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# Contribution of Lianas to Plant Area Index and Canopy Structure in a Panamanian Forest

Maria Elizabeth Rodriguez-Ronderos  
*University of Wisconsin-Milwaukee*

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CONTRIBUTION OF LIANAS TO PLANT AREA INDEX AND CANOPY  
STRUCTURE IN A PANAMANIAN FOREST

by

María Elizabeth Rodríguez-Ronderos

A Thesis Submitted in  
Partial Fulfillment of the  
Requirements for the Degree of

Masters of Science  
in Biological Sciences

at

The University of Wisconsin-Milwaukee

December 2015

## ABSTRACT

### CONTRIBUTION OF LIANAS TO PLANT AREA INDEX AND CANOPY STRUCTURE IN A PANAMANIAN FOREST

by

María Elizabeth Rodríguez-Ronderos

The University of Wisconsin-Milwaukee, 2015

Under the Supervision of Professors Stefan A. Schnitzer and Filipe Alberto

Lianas are an important component of tropical forests, where they reduce tree growth, fecundity and survival. Competition for light among plants may be intense; however the amount of light that lianas intercept is poorly understood. We used a large-scale experiment to quantify light interception by lianas in a 60 year-old Panamanian tropical forest. We measured the change in plant area index (PAI) and forest structure six weeks after cutting lianas in eight 80 x 80 m plots and in eight control plots, and then annually for four years. We used ground-based LiDAR to measure the 3-dimensional canopy structure before liana cutting and annually for two years afterwards. Six weeks after liana cutting, mean plot PAI was 20% higher in control versus liana removal plots. One year after liana cutting, mean plot PAI was ~17% higher in control plots. The differences among treatments diminished two years after liana cutting and, after four years, trees had fully compensated for PAI proportion of lianas. Ground-based LiDAR revealed that lianas were distributed in the upper and middle parts of the canopy, and not just the upper canopy as previously suspected. Therefore, lianas attenuated ~20% of the light in the upper- and mid-canopy of the forest.

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Para  
Mamá, Papá  
y toda mi familia.

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## **CHAPTER 1.**

# **CONTRIBUTION OF LIANAS TO PLANT AREA INDEX AND CANOPY STRUCTURE IN A PANAMANIAN FOREST**

To be submitted with co-authors: Gil Bohrer, Arturo Sanchez-Azofeifa, Jennifer S. Powers  
and Stefan A. Schnitzer

### **Introduction**

Light is often a limiting resource in lowland tropical forests. The amount of photosynthetic active radiation that reaches the top of a mature tropical forest canopy can be high ( $>1000 \text{ mol m}^{-2} \text{ s}^{-1}$ ); however, light is extinguished rapidly as it is transmitted from the canopy to the understory, where only 1% of the incident light reaches this lower portion of the forest (Chazdon and Fetcher 1984, Leigh 1999). To maximize light interception, plants deploy leaves at the top of the forest canopy and stratify additional layers of leaves below them (Kitajima et al. 2005). Plant stems and branches may also decrease light availability, but they are often overlooked in studies of light interception (Kalacska et al. 2005, Sánchez-Azofeifa et al. 2009). As the contribution of woody material from stems (wood area index, WAI) increases, light availability and canopy openness decreases. The attenuation of light by both leaves and stems is plant area index (PAI), which is a measure of total light interception by plants.

Most of the light in tropical forests is intercepted by trees, which constitute the majority of the biomass, leaf area, and basal area in tropical forests (Clark et al. 2008). Researchers have estimated tree leaf contribution to the forest canopy from optical measurements of leaf area index (LAI; total amount of leaf area per unit ground area  $\text{m}^2$ ), canopy cover, leaf litter production, and



manually harvesting leaves (Asner et al. 2003, Kalacska et al. 2005, Clark et al. 2008). For example, in a tropical wet forest in Costa Rica, Clark *et al.* (2008) directly quantified leaf area by harvesting leaves from the forest floor to the top of the canopy in 54 vertical transects and found that trees contributed more than 50% to forest leaf area. In a seasonal tropical forest in Panama, (Avalos and Mulkey 1999) used a canopy crane to access to the top portion of the canopy and reported that tree leaf canopy cover was as high as 78.4% during the dry season. In a moist seasonal tropical forest in Panama, Wright et al. (2004) estimated that trees contributed 83% to 89% to the leaf litter productivity.

