequence after

the second year of our experiment (Figure 7). We only found an effect of forest age on biomass relative increment for both treatments in 2016, but not in the other years of the study (Figure 7). For small and medium sized trees, and for all three sizes combined, the removal of lianas did not have a positive effect on the biomass relative increment (Appendix 11-13).

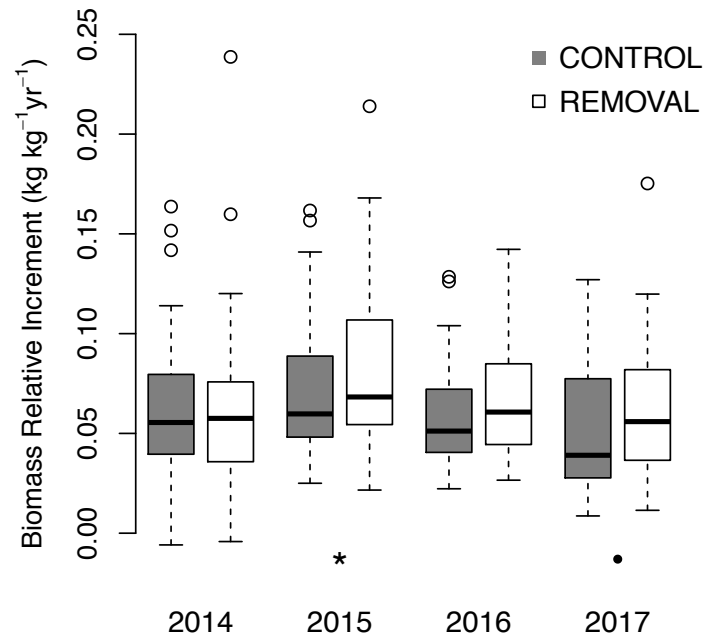


Figure 6. Biomass relative increment for 30 control plots (gray bars) and 30 liana-removal plots (white bars) during four years on Agua Salud Project, Central Panama. Error bars represent one standard error. \* $P < 0.05$ ; • $P = 0.07$ .

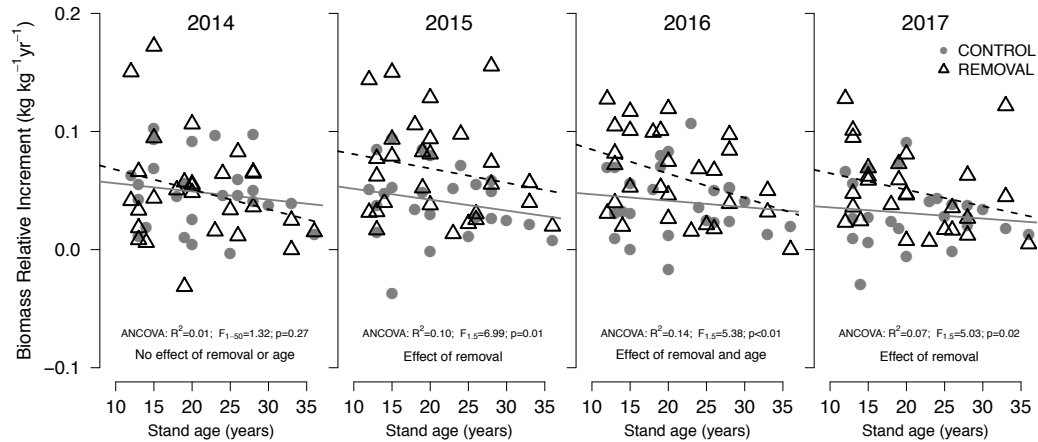


Figure 7. Biomass relative increment for large trees (diameter at breast height > 20cm) across 30 control plots (gray circles) and 30 liana-removal plots (white triangles) during four years in a secondary forest chronosequence in the Agua Salud Project, Central Panama. Gray bars represent line of best fit for control plots, dashed line represents line of best fit for liana removal plots. ANCOVA results are below each figure.

Liana removal had a strong positive effect on biomass relative increment at the tree level after accounting for the effect of crown condition and illumination (Figure 8). Sampling year and forest age had negative effects on biomass relative increment, but only sampling year had a significant effect. The linear mixed model had a low coefficient of determination; fixed factors (crown illumination, removal, crown condition, sampling year and forest age) explained only 14% of the total variance, and fixed factors and random factors (plots nested within sites) explained 0.28% of the total variance.

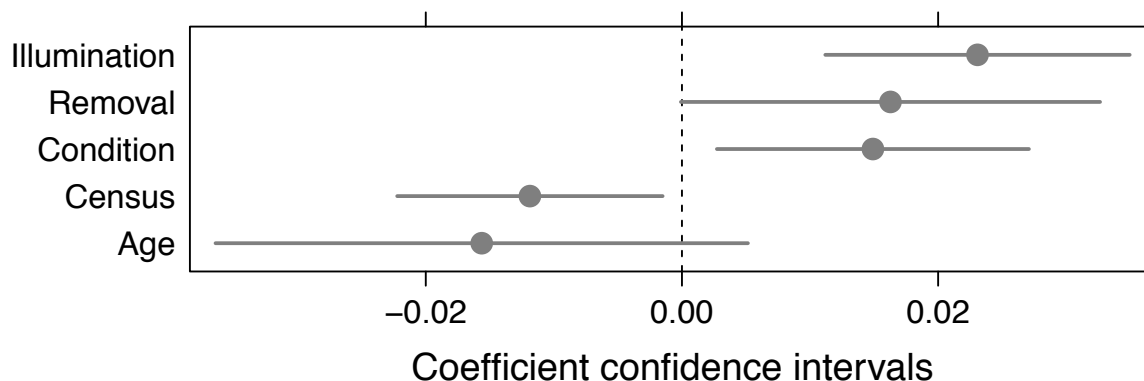


Figure 8. Coefficient confidence intervals of biomass relative increment from Linear Mixed Effects Models for large trees across four years on Agua Salud Project, Central Panama. Points are averaged coefficient estimates and bars correspond to 95% CIs. Intervals that do not overlap with zero value indicate a strong and significant effect. Illumination indicates crown illumination index, removal indicates the liana removal treatment, condition represents crown condition, census indicates year of sampling, and age indicates stand age.

## Discussion

Our study is the first experimental quantification of the effects of lianas on early successional tropical forests. Our results support the hypothesis that lianas dramatically reduce biomass accumulation in early secondary tropical forests. In fact, lianas reduced biomass accumulation on large trees regardless of forest age. Lianas strongly reduced biomass accumulation of large trees even after accounting for the health of the tree crown and canopy illumination. This result is particularly relevant because large trees contain most of the forest biomass (Lutz et al. 2018). In contrast, lianas did not have a negative effect on medium- and small-statured trees. We interpret these findings based on the light-demanding physiology of most liana species (Asner and Martin 2012). Lianas seek high lit areas at the top of the canopy (Avalos et al. 1999), areas also occupied by the foliage of the largest trees (Wirth et al. 2001). By intercepting light and displacing the

leaves of large canopy trees, lianas reduce tree growth and biomass accumulation (van der Heijden et al. 2015b). Once lianas are removed, large trees are able to accumulate more biomass compared to trees that still have lianas on their canopies. The benefit of liana removal to medium and small trees may be much more muted due to the lower prevalence of lianas on non-canopy trees (Muller-Landau and Visser 2018).

Lianas contribute a significant portion of the foliage in the canopy, and trees quickly took up the space vacated by lianas after liana removal. Our results closely resemble what Rodríguez-Ronderos et al. (2016) and Schnitzer and Carson (2010) found in similar studies in Central Panama. After one year of liana removal, Rodríguez-Ronderos et al. (2016) found that LAI was 17% higher in control plots with respect to removal plots. Four years after liana removal, trees in removal plots had fully compensated for the loss of lianas. Similarly to Rodríguez-Ronderos et al. (2016), trees in our removal plots also took four years to compensate for the loss of lianas in the canopy. Our finding that lianas contribute 18% of LAI also resembles the results of Wright et al. (2004), who found that lianas contribute up to 17% of the leaf productivity in the canopy of BCI. However, our results represent pooled data across forests of different ages and might not reflect subtle differences between younger and older forests. The rapid increase in tree photosynthetic machinery, which can be inferred from LAI data, can be one of the reasons why trees in removal plots, and especially large trees, were able to accumulate more biomass in removal plots compared to control plots.

The effect of lianas on biomass accumulation in tropical forests has gained attention recently (Paul and Yavitt 2011, Durán and Sánchez-Azofeifa 2015) due to the detrimental effects of lianas on forest carbon cycling (van der Heijden et al. 2015a).

While we found that lianas reduce biomass accumulation up to 21.9%, the magnitude of the liana removal effect across studies varies greatly. For example, in a 60-year old successional forest in Central Panama, van der Heijden et al. (2015b) found that lianas reduced biomass accumulation by 76% for trees  $\geq 10$  cm diameter. Liana removal experiments with saplings conducted in mid and older successional forests, or in forest gaps, have shown that biomass accumulation can range from 52% up to 436% (Schnitzer et al. 2005, Schnitzer et al. 2014, César et al. 2016, Marshall et al. 2017). This variability may be due to different light conditions across forest age, or the disparity in size classes between studies. For example, seedlings exempt from liana competition and under high light conditions may be able to accumulate more biomass relative to their initial size than small or medium size trees growing in the understory. In sum, our results and those of the other experimental studies, provide compelling evidence that lianas significantly reduce tree biomass in early successional forests.

Our experimental evidence is comparable to a recent observational study in the same field site, but differences between studies on how lianas affect trees with different size classes or across forest age provide important nuances on how lianas might be affecting trees. Using trees of all size classes ( $\geq 1$  cm DBH) on plots that ranged from 3 years to 35 years at Agua Salud, Lai et al. (2017) also found that the lianas significantly reduced tree biomass accumulation. However, and contrary to our results, they found that the effect of lianas increased with forest age (Lai et al. 2017). The contrasting results between these two studies might be due to the correlation between tree size and stand age; larger trees accumulate much more biomass per unit of diametric growth compared to smaller trees (Stephenson et al. 2014), and more trees move to larger size classes as

thinning takes place throughout succession (Saldarriaga et al. 1988). As Lai et al. (2017) sampled more larger trees in progressively older forests, the detrimental effect of lianas seem to increase over time.

In light of our results, we propose an alternative explanation: the per-capita effect of lianas on trees remains constant across forest age as long as the level of liana infestation per tree does not change over time. This would explain why we did not find an effect of liana removal on forest age when tree size is standardized. It would also explain why it was possible to detect a cumulative detrimental effect of lianas over time when sampling more larger trees across forest age (Lai et al. 2017). In other words, the detrimental effects of lianas increase over time because the number of large trees increases throughout succession, but not because the effects of lianas per capita becomes progressively stronger through time. In sum, by standardizing our sampling across the chronosequence, we demonstrate experimentally that lianas have a strong detrimental effect on early successional forests, and the per-capita effect of lianas remains constant as forests age, but because large trees accumulate with forests age, and lianas have a particularly strong negative effect on large trees, the effects of lianas on trees at the forest level can also increase with forest age.

