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Lianas in Gaps Reduce Carbon Accumulation in a Tropical Forest

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Abstract: Treefall gaps are the "engines of regeneration" in tropical forests and are loci of high tree recruitment, growth, and carbon accumulation. Gaps, however, are also sites of intense competition between lianas and trees, whereby lianas can dramatically reduce tree carbon uptake and accumulation. Because lianas have relatively low biomass, they may displace far more biomass than they contribute, a hypothesis that has never been tested with the appropriate experiments. We tested this hypothesis with an 8-year liana removal experiment in central Panama. After eight years, mean tree biomass accumulation was 280% greater in liana-free treefall gaps compared to control gaps. Lianas themselves contributed only 24% of the tree biomass accumulation they displaced. Scaling to the forest level revealed that lianas in gaps reduced net forest woody biomass accumulation by 8.9% to nearly 18%. Consequently, lianas reduce whole-forest carbon uptake despite their relatively low biomass. This is the first study to experimentally demonstrate that plant-plant competition can result in ecosystem-wide losses in forest carbon, and it has critical implications for recently observed increases in liana density and biomass on tropical forest carbon dynamics.

Keywords: Annual increment, Barro Colorado Nature Monument, biomass, carbon storage, lianas, gap-phase regeneration, Panama, treefall gaps, tropical forests

Introduction

Tropical forests store more than one third of all terrestrial carbon and nearly one third of terrestrial net primary productivity on the planet, and thus they are a critical component of the global carbon cycle (Beer et al. 2008, Pan et al. 2011). Nearly all of the aboveground carbon in tropical forests is held in tree biomass, and long-term carbon fluxes are balanced largely by tree growth, which removes carbon from the atmosphere, and tree death, which releases carbon into the atmosphere (Clark et al. 2001). Therefore, the vast majority of research on tropical forest carbon dynamics has focused on the growth and mortality of canopy trees (e.g., Clark et al. 2001, Chave et al. 2008, Asner et al. 2010).

Canopy tree mortality results in the creation of treefall gaps, which is a common form of natural disturbance in tropical forests (e.g., Brokaw 1985, Denslow 1987, Hubbell et al. 1999), and gaps have important consequences for tree regeneration and forest carbon accumulation. In many forests, one to two percent of canopy trees fall each year (e.g., Swaine et al. 1987), and the length of time for a tall canopy to regenerate within a gap typically ranges from eight to ten years or longer (Brokaw 1985). Therefore, at any given time, eight to more than twenty percent of total forest area can be in a state of gap-phase regeneration. The rate of carbon accumulation in gaps is likely to be important because of the rapid woody plant recruitment and growth in these resource rich habitats (e.g., Denslow 1987, Brokaw and Busing 2000). Furthermore, the speed of gap-phase regeneration will determine the amount of carbon accumulation in gaps, which affects the capacity of tropical forests to store carbon and, ultimately, influences the global carbon balance. Nonetheless it remains unknown how the intense competitive sorting of woody species that occurs in gaps contributes to forest-wide carbon dynamics.

Gap-phase regeneration in tropical forests can follow two primary trajectories. In the first, rapid tree recruitment and growth reforms a high-canopy forest within the first ten years, concomitant with the rapid accumulation of forest biomass and thus carbon (e.g., Brokaw 1985). Alternatively, lianas can proliferate rapidly in gaps soon after gap formation, where they compete intensely with trees, reducing tree recruitment, growth, diversity and abundance (Putz 1984, Schnitzer et al. 2000, 2012, Schnitzer and Carson 2001, Dalling et al. 2012). Lianas can thus redirect gap-phase regeneration away from a tree-dominated state to one where lianas are far more prevalent (Schnitzer et al. 2000, Foster et al. 2008). Because lianas allocate little to structural support relative to trees, it is likely that the biomass that would have been stored in trees is not fully compensated by the lianas that supplanted them (van der Heijden and Phillips 2009, Schnitzer and Bongers 2011, van der Heijden et al. 2013).