Lianas (woody vines) may also contribute substantially to light attenuation in lowland tropical forests, despite their relatively small fraction of forest biomass and basal area (Schnitzer et al. 2012, 2014, van der Heijden et al. 2015). Lianas commonly comprise 25% of the woody stems and can contribute significantly to forest productivity (Schnitzer and Bongers 2002, Wright et al. 2004, van der Heijden et al. 2013). For example, in a tropical wet forest in Costa Rica, lianas contributed 12.1% to the forest leaf area (Clark et al. 2008), even though liana density was relatively low in this forest (Mascaro et al. 2004, Yorke et al. 2013). Lianas may be particularly important to forest productivity in seasonal forests, where lianas are most abundant (Schnitzer 2005, DeWalt et al. 2010, 2015). In a seasonally dry tropical forest in Panama, where lianas are relatively abundant, Avalos and Mulkey (1999) reported that lianas contributed more than 40% of the leaf canopy cover during the wet season and more than 20% of the leaf canopy cover during the dry season. On Barro Colorado Island, Panama, lianas contributed 11% to 17% to the forest-level leaf productivity (Wright et al. 2004), and 25% to the woody stem density (stems  $\geq 1$  cm diameter; Schnitzer et al. 2012, 2015). Lianas also contribute to forest wood area index (WAI); Sánchez-Azofeifa et al. (2009) reported that lianas contributed 37% to the forest

wood area index in successional tropical dry forests in Mexico, Costa Rica and Brazil.

The contribution of lianas to tropical forest plant area index may be an indication of their competitive effects on trees. Lianas compete intensely with trees, reducing tree regeneration, growth, fecundity, survival, and, at the ecosystem level, carbon storage (Schnitzer and Bongers 2002, Wright 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Schnitzer et al. 2014, van der Heijden et al. 2015). Furthermore, lianas may be increasing in density and biomass in neotropical forests (Schnitzer and Bongers 2011, Schnitzer et al. 2015), and thus their contribution to forest dynamics and forest-level light interception is likely to increase. However, the contribution of lianas to forest-level PAI and light interception, perhaps the most limiting resource in tropical forests (Graham et al. 2003), remains poorly understood.

We quantified the relative contribution of lianas and trees to forest PAI using a large-scale experimental manipulation in a 60 year-old secondary seasonal tropical forest in the Republic of Panama. We established 16 80 x 80 m plots and cut all of the lianas from eight of them. We measured PAI before liana cutting, six weeks after liana cutting, and then annually for four years. We quantified the speed at which trees recovered from liana removal in terms of increased PAI. We also measured the 3-dimensional structure of the forest using ground-based LiDAR before and annually for 2 years after liana cutting to determine where along the vertical gradient of the forest lianas were intercepting light.

## **Materials and Methods**

### *Study site*

We conducted this experiment on Gigante Península, a protected mainland forest that is part of the Barro Colorado Nature Monument (BCNM) in the Republic of Panamá (9°9' N, 79°

51' W, Figure 1.1). The forest at this site is a mix of early and late secondary seasonal tropical forest (Schnitzer and Carson 2010). Rainfall averages 2616 mm per year, with 90% of the rain falling from May until December (Leigh, 1999). Further information about this forest, climate and geology can be found in (Leigh 1999, Schnitzer and Carson 2010, Álvarez-Cansino et al. 2015).

*Plot selection, liana removal, plant area index (PAI) and forest structural complexity*

In 2008, we established sixteen 80 x 80 m plots and we measured the diameter of all trees and lianas  $\geq 1$ cm diameter in the central 60 x 60 m area of each plot (Martínez-Izquierdo et al. *in press*, Álvarez-Cansino et al. 2015, van der Heijden et al. 2015, Reid et al. 2015). In April 2011, we cut all lianas in eight randomly selected plots, with the remaining eight plots serving as non-manipulated controls. We cut lianas near the forest floor using machetes without removing lianas from the canopy to avoid tree damage (follows Schnitzer and Carson 2010, Schnitzer et al. 2014). Because many lianas resprout copiously after being cut (Schnitzer et al. 2004), we recut liana stems every 3 to 4 months in the liana removal plots. We also visited the control plots with the same frequency as the liana removal plots to avoid a visitation effect (Cahill et al. 2001, Schnitzer et al. 2002).