The reduction in biomass accumulation due to the effects of lianas on trees has important implications for the future of carbon cycling. Early successional tropical forests can accumulate up to 1.6 PgC per year (Pan et al. 2011, Grace et al. 2014, FAO 2015), and if all the young and mid secondary Neotropical forests were left unperturbed for 40 years, they might be able to accumulate 8.48 PgC (Chazdon et al. 2016). In fact, 4.22 PgC could be accumulated in that same time period if only 10% of current pasture area

would be allowed to return to forests and if 60% of the secondary forests are allowed to persist (Chazdon et al. 2016). This huge potential could be thwarted for three key reasons. 1) Lianas may be increasing in tropical forests, especially in the Neotropics (Schnitzer 2015, Pandian and Parthasarathy 2016, Ceballos and Malizia 2017, Hogan et al. 2017). 2) Lianas recruit rapidly in early successional forests (Letcher and Chazdon 2009, Barry et al. 2015, Lai et al. 2017), and 3) lianas reduce biomass accumulation significantly in secondary forests (our results, van der Heijden et al. 2013, van der Heijden et al. 2015a). Future and more accurate forecasts of carbon accumulation and carbon sinks should integrate into their calculations the strength by which lianas reduce tree biomass across young secondary forests (Verbeeck and Kearsley 2016).

## Conclusions

Lianas reduce a significant portion of tree biomass accumulation early in secondary forest regeneration, especially for large trees. Once the effect of lianas was removed, trees quickly grew and took up the space that was once occupied by lianas. Once crown condition and illumination were factored in, liana removal remained a significant and positive factor in biomass accumulation. Overall, the effect of lianas on biomass accumulation might remain high as young forests age, but then the effect of lianas is expected to decline as once liana density starts to decline (Dewalt et al. 2000). As succession progresses and communities accumulate more hard-wooded old growth species, who seemed better capable to withstand higher liana infestation compared to soft-wooded pioneer species (Visser et al. 2018), the effect of lianas may increase over time.



The fact that competition between trees and lianas early in forest succession was intense and experienced by large trees informs the larger discussion about competition intensity during succession, and how competition shapes succession. Competition was intense regardless of forest age, which contrasts with the idea that competition increases steadily during succession (Christensen and Peet 1984, Walker and Chapin 1987, Tilman 1990). Even though Lai et al. (2017) showed that the effect of competition on forest biomass intensifies over time, the results from the liana removal experiment indicate that liana-tree competition is intense on a per capita basis for large trees regardless of forest age. This has important implications for forest succession because the largest individuals, which are those responsible for the largest bulk of ecosystem function in the forest (e.g. biomass accumulation) (Lutz et al. 2018), are those that experience intense levels of competition with lianas. Moreover, results from the removal experiment also indicate that competition between lianas and smaller trees was weak, probably because lianas seek the high lit environment at the top of the canopy, an area occupied by the largest trees. Competition intensity, at least between trees and lianas, seem to be intense for the largest individuals all throughout succession, but as tree density declines due to mortality during succession (Capers et al. 2005), and more trees increase in size, competition intensity at the stand level seems to increase (Lai et al. 2017).

The results from the liana removal experiment also sheds light into how competition between trees and lianas can shape succession. An established pattern across tropical successional forests is that biomass accumulation increases sharply during the first decades of succession, and tapers as time progresses (Saldarriaga et al. 1988, Poorter et al. 2016). Between 80 and 100 years after farmland abandonment, forests have

accumulated roughly the same amount of biomass compared to old growth forests (Martin et al. 2013). Maybe the great variability in biomass accumulation across early tropical secondary forests, as it has been shown by Poorter et al. (2016), may be due to different densities of lianas across these forests even if the effect of rainfall seasonality on liana density is accounted for. The results from our experiment shows that competition might reduce the speed at which early successional forests accumulate biomass, and hamper the capacity of early successional forests to reduce of atmospheric CO<sub>2</sub>. Even though we do not have data yet to determine whether the absence of lianas shifted the tree composition during succession, we know that lianas affect the trajectory of biomass accumulation by decreasing how much large trees uptake biomass.

Now that we have experimental evidence that lianas affect biomass accumulation in early successional tropical forests, is there more experimental evidence that lianas affect other community properties beyond biomass accumulation? Many observational studies have shown the direction and magnitude of the effects of lianas on tropical forests, and these effects have been recently reviewed (Paul and Yavitt 2011, Schnitzer and Bongers 2011, Durán and Sánchez-Azofeifa 2015, Schnitzer et al. 2015a). However, there has not been a systematic literature review summarizing the experimental evidence showing how strong the effect of lianas is on tropical forests. In the next chapter, I will show what does the experimental evidence says about the effect of lianas on tree growth, biomass accumulation, survival, reproduction, and on forest gap formation and tree damage when trees are felled by foresters.

#### IV. A COMPREHENSIVE SYNTHESIS OF LIANA REMOVAL EXPERIMENTS IN TROPICAL FORESTS

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 and 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 and Bongers 2002, Schnitzer et al. 2012, Wyka et al. 2013, Schnitzer et al. 2015a). 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, Schnitzer et al. 2015b). Lianas also provide food sources to insects, birds and mammals, particularly when trees are not flowering or fruiting (Morellato and Leita-Filho 1996). By linking tree crowns, lianas provide aerial pathways that are utilized by many animal species (Yanoviak and 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 and Phillips 2009, Ingwell et al. 2010), fecundity (Kainer et al. 2014, García León et al. 2018), recruitment (Schnitzer and

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 and Carson 2010, van der Heijden et al. 2013, Schnitzer et al. 2014, Schnitzer 2015, van der Heijden et al. 2015b, Ledo et al. 2016). Given that lianas commonly infest up to 75% of the trees in tropical forests (van der Heijden et al. 2008, Ingwell et al. 2010, van der Heijden et al. 2015b), 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 and Schnitzer 2008, Schnitzer et al. 2012, Bongers and Ewango 2015, Schnitzer et al. 2015a, Thomas et al. 2015), only one plot sampled lianas across the entire 50 hectares (Schnitzer et al. 2012, Schnitzer et al. 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, Schnitzer et al. 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, Reid et al. 2015, van der Heijden et al. 2015b, 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, actually 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 years, 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 five months to 10 years (Pérez-Salicrup and Barker 2000, Kainer et al. 2014), to studies on multiple tree species that spanned 28 years (Okali and 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 and Ola-Adams 1987, Parren and Bongers 2001, Dekker and 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 and Bongers 2002, Isnard and Silk 2009, Paul and 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 also 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 also 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 years that used liana removals to explore the role of lianas in tropical and subtropical forest ecosystems (Table 1, Appendix 14). To amass the liana experimental literature, we first searched the public comprehensive liana database 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.

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 of the studies, with one exception, reported that lianas reduced the performance of adult tree, saplings, or seedlings (Table 3, Appendix 14).

Table 3. Number of publications where liana removal experiments have been conducted, 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 days to 10 years	2 months to 18 years	2 months to 28 years



## 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 below ground. 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 measureable 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% one-year following the removal of lianas in 8 80 x 80 m plots (with 8 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 years. 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 and 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 two years 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) five months after liana cutting, and increased deeper soil layers after three years. 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 top soil 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 and Nepstad 2001, Restom and Nepstad 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 top soil 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* (Caesalpinioideae) and reported that leaf water potential increased immediately after removing lianas and remained higher than controls for the five-month study period. Furthermore, trees without lianas grew twice as much as controls over this same period (Pérez-Salicrup and 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, Dillenburg et al. 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 ( $\geq 10$  cm diameter) increased between 25% to 372% (Grauel and Putz 2004, Campanello et al. 2007, Grogan and Landis 2009, Schnitzer and 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 two-year period in liana removal plots for trees larger than 5cm 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 two-year 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 and 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 years 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 x 80 m plots (8 liana-removal and 8 control plots) in Panama, van der Heijden et al. (2015b) examined the effects of lianas over a 3-year 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. 2015b). 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 one year 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 years 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 five years 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 five years (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 four years, fruit production increased three-fold compared to 60 control trees. Kainer and colleagues followed these same trees for six more years and reported that, after 10 years, 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 five-fold one year 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 five years 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 years of liana removal.

However, community composition of all species between control and removal plots did not differ (Schnitzer and Carson 2010). In a dry forest in Brazil, Gerwing (2001) found that the sapling (>25cm tall and <2cm 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 years), 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 and Ola-Adams 1987, Dekker and 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 and de Graaf 2003) or prescribed burnings (Okali and 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. 2015a, Michel et al. 2015, Yanoviak 2015). For example, howler monkeys and marmosets 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 and Leita-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 tree crowns 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 (Schnitzer et al. 2014, van der Heijden et al. 2015b). 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. Out 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 3). All of 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-month 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 and Walker 1977, Putz 1984b, Okali and 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 one year 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 years 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 four years of removing both liana and trees increased tree growth 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 years 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 of 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 and 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 Reduced Impact Logging (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 and 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 and Braz 1995, Johns et al. 1996, Pinard and 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 tree-fall 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 and 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 tree-fall 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 and 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 tree fall 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 of different successional stages, and throughout the tropics. The majority of liana removal studies (43 of the 64) were conducted in the neotropics (Central and South America; Figure 9). Twenty studies were conducted in the paleotropics; nine in Africa, 10 in Asia, and one comparing liana removal experiments between the Africa and Asia (Dawkins 1960). Within the neotropics, the majority have been conducted in Bolivia, followed by Panama and Brazil (Figure 9). Within the paleotropics, the majority have been conducted in Indonesia, Malaysia, and Nigeria (Figure 9). 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.

The number of liana removal studies is relatively balanced in terms of the major tropical forest types (Figure 10a). 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 1050mm in Nigeria (Okali and 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 out of 22 studies performed in tropical moist forests were conducted in Panama, whereas only 3 out 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.

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 years since abandonment), five in mid-secondary (20-60 years since abandonment), four in old growth forests (>200 years since abandonment or stated as old growth by the authors), and three studies in early secondary forests (0-20 years since abandonment) (Figure 10b). 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.