For example, on and in the vicinity of Barro Colorado Island, Panama (BCI), lianas have been shown to have a strong competitive effect on trees (Putz 1984, Schnitzer et al. 2000, Schnitzer and Carson 2001, 2010, Ingwell et al. 2010). Yet, in the BCI 50 ha forest dynamics plot lianas constituted 25% of the rooted woody stem density (trees plus lianas) and 35% of the woody species diversity, but only 3% of the woody plant basal area (Schnitzer et al. 2012). Indeed, lianas commonly constitute less than 5% of the woody plant biomass in tropical forests (DeWalt and Chave 2004). In an Amazonian forest in Peru, the correlation between tree growth and liana infestation revealed that liana biomass increment (based on diameter growth) compensated only one-third of the biomass increment that they displaced in trees (van der Heijden and Phillips 2009). Thus, competition from lianas on trees may reduce net forest biomass accumulation because lianas uptake far less biomass than they displace in trees. Furthermore, lianas are increasing in abundance, productivity, and biomass in neotropical forests (reviewed by Schnitzer and Bongers 2011, Schnitzer in press) and are particularly abundant in treefall gaps (Schnitzer et al. 2000, 2012, Dalling et al. 2012). Thus, the detrimental effect of lianas on gap-phase regeneration and biomass accumulation and storage is also likely to increase (Schnitzer et al. 2011).

To date, however, there have been no experimental tests of the reduction of tree biomass accumulation due to lianas and the contribution of liana stem growth and mortality to forest level biomass. We used an eight-year liana removal experiment to test three main hypotheses. 1) Lianas reduce tree biomass accumulation in treefall gaps by reducing tree recruitment and growth rate (and thus biomass increment) and increasing tree mortality. 2) Liana biomass accumulation does not compensate for the liana-induced loss of tree biomass accumulation (recruitment, growth, and mortality) during gap-phase regeneration. If hypothesis 2 is correct, then the displacement of trees by lianas will reduce carbon sequestration in treefall gaps. We then used our empirical data to parameterize a statistical model to test and quantify our third hypothesis, that: 3) lianas reduce forest-level carbon accumulation through their effect on tree regeneration in treefall gaps. If lianas reduce tree growth and survival rates in gaps, then more gaps will remain in a low biomass state, which will lower the capacity of tropical forests to sequester carbon.

Materials and methods

Study site and experimental design

We conducted the study from 1997 until 2006 in a secondary, seasonally moist lowland tropical forest on Gigante Peninsula, a protected mainland forest that is part of the Barro Colorado Nature Monument, Republic of Panama. Mean annual rainfall of this forest is 2600 mm, with a dry season from December until April. The study site is described in more detail in Schnitzer and Carson (2010).

In 1997, we located all (17) recent (< 1 year old) natural treefall gaps on the relatively flat, upland central plateau of Gigante peninsula. We selected the gaps that were present and did not exclude any gaps because of liana density (high or low). We determined gap age by the presence and condition of the fallen tree, and each gap was defined as the area where a vertical line from the edge of the canopy intersected the ground (Brokaw 1982, van der Meer and Bongers 2001). The gaps varied in size from 145 m^2 to 499 m^2, which is a common gap size range in tropical forests (Brokaw 1985, van der Meer and Bongers 2001, Sanford et al. 1986). Gaps were paired by size for the purpose of randomly assigning treatments, either liana-removal or control. The liana-removal and control gaps were statistically indistinguishable in total gap area (ANOVA: $F_{1,15} = 0.26$, $P = 0.62$; Schnitzer and Carson 2010).