We measured mean per-plot plant area index (PAI) in all sixteen plots 15 days before cutting lianas, six weeks afterwards, and then annually for four years (March 2011 - March 2015). In 2014 we measured PAI during the wet season (June). In each plot, we used a LI-COR LAI-2000 plant canopy analyzer (LI-COR Biosciences, Lincoln, NE, USA; Welles and Norman 1991, Kalacska et al. 2005) to measure PAI along a uniform grid of 7 rows and 7 columns (49 points) total, within the center 60 x 60m area of the plot. The point measurements were at 50 cm and 1m above the soil surface (98 total measurements per plot). Simultaneously, we collected

full-sun light measurements with a second LAI-2000 outside of the forest on the edge of Lake Gatun as a comparison for our within-forest measurements (follows Schnitzer & Carson 2010). To ensure that the open-sky measurements did not intercept forest leaf area and that the within-forest measurements did not include the shadow of the operator, we restricted light measurements to the northern half of the sensor and we positioned the sensors towards the north for each measurement. At every sampling period, we measured the plots in the same order to ensure consistent and comparable measurements.

We characterized the canopy structural complexity in each plot using a ground-based portable canopy light detection and ranging (LiDAR) system (Parker et al. 2004). The LiDAR system consisted of a near-infrared pulsed-laser ( $> 3000$  pulses per second) that recorded the vegetative surfaces distributed at different heights of the forest canopy (Parker et al. 2004, Hardiman et al. 2011). We collected LiDAR measurements one week before liana cutting and one and two years afterwards (March 2011, March 2012, March 2013) along thirteen equally spaced 60m transects that spanned the plot for each of the 16 plots. We measured LiDAR in the same order and directionality in each sampling period.

### *Data analysis*

We used LI-COR FV2000 Analysis Software to pair the full-sun and within-forest measurements and to convert the differences between the measurements into PAI (2005, LI-COR, Biosciences, Lincoln, NE, USA). To calculate the PAI values, we used the horizontal uniform canopy model and the first 4 zenith angles ( $0^\circ$  to  $60^\circ$ ). The results were consistent between the two measurement heights; thus, we used the mean PAI of the two different heights for analysis.

To assess whether removal and control plots were statistically similar in PAI before the liana manipulation, we used a Mann Whitney-U test (R: stats package, (R Core Team 2015)). We analyzed PAI data using a linear mixed effects (LME) model with repeated measures of the same plots over time (Zuur et al. 2009), R: nlme package, (Pinheiro et al. 2015). The linear mixed effect model included treatment (removal or control) and time as fixed effects, and plot as the random effects.

We binned every horizontal meter of the LiDAR data into vertical columns for each of the transects (780 vertical columns per plot). We divided the vertical columns into non-saturated (more than 1% of the laser pulses did not encounter vegetation) and saturated (less than 1% of the laser pulses did not encounter vegetation), based on the first year of data collection (2011). We subdivided saturated columns of each removal and control plot into 6 different categories based on their saturation height: 0 - 5m, 5 - 10m, 10 -15m, 15 - 20m, 0 - 25m, and 25 - 41m. Less than 2% of the vertical columns were not saturated prior to the manipulation, and thus we analyzed only the saturated columns.

We constructed plant surface density profiles from saturated columns to visualize the distribution of plant biomass and their contribution to the forest structure throughout the vertical gradient of the forest in MATLAB (2012). We constructed one surface density profile per year and per category height for each removal and control plot, and compared each profile to 2011-year profiles. We analyzed the fraction of the plant biomass change since 2011 at each category height using a linear mixed effect model (LME; Zuur *et. al* 2009, R: nlme package, Pinheiro *et al.* 2015). The linear mixed effect model included treatment (removal or control) and time as fixed effects, and individual plots were included as a grouping variable in the random effects component, since columns within plots were repeatedly measured over time. The contribution of

each random and fixed effect was assessed by a manual stepwise AIC of the models. We used restricted maximum likelihood (REML) to compare nested models for which random variables differed, and maximum likelihood (ML) to compare nested models for which fix effects differed. Models were considered competitive when  $\Delta AIC \leq 2$  and, if ties were present, a correction for AIC was performed where the number of parameters and log-likelihood were taken in account (Arnold 2010). We used normalized residuals based on the REML fit to validate the final model (Zuur *et. al* 2009, Schnitzer *et al.* 2014).