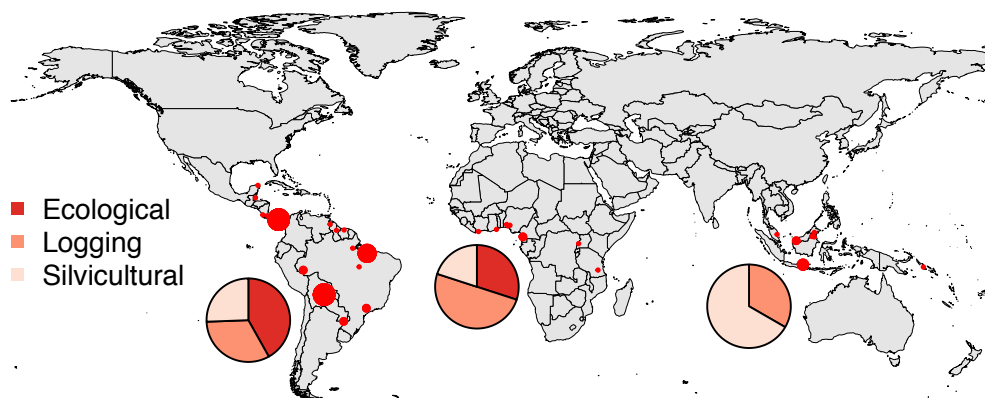


Figure 9. The pantropical distribution of liana removal studies ( $n = 64$ ), including the locations where liana removal experiments have been conducted. The size of the points represents the relative number of studies conducted at each location. Geographical coordinates for each study were obtained 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.

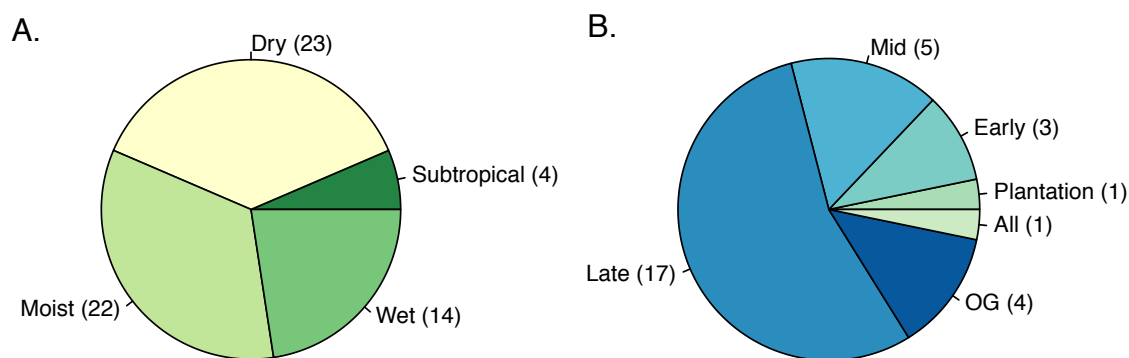


Figure 10. A) The forest types studied in 64 liana removal studies using the Holdridge life zone classification. Dry = Tropical Dry Forests, Moist = Tropical Moist Forests, Wet = Tropical Wet Forests, Subtropical = Subtropical Moist Forests. One study compared different forest types. B) The distribution 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.

### 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 and 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 and 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 and 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 and Chazdon 2012, Ledo and 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 (Schnitzer and 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 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.

## Conclusions

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.

## V. FINAL CONCLUSIONS

Edaphic factors, initial conditions and competition are key drivers of tropical forest succession. My results support the hypothesis that edaphic factors have a

significant effect on the changes of abundance of saplings and large lianas due to changes in soil nutrient availability. Soil nutrients, most likely P, affected the recruitment of saplings and the survival of large lianas over time. However, soil nutrients did not have a significant effect on the trajectories of trees and small lianas. Topography, another dimension of edaphic factors, had a significant effect on the temporal turnover of large lianas, probably because certain species of large lianas are associated with slopes and ridges. Initial conditions also affected successional trajectories. Plots with lower basal in the first forest census showed faster rates of change in structure, richness and biomass for trees and saplings, probably because there was more space available for new species to recruit, and less competition for light. The opposite was also true, plots with more basal area showed slower rates of change in structure, richness, biomass for trees and saplings but not for small and lianas. Higher forest cover, another initial condition, had a positive effect on seedling abundance, probably because forest cover increases seed dispersal and ameliorates harsh environmental conditions that would otherwise preclude sapling establishment. These results indicate that edaphic factor and initial conditions help drive how the trajectories of saplings, trees, small and large lianas change over time.

I was also able to show that competition between trees and lianas has a strong, and it had detrimental effects on biomass accumulation throughout forest succession. Contrary to recent evidence, I showed that lianas affected biomass uptake of large trees in early secondary forest regardless of forest age. Even though liana proliferation was high, the detrimental effect of lianas was only found on large trees, which can be explained by the fact that lianas tend to seek the high lit environments at the top of the canopy, an area occupied by largest trees of the forest. Lianas use a significant portion of the forest

canopy that would have been otherwise used by trees to intercept light. Interestingly, the positive effect of liana removal on biomass uptake on large trees was still significant even after accounting for crown illumination and canopy condition. In other words, the detrimental effect of lianas on biomass uptake is substantial despite different levels of exposure to sunlight and canopy completeness.

Finally, I showed that lianas have a strong detrimental effect on tree establishment, survival, growth, biomass accumulation, reproduction, and tree diversity in tropical forests around the world using the largest literature review on liana removal experiments up to date. Moreover, I also found that lianas increased tree mortality and gap formation during logging operations, lowering the productivity of future logging operation. Additionally, the effects of liana removal did not differ among the global regions where studies have been conducted, which indicates that the detrimental effects of liana tree-competition on trees and forests are significant and widespread. In sum, edaphic factors, initial conditions and competition between trees and lianas all influence the rate and direction of succession in young tropical forests.

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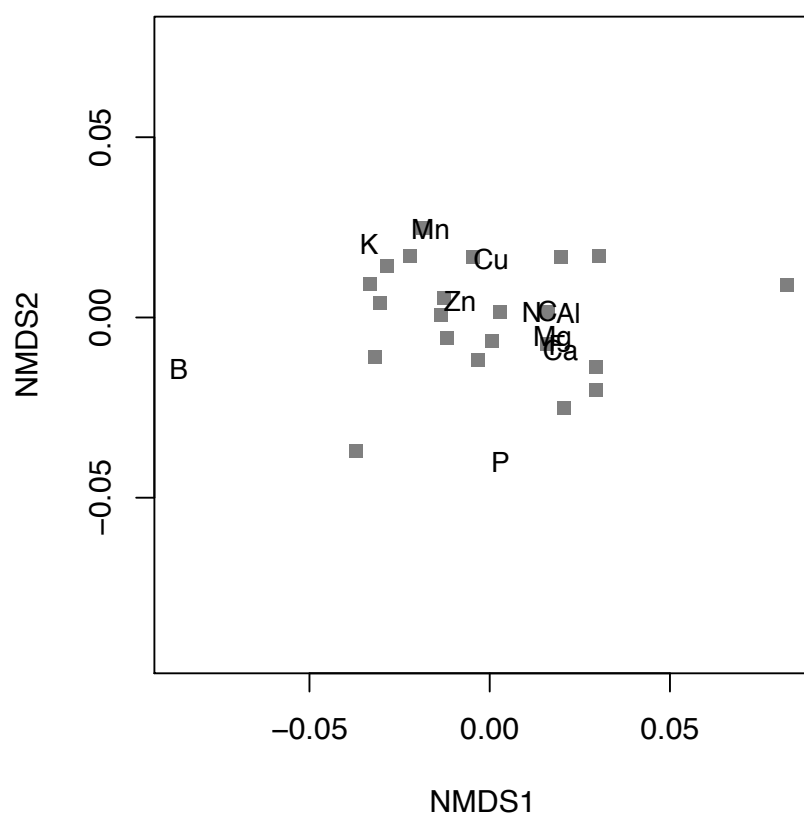
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## APPENDICES

Appendix 1. Ordination plot showing the variation in soil inorganic nutrients across plots. Gray squares represent plots. Letters represent soil elements.



Appendix 2. A) Pearson's correlations and B) Spearman's correlation tests among edaphic factors, initial conditions and forest age. Correlation tests were performed as a preliminary analysis to determine collinearity among all explanatory variables before conducting Linear Mixed Effects Models. Age = Year of pasture abandonment; I.BA = Initial Basal Area; For30 = Forest cover at a radius of 30m around the plots; For50 = Forest cover at a radius of 50m around the plots; For75 = Forest cover at a radius of 75m around the plots; For100 = Forest cover at a radius of 100m around the plots; For300 = Forest cover at a radius of 300m around the plots; Ele = Elevation; Asp = Aspect; Slo = Slope; TPI = Topographic Position Index; TRI = Terrain Roughness Index; Soil1 = First axis of Non Metric Multidimensional Scaling; Soil2 = Second axis of Non Metric Multidimensional Scaling.

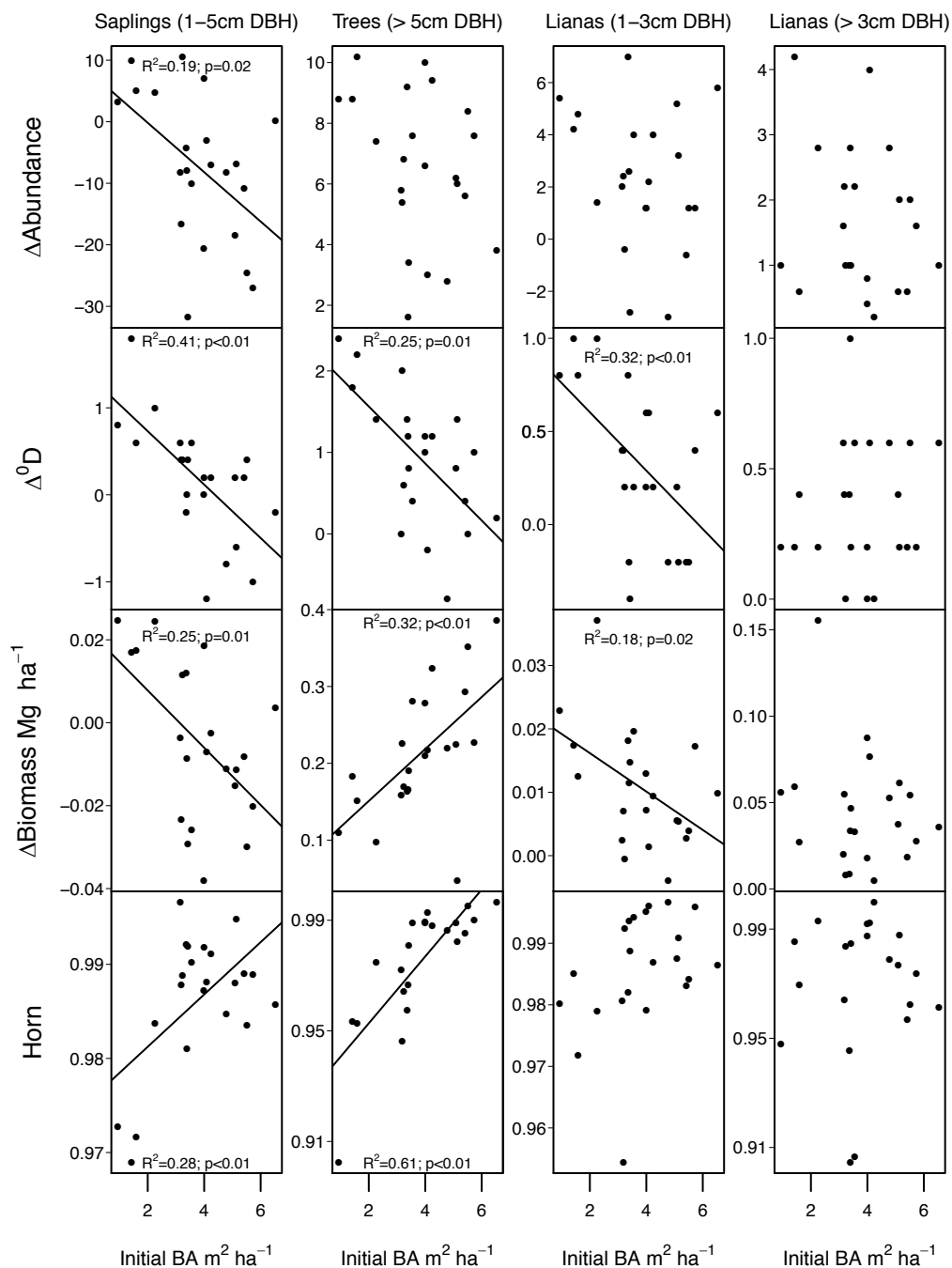
A)