In 1997, we tagged, mapped, measured the diameter, and identified to species all lianas and trees > 1.3 m tall in all 17 gaps. We censused all gaps again in 1998 using identical methods to the 1997 census and then we cut all of the lianas in 8 of the gaps – leaving 9 non-manipulated gaps as controls. The mean number of lianas that we cut in each gap was 109 (± 17 se) comprising 20 (± 2 se) species. We cut lianas near the forest floor using machetes, but we did not attempt to remove the lianas from the trees because of the risk of damaging the tree crowns (Schnitzer and Carson 2010, Tobin et al. 2012). Prior to liana cutting, liana abundance, diversity, basal area, and biomass, as well as tree biomass, recruitment, growth (RGR), and mortality (from 1997-1998) did not differ between the controls and the gaps where lianas were eventually removed (Schnitzer and Carson 2010; see also Appendix A).

We visited all gaps monthly for the first two months after liana cutting and then bi-monthly for the next six months to monitor the gaps and to cut resprouting liana shoots in the removal gaps. After eight months, the cut lianas were no longer resprouting vigorously, and thus we visited the gaps to monitor them and to cut resprouting liana shoots every 3-4 months between censuses. We monitored liana removal and control gaps with the same approximate frequency and intensity so that we did not introduce a researcher visitation bias among the treatments (Cahill et al. 2001, Schnitzer et al. 2002). We recensused the gaps in years 1999, 2000, 2001, 2003, and 2006 to quantify tree and liana growth, recruitment, and mortality. We omitted the 2006 measurement for two gaps because they were completely covered by the crowns of newly fallen trees in that year (see Schnitzer and Carson 2010). We calculated biomass for lianas and trees using allometric equations from Schnitzer et al. (2006) and Chave et al. (2005), respectively. We calculated biomass accumulation per gap as the sum of stem growth plus recruitment minus mortality for both trees and lianas.

Data analysis and modeling

We analyzed our data using a linear mixed effects (LME) model, which can handle repeated measurements of the same gaps over time, as well as missing data and unbalanced designs without compromising the results (Zuur et al. 2010). Linear mixed effects models include fixed effects, which are explanatory variables associated with an entire population or with repeatable experimental treatments, and random effects, which are associated with individual experimental units, in this case, the individual gaps, drawn at random from a population (Pinheiro and Bates 2000). We constructed a LME model to test whether cumulative tree biomass accumulation (stem growth plus recruitment minus mortality), biomass increment due to growth, and biomass loss due to mortality over time differed between the treatments. Recruitment represented less than 1% of tree biomass accumulation, so we did not model it separately. We included initial tree biomass in the model because gaps with higher initial biomass may have stronger responses in their cumulative rate of biomass increment (growth and recruitment) and loss (mortality) compared to gaps with lower initial biomass. The response variables were cumulative and all started at zero at the time of liana cutting, so we excluded the intercept from the model. The initial fixed effects component of the model was: $y = \beta_1\ \mathrm{treat}_i + \beta_2\ \mathrm{time}_i + \beta_3\ \mathrm{AGBin}_i + \beta_4\ \mathrm{treat}_i{*}\mathrm{time}_i + \beta_5\ \mathrm{time}_i{*}\mathrm{AGBin}_i + \beta_6\ \mathrm{treat}_i{*}\mathrm{time}_i{*}\mathrm{AGBin}_i$

(1)

where y is the response variable, i.e. biomass increment due to growth or biomass loss due to mortality, the cumulative increase in biomass increment (sum of biomass increment, recruitment, and loss), treat is treatment (i.e. control or removal), AGBin is initial tree biomass and β's are the fixed effects parameters. Polynomial terms for time were included as necessary.

Individual gaps were included as a grouping variable in the random effects component of the model because the cumulative biomass variables in the gaps were repeatedly measured over time. Individual gaps may experience different abiotic and biotic conditions, which may influence the extent of the change in cumulative biomass over time. Therefore, we allowed individual gaps to vary in their rate of change in biomass accumulation by including gap size, initial biomass (Appendix A) and their interactions with time into the random effects model. Our full initial model including fixed and random effects was:

$y_{\mathrm{gap}} = \text{fixed effect model (1)} + \alpha_{1\mathrm{gap}}\ \mathrm{gapsize}_i + \alpha_{2\mathrm{gap}}\ \mathrm{time}_i * \mathrm{gapsize}_i + \alpha_{3\mathrm{gap}}\ \mathrm{time}_i{*}\mathrm{AGBin}_i$ (2)

where α's are the random effects parameters.