## Results

### *Plant area index*

Six weeks after cutting lianas, mean PAI was  $\sim 20\% \pm 3.4\%$  (Mean  $\pm$  95% CI) higher in the control plots than in the liana-removal plots relative to the pre-treatment measurements. PAI decreased 16.6% in the liana-removal plots and increased 3.2% in control plots ( $Z_{(18)} = -4.20$ ,  $P < 0.01$ ; Figure 1.2a). One year after liana cutting, PAI was  $\sim 17\%$  higher in the control plots; PAI decreased 21.3% in the liana-removal plots and 4.5% in control plots relative to the pre-treatment measurements ( $Z_{(18)} = -5.44$ ,  $P < 0.01$ ; Figure 1.2a). Two years after liana cutting (2013), the differences among treatments were no longer significant and, by the fourth year (2015), PAI was nearly identical among the treatments (Figure 1.2a). The higher PAI for all plots in 2014 was apparently because we took the measurements during the wet season of that year (Figure 1.2b).

### *Forest Structural Complexity*

Prior to the manipulation, more than 95% of the columns were saturated and we used these columns to determine the change in forest structure following the liana removal manipulation. There was no difference between treatments in forest structure for the lowest

portion of the forest (0-5m) after liana removal, indicating that there were few liana stems and leaves attenuating light near the forest floor (Figure 1.3a). However, in each of the higher forest strata (above 5 m), the liana removal plots had significantly reduced plant structure compared to the pre-manipulation measurements, indicating that lianas had occupied the middle and upper portions of the forest (Figure 1.3b– e). Differences in plant structure were still significant two years after liana removal for most of the middle and upper portions of the forest (Figure 1.3b-e), except for the highest portion of the upper canopy (25 to 41m; Figure 1.3f). Profiles for all of the saturation height categories and plots are listed in Appendices A and B.

## **Discussion**

Lianas contributed approximately 20% to the plant area index (PAI) in the Gigante Peninsula forest. The contribution of lianas to light interception in the Gigante Peninsula forest was greater than what was reported in dry forest stands of Mexico, Costa Rica and Brazil, where lianas attenuated ~11% of the light interception (Sánchez-Azofeifa et al. 2009). In the old-growth tropical wet forests at La Selva Biological Station, Costa Rica, lianas contributed up to 12% to the forest leaf area (Clark et al. 2008). Our findings were more similar to data from the nearby old-growth forest of BCI, where the proportional contribution of lianas to total leaf litter was 17% (Wright et al. 2004). Neither Clark et al. (2008) nor Wright et al. (2005) included wood area index, which may explain their lower estimates of light interception by lianas compared to our findings. Wood area index can be an important component of light interception. For example, 15% of the light interception in tropical dry forests was attributed to liana stems WAI; (Sánchez-Azofeifa et al. 2009). Furthermore, lianas are more abundant in highly seasonal tropical forests than in wet forests such as La Selva (Mascaro et al. 2004, Schnitzer 2005, Schnitzer et al. 2012,

Yorke et al. 2013, DeWalt et al. 2015), which may also account for the rather large discrepancy among our finding and that of Clark et al. (2008).

The amount of PAI and thus light interception was variable among years. During the dry season, PAI ranged from less than 6 in 2015 to more than 7.5 in 2014, indicating that resource availability strongly influence PAI. Predictably, higher amounts of precipitation and the absence of deciduousness during our wet-season measurement in 2014 likely explained the relatively high PAI in both the liana-removal and control plots for that year. By contrast, PAI was relative uniform in the control plots during the dry season (in 2012, 2013, and 2015), ranging from slightly less than 6 to 6.5.

Lianas and trees appear to compete intensely for light, and trees responded rapidly to the decrease in PAI following liana cutting. Four years after cutting lianas, trees had completely compensated for the fraction of PAI that lianas had previously contributed. Initially, we had hypothesized that PAI of the liana-removal plots would approach to that of the control plots after liana cutting, but never return to pre-cutting conditions. Our hypothesis was predicated on the idea that crown shyness (e.g., Putz et al. 1984) maintains spaces among tree crowns, but that lianas can fill these inter-crown spaces. Contrary to our hypothesis, however, trees compensated 100% for the loss in liana PAI within 4 years, which may have been the result of both trees in the canopy expanding to take the space vacated by lianas, as well as trees in the upper understory expanding their crowns. We were surprised at the rapid speed at which trees compensated for liana removal in terms of light interception, which suggests that competition for light is a powerful interaction between lianas and trees in tropical forests (Schnitzer and Carson 2010, Toledo-Aceves 2015).