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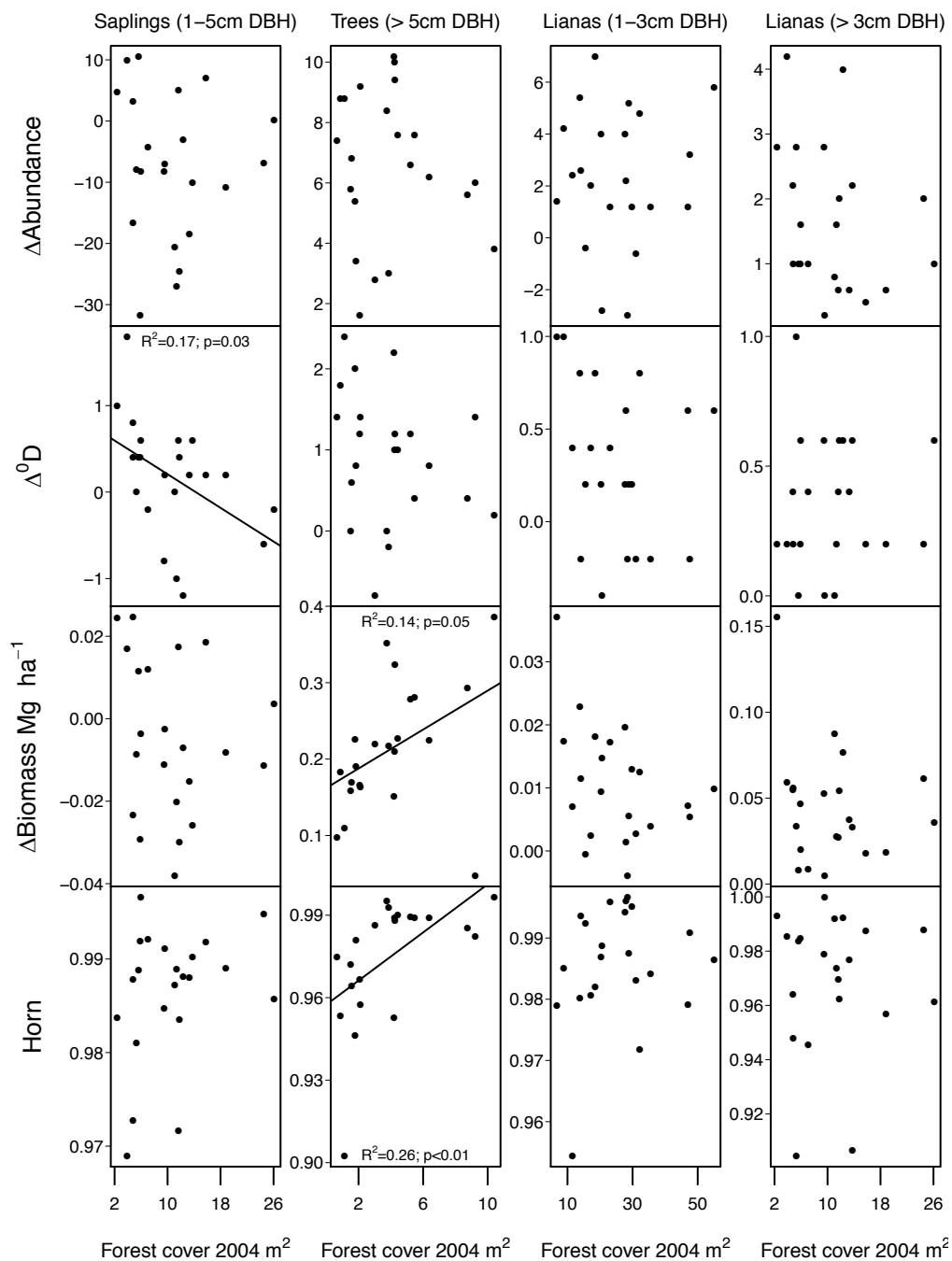
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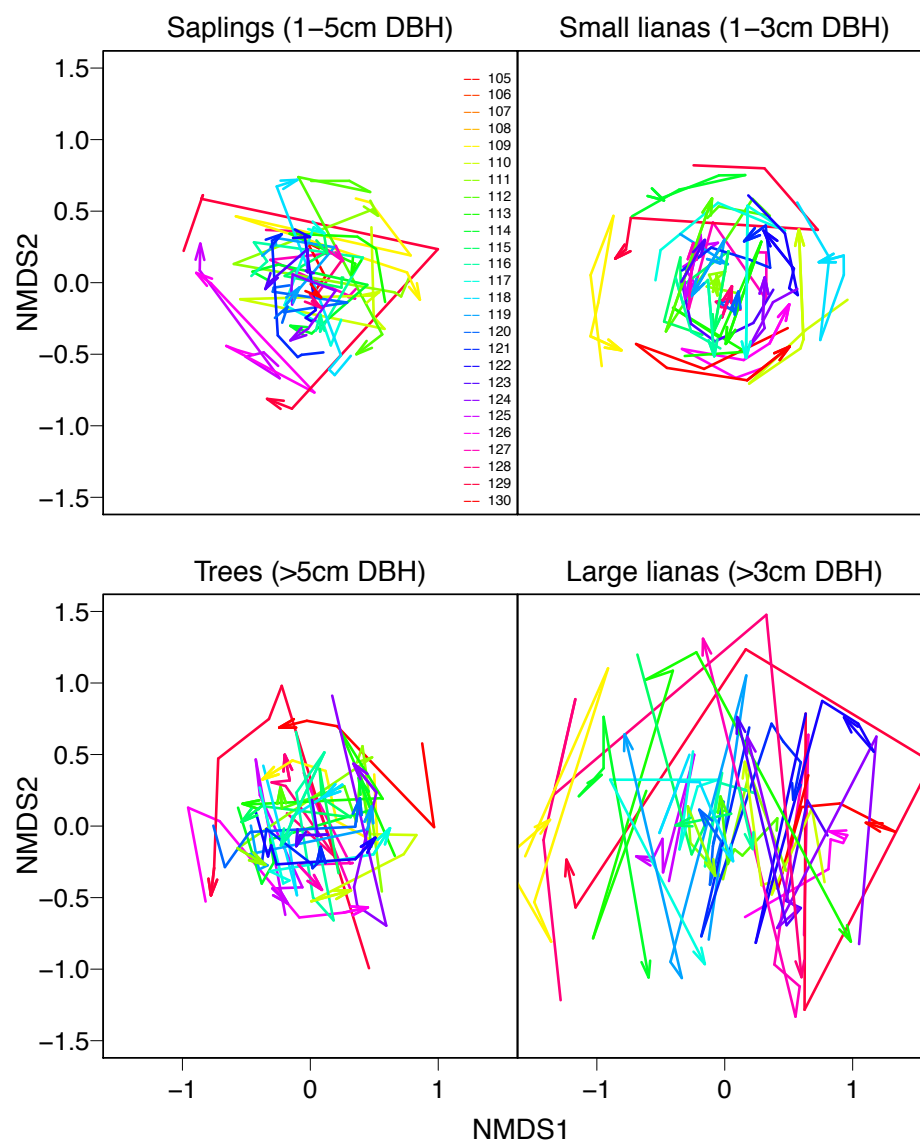
Appendix 3. Changes in community properties with respect to initial basal area (i.e. initial conditions when forest censuses began).  $\Delta$  represents rate of change. Regression lines are only for statistically significant correlations.



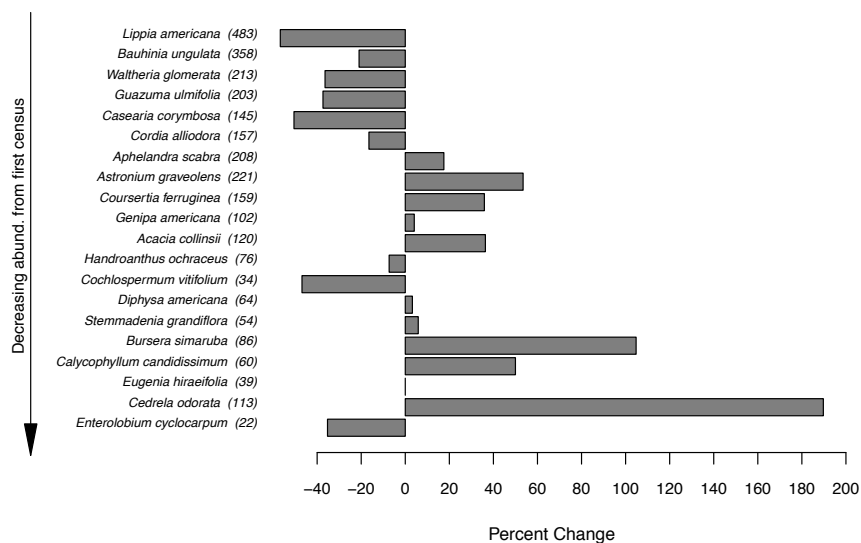
Appendix 4. Changes in community properties with respect to forest cover in 2004 inside and 30 m around each plot (i.e. initial conditions when succession began).  $\Delta$  represents rate of change. Regression lines are only for statistically significant correlations.