The contribution of each fixed and random effect was assessed by deleting variables one at a time from the full model and comparing the depleted models with the full model using an χ^2-test based on log-likelihood ratios (Pinheiro and Bates 2000) and Akaike Information Criterion with a correction for finite sample sizes (AICc), favoring models with low AIC (Burnham and Anderson 2002). We used restricted maximum likelihood (REML) to compare nested models in which only the random effects differed and maximum likelihood to compare nested models where the fixed effects differed (Burnham and Anderson 2002). Models were considered competitive when ΔAICc ≤ 2, and in these instances the most parsimonious model (i.e. the model with the fewest parameters) was used. We used REML to calculate the estimates of the parameters for the 'best' model.

To estimate the effect of lianas on biomass accumulation in gaps, we generated two models for each of the three response variables: a) cumulative biomass accumulation (growth plus recruitment minus mortality); b) cumulative biomass accumulation due to growth; and c) cumulative biomass loss due to mortality. In the first model, we examined only tree biomass accumulation with the aim of assessing the effect of liana removal on tree biomass dynamics. In the second model, we included the biomass accumulation of both trees and lianas for the control gaps to quantify the extent to which liana biomass dynamics compensate for the liana-induced reduction in tree biomass accumulation. The difference between biomass accumulation of the control gaps excluding lianas and the control gaps including lianas was taken to be the extent of the compensatory effect of lianas.

The resulting best-fit models for each of the response variables followed a similar format:

$$y_{gap} = \beta_1 \text{ time}_i{*}\text{treat}_i{*}\text{AGBin}_i + \alpha_{1gap} \text{ time}_i{*}\text{AGBin}_i \tag{3}$$

Only the model for biomass increment due to growth contained β_2 time for the first model, and β_2 time + β_3 time^2 for the models including lianas (Appendix B). Initial tree biomass and gap size were positively correlated, but initial biomass in the fixed effect part of the model resulted in a better overall model fit (ΔAICc >2). To test whether predicted values from the model matched the empirical data that we collected over the eight-year period, we used the model to predict cumulative biomass accumulation for each time period for each gap and compared this with the observed values. The model output closely matched the empirical data (Appendix C).

To extend the gap-level effects to the forest-level, we estimated the effects of lianas in gaps by using the conservative assumptions of a 1% annual canopy tree mortality rate, a more realistic 2% annual canopy tree mortality rate (Swaine et al. 1987), and a gap-phase regeneration rate of 8 years, i.e. 8% of the total forest area is in gap state. Based on the fixed effects model using average initial biomass values, we then calculated the mean cumulative biomass increment for each year over the eight-year period for trees in the liana-free gaps and in the control gaps, and the relative contribution of liana biomass increment to that of trees in the control gaps and extrapolated this over 0.08 ha of forest (the proportion of forest in some stage of gap-phase regeneration assuming a 1% disturbance rate).

Results

Lianas substantially reduced tree biomass accumulation in gaps. At every census period the relative tree biomass accumulation was higher in liana-free gaps than in control gaps where lianas were present (Fig.1). After 8 years, tree biomass accumulation was 280% higher in the liana-free gaps than the control gaps (dashed black line versus the solid black line in Fig. 2). Liana-free gaps accumulated a mean tree biomass of 2.47 kg m^2 in this time period, whereas control gaps gained a mean tree biomass of 0.88 kg m^2, demonstrating that lianas reduced mean tree biomass accumulation in gaps by 1.59 kg m^2.

Adding the contribution of liana biomass accumulation to tree biomass accumulation in the control gaps did not compensate for the large liana-induced loss of tree biomass. Over the 8-year period, liana biomass accumulation added 24% (0.38 kg biomass m^2) of the biomass accumulation that lianas displaced in trees (grey line versus solid black line in Fig. 2). These findings demonstrate that lianas displaced 76% more tree biomass accumulation than they themselves contributed to woody plant biomass regeneration in treefall gaps.