Lianas were once thought to deploy the majority of their leaves over those of their host



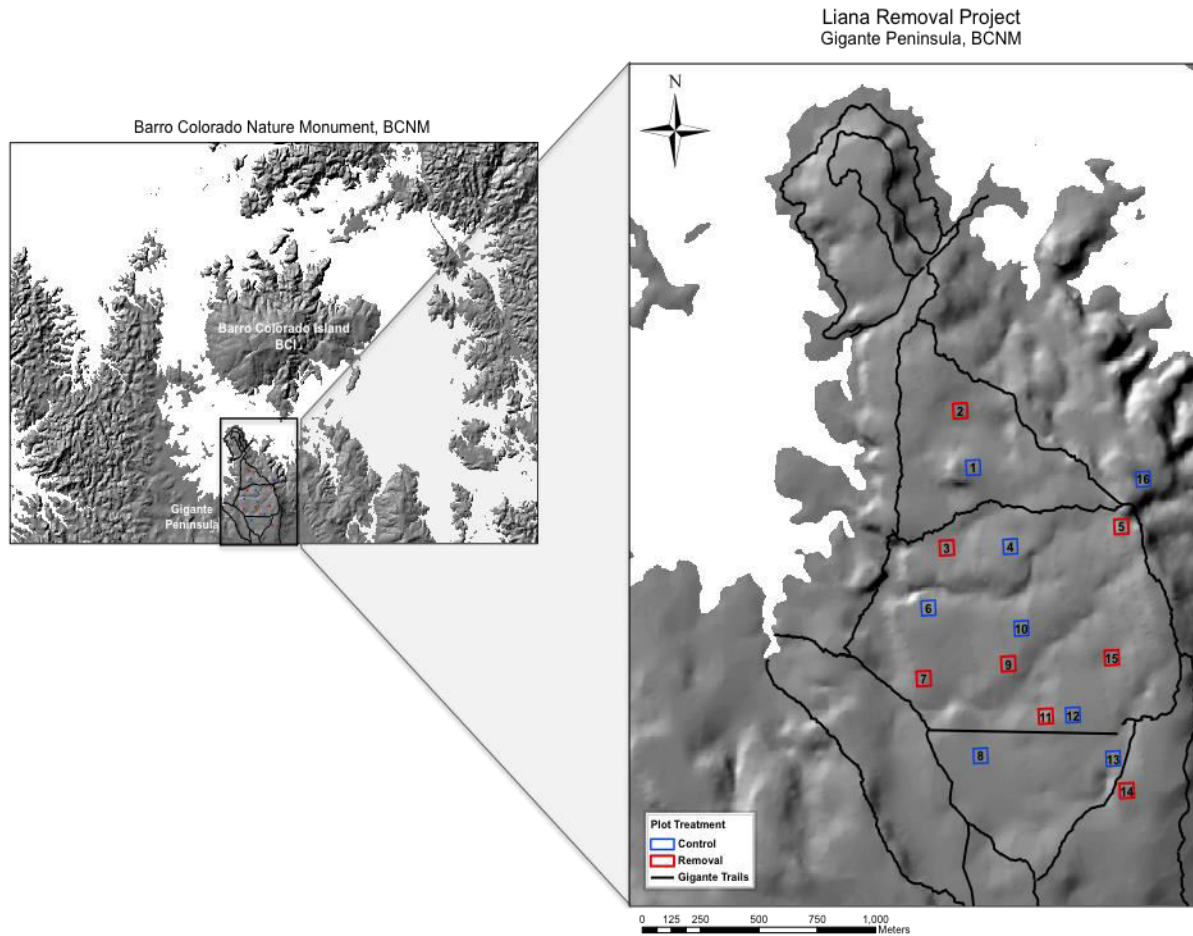
trees (Ogawa et al. 1965, Ingwell et al. 2010). However, our data indicate that lianas contribute strongly to forest structure in both the upper and middle fraction of the forest, where lianas attenuated light as it filtered through the canopy. Liana stems may have accounted for a large degree of light attenuation in the lower- and mid-canopy strata. Indeed, two years after the liana removal, there were no significant differences between removal and control plots in the top stratum of the forest (25 - 41m), possibly because trees responded most rapidly to the loss of liana leaves in the upper canopy, where light is most abundant. By contrast, trees would have to allocate more resources for a lower return on investment to replace the loss of liana stems in the mid-canopy strata of the forest.

Taken together, our findings indicate that lianas attenuate approximately 20% of the light in this tropical forest. Lianas intercept light throughout most of the forest vertical strata, and the effects of lianas are not concentrated only above the crown of their host trees as was previously suspected. Furthermore, competition for light between lianas and trees appears to be intense as trees were able to fully compensate the loss of liana structure within four years. If lianas continue to increase in neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015) then we would expect a reduction in tree leaf area and structure throughout the mid- and upper strata of these forests.