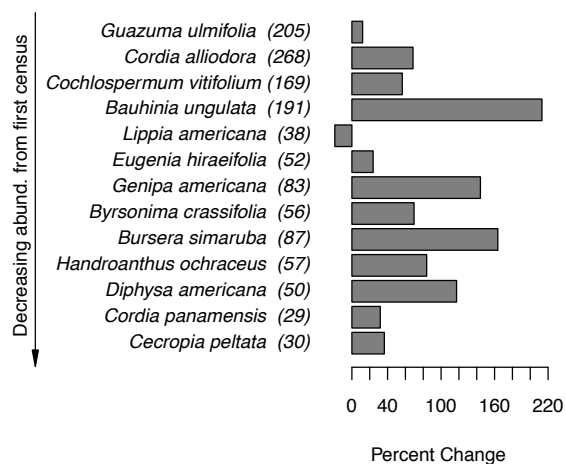
Appendix 5. Successional trajectories of species composition of saplings, trees, small lianas and large lianas through seven years of succession in a dry forest in Panama. Each arrow represents the trajectory of changes in community composition between censuses for each transect, and each color represents a different plot.



Appendix 6. Changes in species abundances of saplings after six years of early succession in a tropical dry forest in Panama. Species are organized in descending order of abundance measured on the initial census. Numbers in parenthesis are abundances in last census.

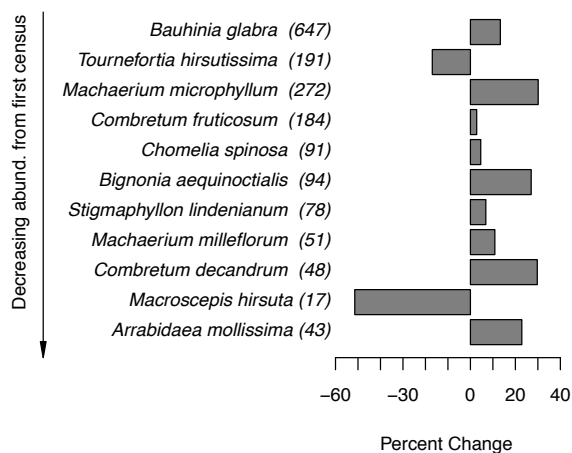


Appendix 7. Changes in species abundances of trees after six years of early succession in a tropical dry forest in Panama. Species are organized in descending order of abundance measured on the initial census. Numbers in parenthesis are abundances in last census.

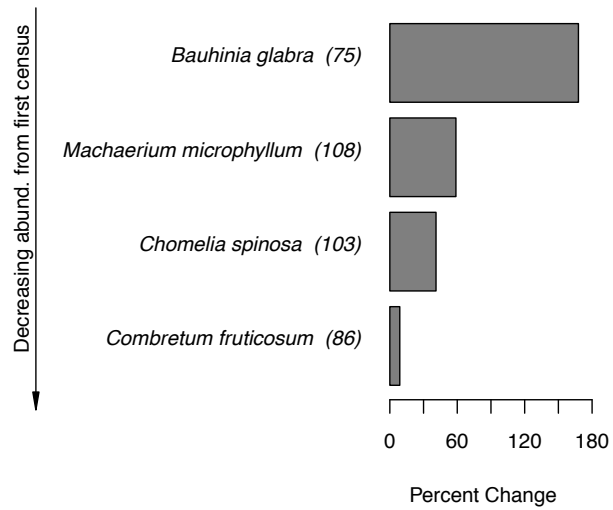




Appendix 8. Changes in species abundances of small lianas after six years of early succession in a tropical dry forest in Panama. Species are organized in descending order of abundance measured on the initial census. Numbers in parenthesis are abundances in last census.



Appendix 9. Changes in species abundances of large lianas after six years of early succession in a tropical dry forest in Panama. Species are organized in descending order of abundance measured on the initial census. Numbers in parenthesis are abundances in last census.

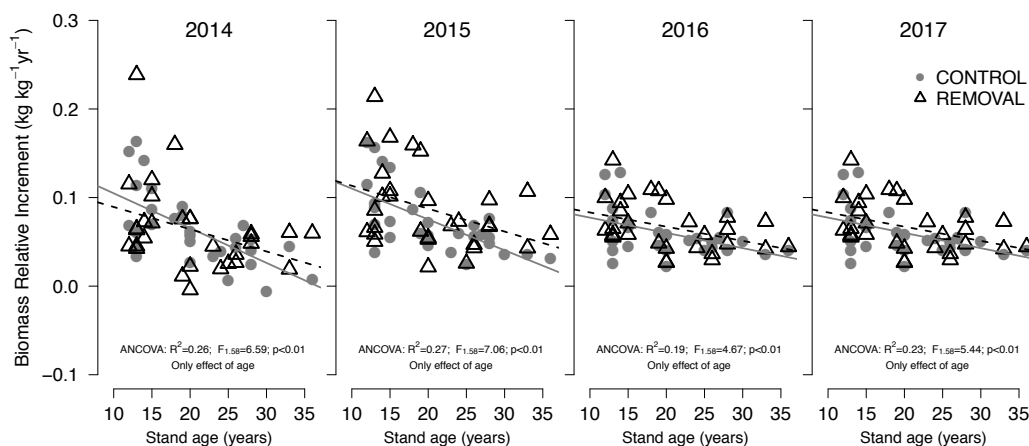


Appendix 10. Species selected (24) across the chronosequence in the Agua Salud Project, Central Panama, and their grouping according to their wood densities. Measurements of wood density were obtained from Agua Salud (Dylan Craven pers. com.) and from Barro Colorado Nature Monument, which is in the same region as Agua Salud (Wright et al. 2010)

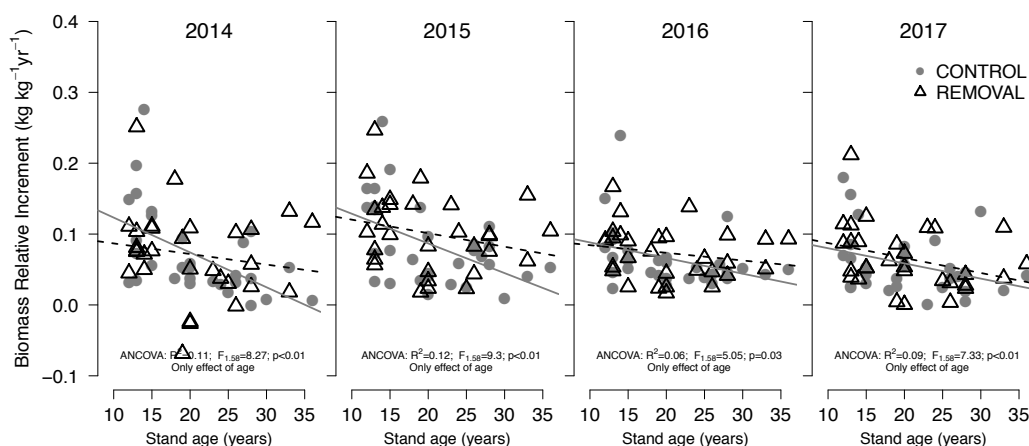
<b>Species</b>	<b>Family</b>	<b>Wood density category</b>
<i>Brosimum guianense</i>	Moraceae	Dense
<i>Coccoloba manzinellensis</i>	Polygonaceae	Dense
<i>Miconia argentea</i>	Melastomataceae	Dense
<i>Andira inermis</i>	Fabaceae: Papilionoideae	Dense
<i>Lonchocarpus heptaphyllus</i>	Fabaceae: Papilionoideae	Dense
<i>Casearia sylvestris</i>	Salicaceae	Dense
<i>Terminalia amazonia</i>	Combretaceae	Dense
<i>Cupania scrobiculata</i>	Sapindaceae	Dense
<i>Banara guianensis</i>	Salicaceae	Medium
<i>Annona spraguei</i>	Annonaceae	Medium
<i>Lacistema aggregatum</i>	Lacistemataceae	Medium
<i>Inga cocleensis</i>	Fabaceae: Mimosoidae	Medium
<i>Conostegia xalapensis</i>	Melastomataceae	Medium
<i>Xylopia frutescens</i>	Annonaceae	Medium
<i>Byrsonima crassifolia</i>	Malpighiaceae	Medium
<i>Schefflera morototoni</i>	Araliaceae	Medium
<i>Saurauia yasicae</i>	Actinidiaceae	Light
<i>Vismia baccifera</i>	Clusiaceae	Light
<i>Pachira sessilis</i>	Bombacaceae	Light
<i>Turpinia occidentalis</i>	Staphyleaceae	Light
<i>Cordia bicolor</i>	Boraginaceae	Light
<i>Trichospermum galeottii</i>	Malvaceae	Light
<i>Apeiba tibourbou</i>	Malvaceae	Light
<i>Cochlospermum vitifolium</i>	Cochlospermaceae	Light

Appendix 11. Biomass relative increment for all tree sizes (diameter at breast height  $\text{DBH} \geq 5\text{cm}$ ), small trees ( $5 \leq \text{DBH} \leq 10$ ) and medium size ( $10 \leq \text{DBH} \leq 20$ ) across 30 control plots (gray circles) and 30 liana-removal plots (white triangles) during four years in a secondary forest chronosequence in the Agua Salud Project, Central Panama. Gray bars represent line of best fit for control plots, dashed line represents line of best fit for liana removal plots. ANCOVA results are below each figure.

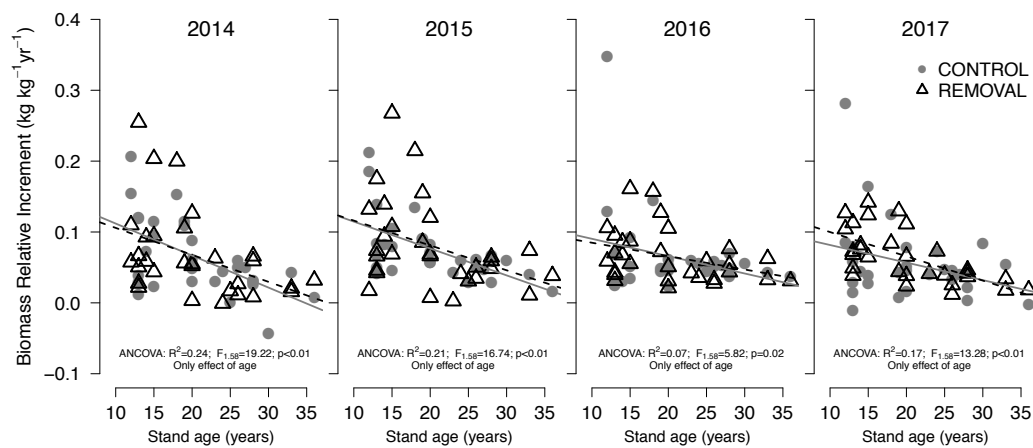
All trees combined.