Over the 8-year period, lianas reduced biomass accumulation by both reducing tree growth (i.e., increment; Fig. 3a) and increasing tree mortality (Fig. 3b). Tree biomass increment due to growth was two-times greater in liana-free gaps compared to control gaps (Fig 3a). Trees in liana-free gaps accumulated 2.23 kg m^2 biomass from growth over the 8-year period, whereas trees in control gaps accumulated 1.12 kg m^2 biomass from growth. Thus, lianas substantially limited tree biomass increment by reducing tree growth. Lianas also reduced tree biomass accumulation by increasing tree mortality (Fig. 3b). However, the loss of biomass increment due to liana-induced tree mortality was relatively minor (16% loss of gap-level tree biomass accumulation) compared to the 84% loss due to liana-induced reduction in tree growth (Fig. 3a). Liana biomass increment (from growth) largely offset the liana-induced reduction in tree biomass from decreased growth (Fig. 3a); however, liana mortality was high (Fig. 3b), which reduced their cumulative contribution to woody plant biomass accumulation to only 24% of what they displaced in trees (Fig. 2).

The degree to which lianas reduced tree annual biomass accumulation depended on the initial tree biomass in the gap. Lianas in gaps with high initial tree biomass had a relatively large effect on total annual biomass accumulation, whereas the lianas in gaps with low initial tree biomass had a much smaller effect on total annual biomass accumulation (Fig. 4, Appendix D). Nonetheless, the mean effect of lianas on total annual biomass accumulation considering all gaps was substantial, demonstrating that lianas in gaps can have a large effect on forest-level biomass accumulation.

We expanded these findings to the forest level to test the hypothesis that lianas reduce forest-level carbon sequestration using the assumptions of a gap phase regeneration rate of 8 years and a 1% or 2% canopy tree mortality rate (Swain et al. 1987). Using the conservative 1% canopy tree mortality rate, we found that lianas in gaps reduced forest-level tree biomass accumulation by 0.159 Mg ha^{-1} yr^{-1} (equivalent to 0.08 Mg C ha^{-1} yr^{-1}). Lianas themselves, however, added just 0.038 Mg ha^{-1} yr^{-1} (equivalent to 0.019 Mg C ha^{-1} yr^{-1}) to forest-level biomass accumulation. In total, the net liana-induced loss of annual biomass increment (the effect of lianas on trees minus the contribution of lianas to annual biomass increment) was 0.121 Mg ha^{-1} yr^{-1} (0.06 Mg C ha^{-1} yr^{-1}) for a 1% tree mortality rate. Doubling the tree mortality rate doubled the forest-level biomass and carbon accumulation to 0.242 Mg ha^{-1} yr^{-1} and 0.12 Mg C ha^{-1} yr^{-1}, respectively. Tree annual increment of the surrounding forest on Gigante Peninsula was 1.356 Mg ha^{-1} yr^{-1}, based on tree biomass increment of more than 2000 trees ≥ 10 cm diameter from 2008 – 2011 in sixteen 60 x 60 m plots (Schnitzer et al. unpublished data). Thus, lianas in gaps displaced 8.9% – 17.8% of the forest-level annual biomass accumulation in this forest.

Discussion

This is one of the first studies to demonstrate experimentally that competition between plants (in this case lianas and trees) in tropical forests can lead to substantial decreases in biomass accumulation. Competition is often thought to be a zero-sum-game with respect to annual biomass accumulation because biomass displaced in one individual is incorporated into another, and the overall productivity of an ecosystem is thought to be regulated by the total amount of resources available (e.g., Tilman 1982, Hubbell 2001). Indeed, this scenario may be largely true for competition within a given growth form (e.g., tree vs. tree, liana vs. liana, herb vs. herb). Among growth forms, however, the zero-sum-game assumption breaks down because biomass storage capacities among competing growth forms can differ far more than among competing individuals within a given growth form.