## **ACKNOWLEDGEMENTS**

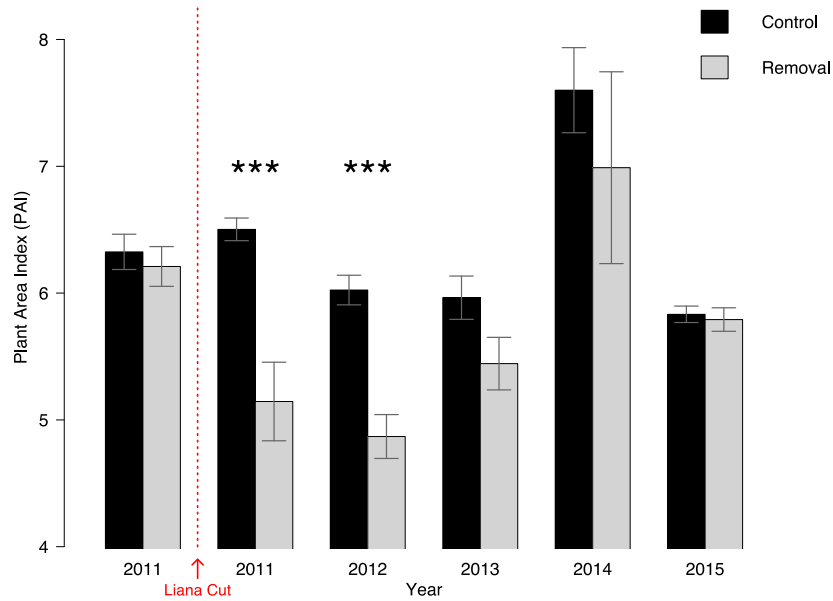
We thank Salomé Pérez, Oldemar Valdés, Abelino Valdés, Severino Valdés, Boris Bernal, Laura Martínez-Izquierdo, Jeremy La-Che, Kyle Maurer, Timothy Morin, Alexander Fotis, William Kenny and Ashley Matheny for valuable assistance in the field. We are grateful to Kathryn

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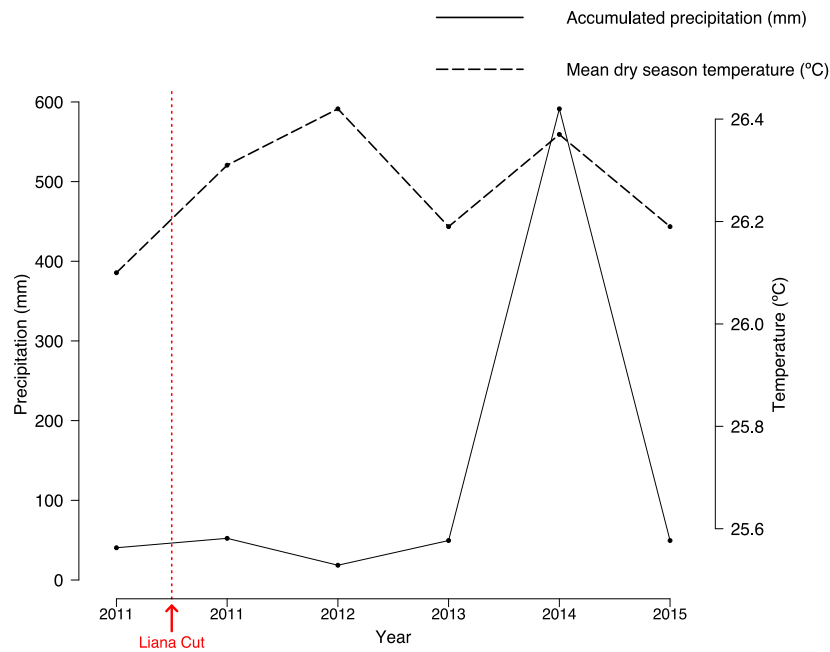


**Figure 1.1.** Map of the Gigante Peninsula where the liana removal project took place. The Gigante Peninsula is part of the Barro Colorado Nature Monument (BCNM, República of Panama, 9°9' N, 79° 51' W).