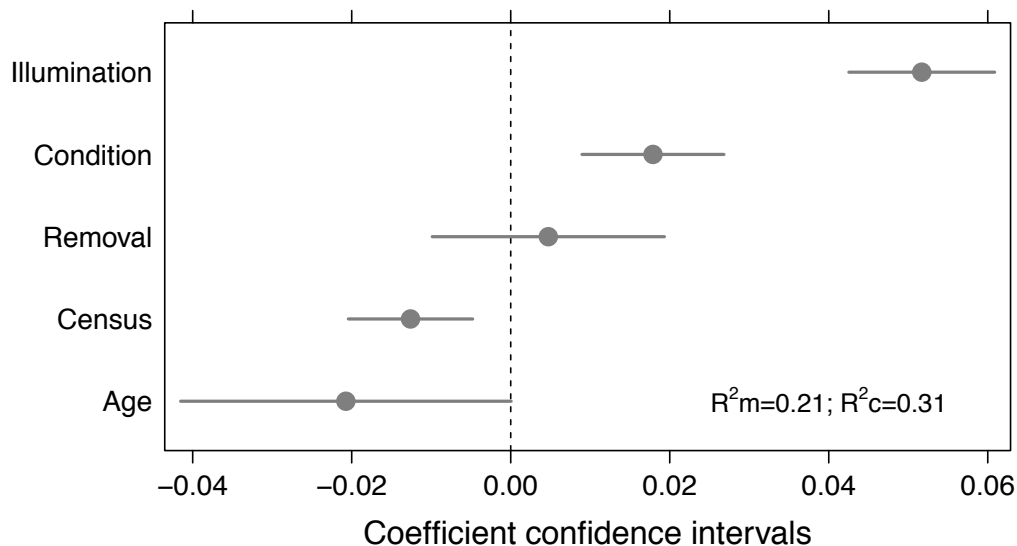
Small trees



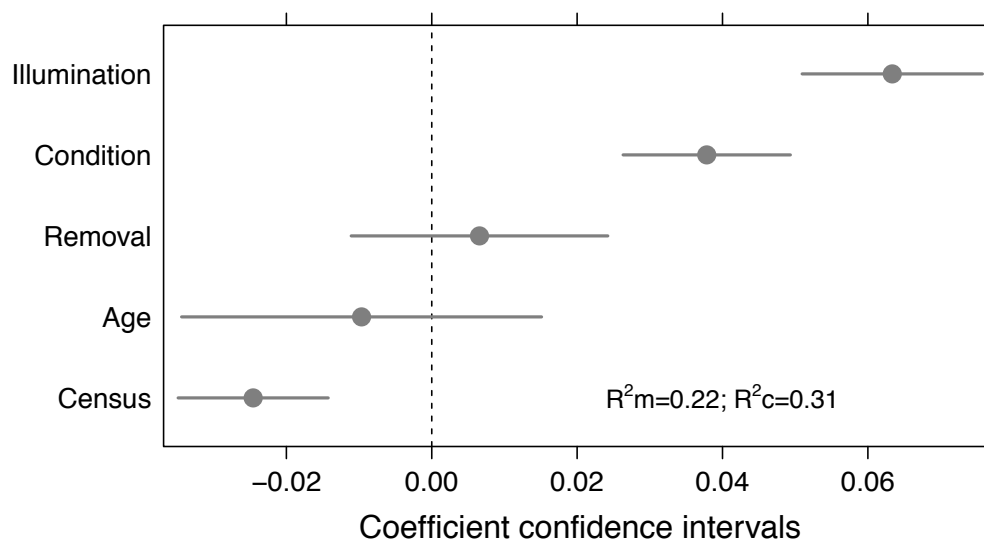
Medium trees



Appendix 12. Coefficient confidence intervals of biomass relative increment from Linear Mixed Effects Models for medium size trees across four years on Agua Salud Project, Central Panama. Points are averaged coefficient estimates and bars correspond to 95% CIs. Intervals that do not overlap with zero value indicate a strong and significant effect. Illumination indicates crown illumination index, removal indicates the liana removal treatment, condition represents crown condition, census indicates year of sampling, and age indicates stand age.  $R^2_m$  represents the marginal coefficient of the variance explained by the fixed factors,  $R^2_c$  represents the conditional coefficient of the variance explained by fixed and random factors.



Appendix 13. Coefficient confidence intervals of biomass relative increment from Linear Mixed Effects Models for small size trees across four years on Agua Salud Project, Central Panama. Points are averaged coefficient estimates and bars correspond to 95% CIs. Intervals that do not overlap with zero value indicate a strong and significant effect. Illumination indicates crown illumination index, removal indicates the liana removal treatment, condition represents crown condition, census indicates year of sampling, and age indicates stand age.  $R^2_m$  represents the marginal coefficient of the variance explained by the fixed factors,  $R^2_c$  represents the conditional coefficient of the variance explained by fixed and random factors.



Appendix 14. Publications reviewed in this chapter. The list is sorted by focal area and then by year of publication. NA = not mentioned or not specified. MAP = Mean Annual Precipitation. Elev = Elevation.

Focal area	Year	Author	Title	Synthesis statement	Method	Spatial Scale of removal	Time for effect	Country	Holdridge life zones	Successional stage	MAP (mm)	Elev.
Effect of liana cutting on trees	1987	Stevens, G.	Lianas as structural parasites: the <i>Bursera simaruba</i> example	Experimental reduction of liana loads on trees' canopies increased fruit tree production	Pole pruners	5 trees with lianas removed. 100 trees for control.	1-2 years	Costa Rica	Tropical dry forest	Old growth	1500	NA
Effect of liana cutting on trees	2000	Barker, M.G. and Pérez-Salicrup, D.R.	Comparative water relations of mature mahogany ( <i>Swietenia macrophylla</i> ) trees with and without lianas in a sub humid, seasonally dry forest in Bolivia.	Removal of lianas had no effect on tree's water relations, even at the end of the dry season	NA	8 trees (4 for removal).	3.5 months	Bolivia	Tropical dry forest	NA	1450	200
Effect of liana cutting on trees	2000	Pérez-Salicrup, D.R. and Barker M.G.	Effect of liana cutting on water potential and growth of adult <i>Senna multijuga</i> (Caesalpinioideae) trees in a Bolivian tropical	Lianas interfere with tree water availability during the dry season. Lianas also hinder tree growth during the same period	NA	20 trees (10 for removal).	5 months	Bolivia	Tropical dry forest	NA	1450	200
Effect of liana cutting on trees	2001	Pérez-Salicrup, D.R.	Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia	Lianas hinder the growth of tree seedlings but with different effect between species. Differential effects shift the balance in competitive interactions between species	Machete cutting near the ground and arm height	Cutting area: 12 plots (30X30 m) plots with 10 m buffers. Same for controls.	1 year	Bolivia	Tropical dry forest	NA	1450	200



Effect of liana cutting on trees	2004	Schnitzer, S.A. et al.	Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon	Pre-logging liana cutting significantly reduced the number of lianas and the number of liana-infested trees in logging gaps. This method minimizes liana detrimental effects on regenerating trees in logging gaps	NA	Cutting area: 6 1-ha plots, 100 m buffer zone. Within, 15 subplots (1X5 m) in six tree gaps. Same for control.	1 year	Cameroon	Tropical moist forest	NA	2000	NA
Effect of liana cutting on trees	2005	Schnitzer, S.A. et al.	Disentangling above- and below-ground competition between lianas and trees in a tropical forest	Tree seedlings grown in liana removal plots had higher biomass and allocated more biomass to stems compared to control plots	Clippers at ground level.	30 9X12 plots. 360 planted seedlings.	2 years	Côte d'Ivoire	Tropical dry forest	Mid succession	1900	50
Effect of liana cutting on trees	2009	Grogan, J. and Landis, R.M.	Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany <i>Swietenia macrophylla</i> in Brazil	Liana cutting allowed trees to grow faster than control trees, but it took five years for trees to show growth rates similar to naturally liana-free trees	NA	22 trees, (8 for removals).	10 years	Brazil	Tropical dry forest	NA	1859	NA
Effect of liana cutting on trees	2010	Schnitzer, S.A. and Carson, W.P.	Lianas suppress tree regeneration and diversity in treefall gaps	Liana-tree competition constrains shade-tolerant tree recruitment, growth and richness in gaps. Lianas were particularly harmful to shade-tolerant species, but not to pioneers	Machete cutting near the ground	17 forest gaps (9 controls, 8 removal), 145–499 m <sup>2</sup>	2 years	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2012	Tobin M. et al.	Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees	Release from liana competition, but not tree competition, resulted in increased water transport in canopy trees. Relative to their biomass, lianas have greater competitive effects on	Machete cutting near the ground	Cutting area: 16 plots (30X30 m), 4 trees measured per plot.	3 days.	Panama	Tropical moist forest	Late succession	2600	NA

				canopy tree performance than competing trees								
Effect of liana cutting on trees	2014	Schnitzer, S.A. et al.	Lianas in gaps reduce carbon accumulation in a tropical forest	Lianas reduce carbon uptake, despite their relatively low biomass, at the scale of forest gaps and when scaled to the forest level	Machete cutting near the ground	Seventeen forest gaps, 9 controls and 8 removals (145–499 m <sup>2</sup> )	8 years	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2014	Kainer, K.A. et al.	Testing a silvicultural recommendation- Brazil nut responses 10 years after liana cutting	Liana cutting enhances fruit production three-fold but only after 4 years of treatment	NA	138 trees: 78 experimental trees, 60 controls	10 years	Brazil	Tropical moist forest	NA	1800	NA
Effect of liana cutting on trees	2015	Ried, J.P. et al.	Short and long-term soil moisture effects of liana removal in a seasonally moist tropical forest	Liana reduction increases water availability near the surface in the short term (months) and in deeper soil layers in the long run (three years)	Machete cutting near the ground	0.64-ha X 8 plots	3 years.	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2015	Álvarez-Cansino, L. et al.	Liana competition with tropical trees varies seasonally but not with tree species identity	Tree sap velocity increased significantly after liana removal, especially during the dry season when soil moisture is low. Response did not differ between tree species	Machete cutting near the ground	0.64-ha X 8 plots	1 year	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2015	van Der Heijden et al.	Lianas reduce carbon accumulation and storage in tropical forests	Lianas decrease forest biomass accumulation by reducing biomass tree growth, increasing tree mortality, and by changing carbon	Machete cutting near the ground	0.64-ha X 8 plots	3 years.	Panama	Tropical moist forest	Late succession	2600	NA

				allocation from wood to leaves.								
Effect of liana cutting on trees	2015	Wright et al.	Unique competitive effects of lianas and trees in a tropical forest understory	Lianas and trees have unique and differential effects on understory plants; lianas seem to compete more strongly during the dry season, whereas trees compete more strongly for light.	NA	40 8m circular plots (10 liana removal, 10 tree removals, 20 controls)	3 years	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2016	César, R.G. et al.	Evaluating climber cutting as a strategy to restore degraded tropical forests.	Liana cutting can be used as a restoration tool because it increases understory light and enhances biomass accumulation of shrubs and small trees, either planted or from advanced regeneration	Machete cutting near the ground and arm height	30 circular plots (10-m radius). Liana cutting: 20 plots	1 year	Brazil	Subtropical Moist forest	Mid succession	1565	550
Effect of liana cutting on trees	2016	Martínez-Izquierdo, L. et al.	Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest	Tree seedlings survived 75% more, grew 300% taller, and had twice the aboveground biomass in liana-removal plots than seedlings in control plots. Lianas had a similar negative effect on all 14-tree species	Machete cutting near the ground	0.64-ha X 8 plots	2 years	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2016	Rodríguez-Ronderos, M.E. et al.	Contribution of lianas to plant area index and canopy structure in a Panamanian Forest	Lianas intercept light in the upper and mid canopy, with an increase in Plant Area Index of about 20% once lianas were removed. Treatment effect disappeared four years after liana cutting	Machete cutting near the ground	0.64-ha X 8 plots	1 year	Panama	Tropical moist forest	Late succession	2600	NA