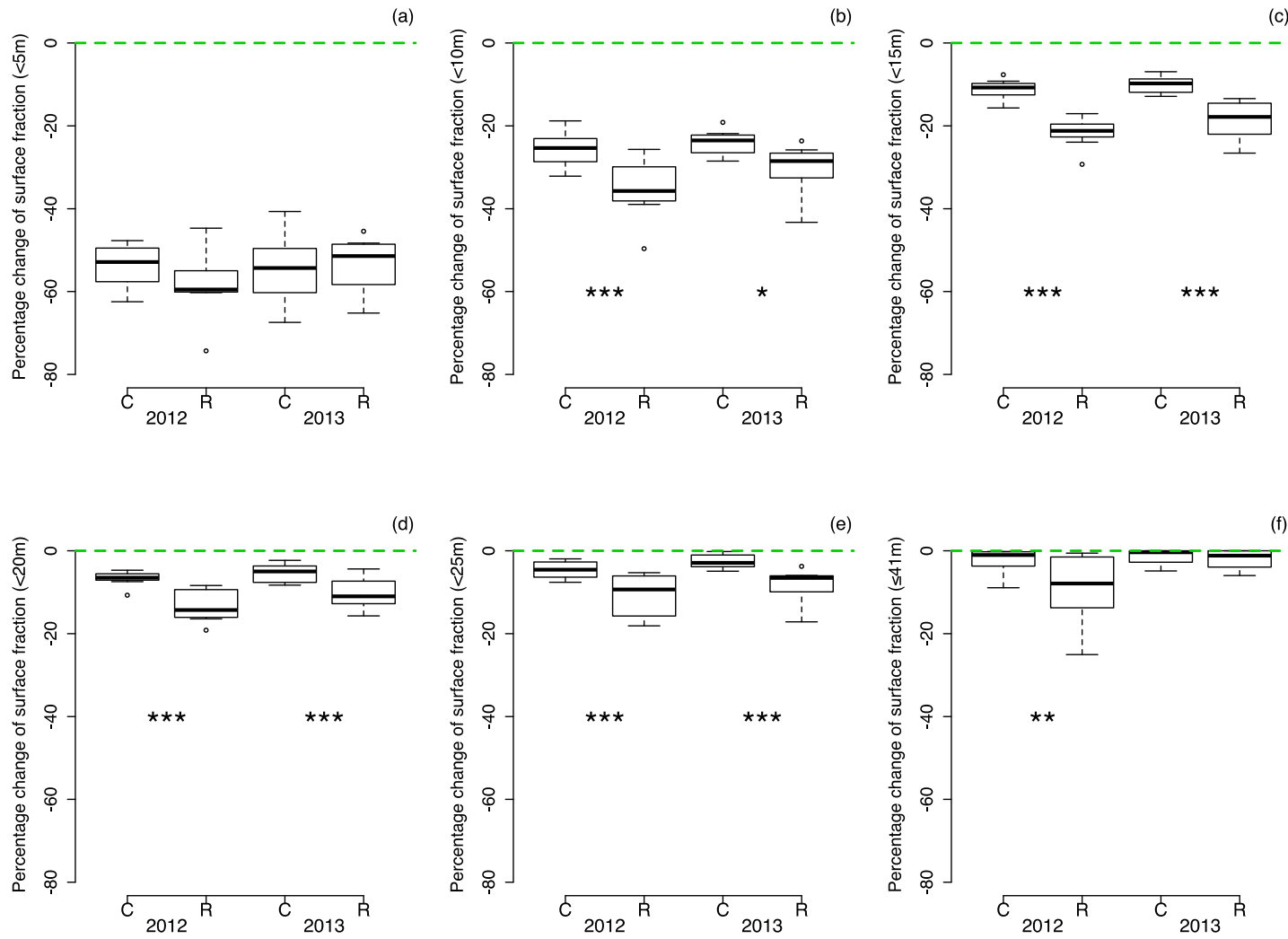
(a)



(b)



**Figure 1.2 (a).** Mean plant area index (PAI) for 8 control plots (black bars) and 8 removal plots (light bars) on Gigante Peninsula, Panama. Error bars represent one standard error. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ . **(b)** Mean dry seasonal temperature ( $^{\circ}\text{C}$ ) and accumulated precipitation (mm) before and after liana removal. An increase in dry-season precipitation appeared to increase PAI in 2014 (LME,  $p < 0.05$ ).



**Figure 1.3.** The percent change in surface fraction over two years in control and removal plots after liana removal in 16 80 x 80 m plots on Gigante Peninsula, Panama. The forest strata are binned in six different height above the ground categories: **(a)** <5m, **(b)** <10m, **(c)** <15m, **(d)** <20m, **(e)** <25m and **(f)** ≤41m of vertical height. \* p<0.05; \*\* p<0.01; \*\*\* p<0.001.

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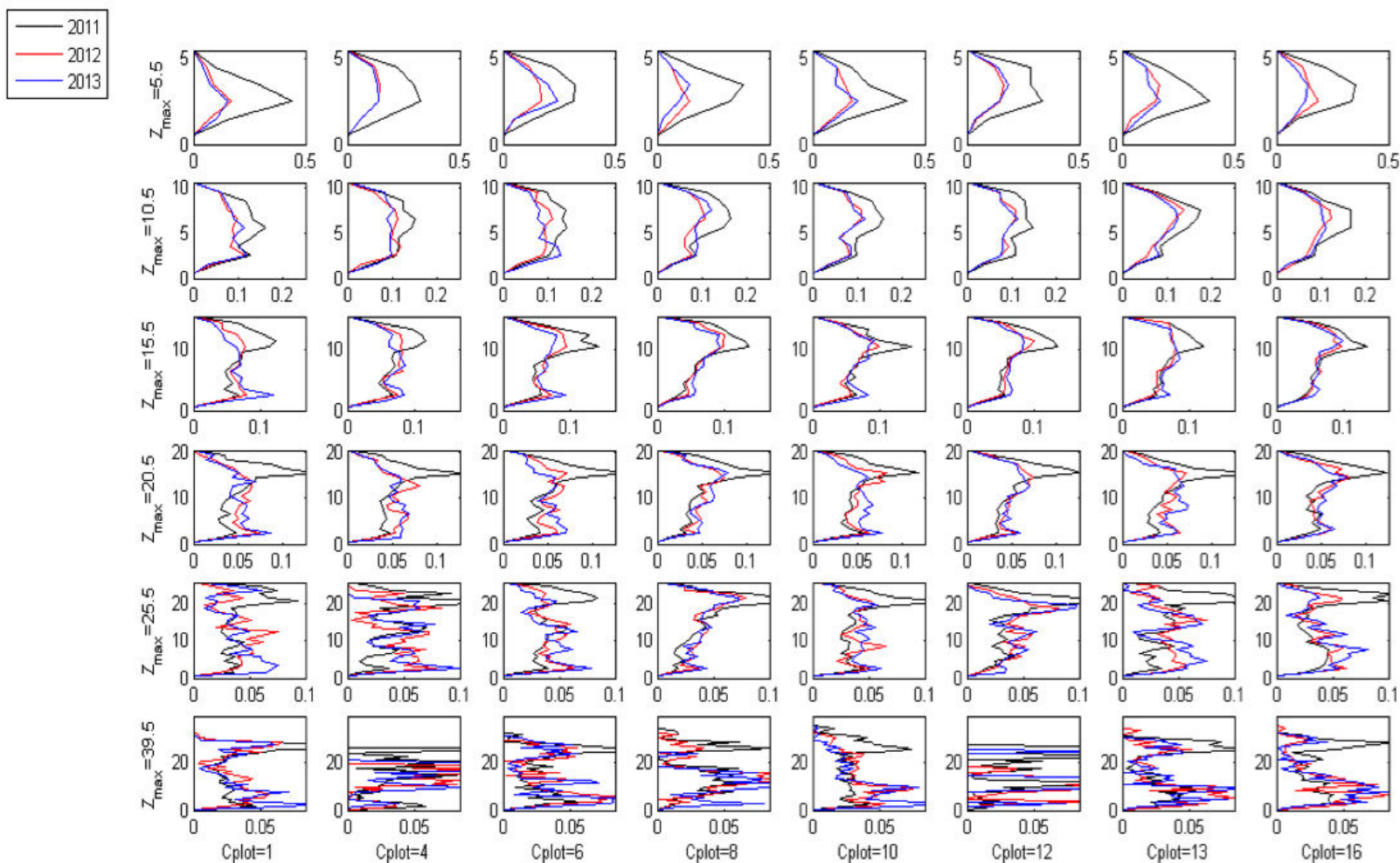
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**APPENDIX A: Profiles for the average saturated columns at different heights for control plots.** Saturated columns at different heights in 2011 were always maintained in the same stratum and compared throughout the experiment: before liana removal (2011) and, one and two years after the removal (2012 and 2013).



**APPENDIX B: Profiles for the average saturated columns at different heights for liana-removal plots.** Saturated columns at different heights in 2011 were always maintained in the same stratum and compared throughout the experiment: before liana removal (2011) and, one and two years after the removal (2012 and 2013).