Effect of liana cutting on trees	2017	Marshall, A.R. et al.	Liana cutting for restoring tropical forests: A rare paleotropical trial	Liana removal increases tree sapling growth, biomass and survival. Wildfires and liana removal have a modest effect on tree biomass accumulation via recruitment	Clippers at ground level and shoulder height, and burning.	18- 5X5 m plots. 10 cut, 8 uncut.	5 years	Tanzania	Tropical moist forest	Mid succession	1514	270
Effect of liana cutting on trees	2017	García-León, M. et al.	Lianas reduce community-level reproduction in canopy and understory tropical trees	After liana cutting far more canopy tree individuals and species produced flowers and fruits. Each reproductive individual had more flowers and fruits, and these effects were strong even after 5 years of liana cutting	Machete cutting near the ground	0.64-ha X 8 plots. Three 20X20 m subplots per plot for understory. 36 canopy trees per plot.	5 years	Panama	Tropical moist forest	Late succession	2600	NA
Effect of liana cutting on trees	2017	César, R.G. et al.	Early response of tree seed arrival after liana cutting in a disturbed tropical forest	The presence of lianas can contribute to more abundant and richer seed rain in liana infested forest fragments	Machete cutting near the ground and arm height	12 circular plots (10-m radius). Liana cutting: 6 plots	1 year	Brazil	Subtropical Moist forest	Mid succession	1565	550
Liana cutting and tree elimination /harvesting as silvicultural treatments	1927	Stevenson, N.S.	Silvicultural treatment of mahogany forests in British Honduras	Silvicultural treatment (liana cut plus canopy thinning) produced higher numbers of merchantable seedlings and saplings.	Cutting NA. Poisson girdling of trees	NA	17 months	Belize	Tropical wet forest	NA	NA	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	1955	Barnard, R.C.	Silviculture in the tropical rainforest of Western Nigeria compared to Malayan methods	Liana cutting enhances tree growth of different size classes because lower liana abundance increases light availability	Cutting NA. Poisson girdling of trees and lianas with sodium arsenite	NA	7 years	Nigeria	Tropical wet forest	Late succession	1651	NA

Liana cutting and tree elimination /harvesting as silvicultural treatments	1970	Baidoe, J.F.	The selection system as practiced in Ghana	Liana cutting enhances tree growth	Cutting NA. Poisson girdling of trees and lianas with sodium arsenite	NA	25 years	Ghana	5 different ecosystems	NA	NA	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	1977	Lowe, R.G. and Walker, P.	Classification of canopy, stem, crown status and climber infestation in a tropical forest of Nigeria	Silvicultural treatment (liana cutting plus canopy thinning) produced higher initial basal areas, which in turn produced higher annual growth rates. Decreasing liana infestation increase growth rates in one species	Cutting NA. Poisson girdling of trees	8-ha, two species analyzed	14 years	Nigeria	Tropical wet forest	NA	NA	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	1984	Putz, F.E. et al.	Effects of post-felling silvicultural treatments on woody vines in Sarawak	Liana removal increases tree basal area and has a moderate effect on the percentage of trees with lianas	NA	5 plots between 12 and 65-ha. All treatments applied in each plot.	4-7 years	Malaysia	Tropical wet forest	Late succession	NA	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	1985	Putz, F.E.	Woody vines and forest management in Malaysia	Liana cutting contributes to less logging damage. Intense logging increases light availability, which increases liana abundance. Trees with lianas grow slower	Cutting NA. Poisson girdling of trees	NA	4 or 5 years. 6 years after logging.	Malaysia	Tropical wet forest	Several studies are reviewed.	NA	>100 From internet

Liana cutting and tree elimination /harvesting as silvicultural treatments	1987	Okali, D.U.U. and Ola-Adams, B.A.	Tree population changes in treated rain forest at Omo Forest Reserve, south-western Nigeria	Increase in light availability via canopy opening and liana cutting changed tree species abundances and size classes, but did not change tree species richness. Cutting and burning were not as effective as other methods	Machete cutting and poison girdling of trees. Machete cutting and burning.	1952: 4 plots, 4.05-ha each. Treatment A: and B. Liana cutting and canopy opening by tree poisoning. Treatment C: clearing and burning. Treatment D: Only Liana cutting in 1951 and 1980: 3 plots (50X50 m each) X 3 treatments = 3-ha	28 years	Nigeria	Tropical dry forest	Late succession	1050	150
Liana cutting and tree elimination /harvesting as silvicultural treatments	1996	Johns, J.S. et al.	Logging damage during planned and unplanned logging operations in the eastern Amazon	Liana removal and planned felling produced smaller logging gaps, fewer trees were damaged, less volume was lost, and bole damage was lower. Liana cutting and directional felling are the most cost-effective strategy to avoid tree damage during logging	NA	105-ha of planned logging where lianas were cut. 75-ha unplanned logging. Permanent plots established within. 30 tree gaps per 105-ha and 75-ha respectively.	2 years	Brazil	Tropical dry forest	NA	1700	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	1999	Guariguata, M.R.	Early response of selected tree species to liberation thinning in a young secondary forest in Northeastern Costa Rica	Liana cutting and canopy thinning significantly increased tree diameter growth with respect to controls.	Machete cutting. Chainsaw girdling of trees.	Treatment: 2 plots (30X70 m). 68 trees within. Control: 2 plots (same dimensions). 71 trees within.	1 year	Costa Rica	Tropical wet forest	Early succession	3800	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	2001	Pérez-Salicrup, D.R. et al.	Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia	Liana cutting reduces the number of lianas in infested forests. The effect lasts more than 2 years, but the method is expensive and should be used as a	Machete cutting near the ground and arm height	Cutting area: 12 plots (30X30 m) within 10m buffers. Same for controls.	2 months for sprouting, 2 years for infestation	Bolivia	Tropical dry forest	NA	1450	200

				preventive activity to avoid infestation								
Liana cutting and tree elimination /harvesting as silvicultural treatments	2002	Gerwing, J.J. and Vidal, E.	Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonia forest.	Complete liana removal and reduced impact logging reduces liana richness, abundance, basal area and biomass. The silvicultural benefits of liana cutting needs to be evaluated	NA	100-ha forest patch. 1 plot (2X1000 m).	8 years	Brazil	Tropical dry forest	NA	1700	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	2002	Gerwing, J.J. and Uhl, C.	Pre-logging liana cutting reduces liana regeneration in logging gaps in the eastern Brazilian Amazon	Pre-logging liana cutting and reduced impact logging can significantly reduce post-logging liana proliferation in gaps, with no negative impact on the species diversity of regenerating lianas	NA	Cutting area: 8 forest gaps (4 with a single gap tree, 4 with multiple gap trees). 8 gaps for controls. In each gap 5X10 m plot.	6 years	Brazil	Tropical dry forest	Old growth	1700	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	2002	Heuberger, K. et al.	Mechanical cleaning and prescribed burning for recruiting commercial tree regeneration in a Bolivian dry forest	Liana cutting and canopy thinning prior to burning can reduce recruiting vegetation around merchantable trees in post-logging gaps, but the treatment did not elicit a significant response in density and growth of merchantable trees	Machete, chainsaw and prescribed burning	40 gaps ranging 240-840 m <sup>2</sup> . 10 gaps per treatment	8 months	Bolivia	Tropical dry forest	NA	1130	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	2003	Zagt, R. et al.	Logging effects on liana diversity and abundance in Central Guyana	Logging produced a net increase liana richness and abundance. However, this increase was only found in the most heavily logged plots. Species showed idiosyncratic responses to logging and pre-existing spatial patterns of species composition remain	NA	Sample A = 3.75-ha. All lianas >2 m height in 10X10 m subplot Sample B = 0.9375-ha. Lianas >0.5 m height in 5X5 m subplots.	4 years	Guyana	Tropical wet forest	NA	2750	50

				similar to nearby control sites								
Liana cutting and tree elimination /harvesting as silvicultural treatments	2003	Sist, P. et al.	Reduced-impact logging in Indonesian Borneo: some results confirming the need for new silvicultural prescriptions	Reduced impact logging (liana cutting prior to felling) showed lower damage on nearby trees, higher remaining basal area and smaller canopy gaps. However, at high logging intensities, Reduced impact logging and conventional methods are similar	NA	24 plots (1-ha each). 9 conventional logging, 3 logging intensities, 9 RIL, 3 logging intensities	8 months	Indonesia	Tropical wet forest	NA	4000	100-300
Liana cutting and tree elimination /harvesting as silvicultural treatments	2003	Dekker, M. and de Graaf, N.R.	Pioneer and climax tree regeneration following selective logging with silviculture in Suriname	No effect of liana removal and canopy thinning after 20 years of logging. Density of old growth species showed no difference between controls and removals, but there was higher liana density on two out of three replicates where logging was highest	Cutting NA. Poisson girdling of trees	9-ha total plus 3 for controls. Assessments on 240 10X10 m subplots, 60 per refinement treatment and 60 for control.	20 years	Suriname	Tropical moist forest	Late succession	2385	25-36
Liana cutting and tree elimination /harvesting as silvicultural treatments	2003	Duncan, R.S. and Chapman C.A.	Tree-shrub interactions during early secondary forest succession in Uganda	Vegetation removal (including vines) has limited effects on tree growth and richness. Some species showed a positive response after one year but on the second the effect disappeared.	Uprooting	42 5X5m plots. 20 plots in low density sites (cypress plantations), 22 plots in high density sites (pine plantations). 25 circular, 25 m <sup>2</sup> control plots	1 year	Uganda	Tropical moist forest	Early succession	1543	1500



Liana cutting and tree elimination /harvesting as silvicultural treatments	2006	Felton, A. et al.	Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest	Reduced Impact Logging gaps were significantly larger, had significantly lower coverage of lianas, and higher prevalence of seedlings than in natural tree-fall gaps. In larger gaps, microclimatic conditions favor the regeneration of non-commercial pioneer species	NA	72 gaps. 36 logging gaps, 36 natural gaps. 20X20 m plot per gap = 2.88-ha	1-4 years	Bolivia	Tropical dry forest	NA	1560	320
Liana cutting and tree elimination /harvesting as silvicultural treatments	2008	Peña-Claros, M. et al.	Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees.	Silvicultural treatments after logging (liana cutting around merchantable trees and future merchantable trees, coupled with canopy thinning and Reduce Impact Logging practices) increased timber volume after the first cutting cycle than just using Reduce Impact Logging practices	NA	12 plots (27-ha each).	4 years	Bolivia	Tropical dry forest	NA	1580	NA
Liana cutting and tree elimination /harvesting as silvicultural treatments	2008	Peña-Claros, M. et al.	Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest	Intensive silvicultural treatment (liana cutting around merchantable trees and future merchantable trees, coupled with canopy thinning) had the strongest impact on tree density and growth of long lived pioneer commercial species	NA	12 plots (450X20 m)	3 years.	Bolivia	Tropical dry forest	NA	1580	400-600

Liana cutting and tree elimination /harvesting as silvicultural treatments	2009	Villegas Z. et al.	Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest	Tree growth rates increased with silvicultural treatments, with long-lived pioneer species showing the strongest response to intense liana cutting and canopy thinning. Tree growth rates increased with higher light availability, higher logging intensity and decrease with higher liana infestation	Machete cutting. Chainsaw girding of trees.	8 plots, 2 per treatment. Average plot size 21.21-ha.	4 years	Bolivia	Tropical dry forest	NA	1160	400-500
Liana cutting and tree elimination /harvesting as silvicultural treatments	2013	Schwartz, G. et al.	Post-harvesting silvicultural treatments in logging gaps: A comparison between enrichment planting and tending of natural regeneration	Tree seedlings showed higher survival and higher growth on gaps where lianas and other vegetation were removed	NA	62 logging gaps	4 years	Brazil	Tropical moist forest	NA	2200	150
Liana cutting and tree elimination /harvesting as silvicultural treatments	2015	Venturoli et al.	Tree diameter growth following silvicultural treatments in a semi-deciduous secondary forest in central Brazil	Lianas and other woody vegetation reduce tree diameter increments by 20%	NA	4 30X25 m removal plots, four controls	4.5 years	Brazil	Tropical dry forest	NA	1800	770
Liana cutting as silvicultural treatments	1960	Dawkins, H.C.	New methods of improving stand composition in tropical forests.	Liana cutting can increase liana densities but lianas will not regain vigor once a canopy is formed above the liana sprouts	NA	NA	NA	Several	Tropical wet forest	NA	NA	NA

Liana cutting as silvicultural treatments	1968	Fox, J.E.D.	Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah	Liana removal decreased the number of trees that were knocked down and reduced total damage when logging. There was lower damage with increasing extracted basal area in removal plots, the opposite was found on controls	Cutting NA. Poisson lianas with sodium arsenite	1.62-ha per plot (10 plots, 5 treatment, 5 controls)	1 year	Indonesia	Tropical wet forest	NA	NA	NA
Liana cutting as silvicultural treatments	1984	Appanah, S. and Putz, F.E.	Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage	Liana removal helped to reduce the number and the size of damaged trees after logging. Poisoning after liana cutting is an appropriate method to reduce liana densities	Machete cutting, poisoning with 2 4 5-T butyl ester	13 plots, 1-ha each. 25 trees per logging treatment.	3 months for cut vs poison. 9 months for logging damage.	Malaysia	Tropical moist forest	Old growth	NA	85
Liana cutting as silvicultural treatments	1984	Neil, P.E.	Climber problems in Solomon Islands Forestry	Lianas can be controlled at a small scale by cutting, using herbicide and allowing cattle grazing.	Machete cutting, poisoning with 2,4,5-T, and use of cattle.	NA	NA	Solomon Island	Tropical wet forest	Row forest plantations	NA	NA
Liana cutting as silvicultural treatments	1995	D'Oliveira, M.V.N. and Braz, E.M.	Reduction of damage to tropical moist forest through planned harvesting	Although logging damage increased with the size of the felled tree, it is uncertain whether liana cutting reduced damage because there was no experimental control.	NA	20-ha	NA	Brazil	Tropical moist forest	NA	NA	NA
Liana cutting as silvicultural treatments	1995	Pinard, M.A. et al.	Creating timber harvest guidelines for a reduced-impact logging project in Malaysia	Liana removal under Reduced Impact Logging practices helps to reduce the number of trees killed when logging	NA	1400-ha	NA	Indonesia	Tropical moist forest	NA	2700	NA

Liana cutting as silvicultural treatments	1996	Mason, D.	Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting	Liana cutting had no effect on understory bird communities	Machete cutting near the ground	Cutting area 2 200x200 m plots. (3 control plots)	4 years	Venezuela	Tropical moist forest	Old growth	1631	140
Liana cutting as silvicultural treatments	1996	Pinard, M.A. and Putz F.E.	Retaining forest biomass by reducing logging damage	Liana removal under Reduced Impact Logging practices helps to keep more and larger trees, hence higher future biomass increments and yields of marketable timber	NA	Reduced-Impact Logging: 4 areas of 30-60-ha each, same number for conventional logging. 20-25 plots (1600 m <sup>2</sup> ) with nested subplots to measure trees.	8-12 months	Indonesia	Tropical moist forest	NA	2700	NA
Liana cutting as silvicultural treatments	1997	Vidal, E. et al.	Vine management for reduced-impact logging in eastern Amazonia	Liana cutting prior to logging reduces logging damage, but it is costly. Removing aggressive species can reduce operation costs.	NA	Cutting area: 2 plots (2X1400 m). Liana cutting cost estimation: 10 plots (50X50 m) X3 forest types.	18 months for type of sprouting	Brazil	Tropical dry forest	Early, mid and old succession	1700	NA
Liana cutting as silvicultural treatments	1998	Sist, P. et al.	Reduced-impact logging guidelines for lowland and hill dipterocarp forests in Indonesia	Liana removal under Reduce Impact Logging practices helps to reduce the number of trees killed when logging	NA	NA	NA	Indonesia	Tropical wet forest	NA	NA	NA
Liana cutting as silvicultural treatments	2000	Fredericksen, T.S.	Selective herbicide applications for control of lianas in tropical trees.	Liana mortality using herbicides is more effective than cutting with machete, however more expensive due to product and operation costs	Machete cutting, poisoning with three herbicides	Exp 1. 100 stems. 20 cut, 20 cut+10% 2,4-D. 20 cut+25% 2,4-D. 20 stems+25% 2,4-D in oil solution. 20 stems+50% 2,4-D in oil solution. Exp 2. 80 stems. 20 stems+Triclopyr 50% in oil. 20 stems+Imazapyr 50% in oil. 20	Exp 1. 2 months. Exp 2. 4 months and 7 months.	Bolivia	Tropical dry forest	NA	1200	NA

						cut +10% 2,4-D, 20 machete. Exp 3. 6 plots (50X50m)= 0.25 ha. 2 cut, 2 cut + water. 2 no cut + oil on base.						
Liana cutting as silvicultural treatments	2001	Gerwing, J.J.	Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon	Liana cutting increased tree diametric growth, basal area, and survival. Cutting also affected the species composition of tree saplings. Trees were quickly infested by after burning	Machete cutting near the ground and arm height	6 blocks total, (40X40 m) 3 controls, 3 removals and 3 burning (all treatments per block).	2 years	Brazil	Tropical dry forest	Late succession	1700	NA
Liana cutting as silvicultural treatments	2001	Parren, M and Bongers, F.	Does climber cutting reduce felling damage in southern Cameroon?	Pre-felling liana cutting had no significant effect on logging gap sizes, tree mortality and damage levels. Liana cutting should be applied on a tree-by-tree basis	NA	33 plots (1-ha each). 5 controls. 28 of them logged, 16 out of 26 with pre-logging liana cutting. 100 m buffer. 161 logged trees in total.	1 year and 10 months.	Cameroon	Tropical moist forest	Late succession	2000	NA
Liana cutting as silvicultural treatments	2004	Grauel, W.T. and Putz, F.E.	Effects of lianas on growth and regeneration of <i>Prioria copaifera</i> in Darien, Panama	Mean annual diameter growth doubled when lianas were cut relative to control. Heavy liana infestation reduces tree regeneration	Machete cutting near the ground	3 plots (25X25 m each). 3 controls. Lianas cut on a 10 m perimeter.	2 months for canopy openness. 2 years for other variables.	Panama	Tropical wet forest	NA	2864	NA
Liana cutting as silvicultural treatments	2004	Alvira, D. et al.	Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia	Pre-logging liana cutting reduces post-logging liana proliferation in logging gaps. Tree crown area, shape, and height help determine the likelihood of liana colonization of canopy trees	NA	22 trees of 6 species for removal. 22 controls. Then 44 trees logged. Liana cutting at 30m radius per tree. (2827 m <sup>2</sup> ).	1 year after liana cutting. 8 months after tree logging	Bolivia	Tropical dry forest	NA	1562	400-600

Liana cutting as silvicultural treatments	2005	Terceros-Gamarra, C.	Densidad, cobertura y altura de bejucos en claros formados por árboles con y sin corta antes del aprovechamiento	Cutting lianas in logging gaps did not affected liana density, cover, height, and percent of resprouting	NA	20 removal gaps, 20 control gaps. 200 subplots (2 m <sup>2</sup> )	3 years.	Bolivia	Tropical dry forest	NA	1580	400-600
Liana cutting as silvicultural treatments	2007	Campanello, P.I. et al.	Lianas in a subtropical Atlantic forest: host preference and tree growth	Tree stem diameter growth was more than 100% higher in two out of the four species studied in removal plots	NA	Cutting area: 3 plots, 1-ha each. 3 controls. Lianas cut on a 10 m perimeter. Both treatments were selectively harvested.	2 years	Argentina	Subtropical Moist forest	Late succession	2000	NA
Liana cutting as silvicultural treatments	2007	Campanello, P.I. et al.	Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest	Bamboo and liana cutting increased solar radiation and increased water availability, which promoted growth of tree saplings	NA	6 plots (1-ha each).	4 years	Argentina	Subtropical Moist forest	Mid succession	2000	250
Liana cutting as silvicultural treatments	2008	Garrido-Pérez et al.	Effects of lianas and Hurricane Wilma on tree damage in the Yucatan Peninsula, Mexico	Liana cutting in older successional forests reduces tree damage by hurricanes, but liana cutting increased tree damage in younger forests.	NA	Cutting area: 6 plots (20X20 m) 6 controls.	20 months	Mexico	Tropical dry forest	Early succession	1250	NA
Liana cutting as silvicultural treatments	2016	Lussetti, D. Et al.	Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo	Supervised logging in combination with liana cutting improved growth of dipterocarp trees, improved stand volume recovery, and reduced overall tree mortality	Machete cutting near the ground	16 plots (1-ha each). plus 4 controls.	18 years	Malaysia	Tropical wet forest	Old growth	3050	300-600