Lianas competed intensely with trees in this forest, but failed to compensate for the tree biomass accumulation that they displaced because lianas have relatively low wood volume, low wood density, and a high rate of turnover. Liana wood volume is low because, as structural parasites that use the architecture of trees to ascend to the forest canopy, they do not develop a large supportive stem (Ewers et al. 1991, Schnitzer et al. 2006). Lianas tend to have relatively low wood density because their stems are generally porous and maximized for water transport rather than structural support (e.g., Ewers et al. 1991). Relatively high liana mortality found in this study further limited the contribution of lianas to forest carbon accumulation.

Our study, along with three previous studies (Phillips et al. 2005, Ingwell et al. 2010, Yorke et al. 2013), document the relatively rapid turnover of lianas compared to trees. Phillips et al. (2005) suggested that lianas were a "hyperdynamic" element in tropical forests because they had a fast rate of disappearance compared to trees, presumably from death. Ingwell et al. (2010) corroborated the idea of lianas being extremely dynamic by showing that over a 10-year period, liana-free trees could become completely inundated by lianas (> 75% of the crown covered), and some trees that were completely covered by lianas could become liana-free during this period. Yorke et al. (2013) highlighted the complexities of liana turnover, demonstrating that many liana stems recruit into the community by falling from the canopy and subsequently rooting and re-establishing in the understory, which indicates that a liana individual can theoretically disappear from one location and reappear in another.

Our finding that lianas displace more biomass than they contribute is consistent with two other studies. Tobin et al. (2012) tested whether lianas have a stronger competitive effect than trees in the Gigante Peninsula (Panama) forest by removing the same amount of either liana biomass or tree biomass from around selected target trees. The authors found that tree sap velocity increased immediately following liana removal, whereas tree sap velocity did not change following tree removal, indicating that lianas have a much stronger competitive effect per unit biomass than do trees. Similarly, van der Heijden and Phillips (2009) examined the correlative relationship between tree growth and liana infestation in a mature forest in Amazonian Peru and estimated that lianas reduced tree biomass increment by 10%, and that lianas compensated 30% of this liana-induced reduction in biomass increment. Biomass accumulation from liana growth in our study was higher than that reported by van der Heijden and Phillips (2009), which may have been due to our focus on gaps and the high concentration of lianas in gaps (Putz 1984, Dalling et al. 2012, Schnitzer et al. 2012, Schnitzer and Carson 2000, 2001, 2010), as well as the presumably greater number of lianas in secondary forests such as Gigante Peninsula (DeWalt et al. 2000). However, the high loss of biomass due to liana mortality (Fig. 3b) substantially reduced total liana biomass accumulation, resulting in lianas compensating only 24% of the biomass uptake that they displaced in trees.

Lianas and whole-forest biomass accumulation

Considering the huge contribution of tropical forests to aboveground terrestrial carbon stocks and net primary productivity (Beer et al. 2008, Pan et al. 2011), even small losses in carbon storage capacity represent an enormous absolute volume of carbon that will remain in the atmosphere. We found that the net reduction in biomass accumulation from lianas was 8.9% to 17.8% − a substantial loss in the capacity of this forest to sequester biomass. Furthermore, we believe that our estimate is conservative and that lianas likely have a much greater effect on forest biomass increment and thus carbon accumulation. Canopy tree mortality and forest turnover rates are typically much greater than 1% and can even exceed 2% in many tropical forests (Swaine et al. 1987). Carbon accumulation in the Gigante Peninsula forest using more realistic forest turnover rate of 2%, keeping constant the conservative 8-year gap regeneration estimate for which we had empirical data (Schnitzer and Carson 2010), revealed that lianas could reduce total forest biomass accumulation by nearly 18%.

Our estimated gap closure rate of 8 years is also likely to be conservative. Treefall gaps can take far longer than 8 years to regenerate, particularly when lianas are present (Brokaw 1985, Schnitzer et al. 2000). Lianas reduce tree recruitment, growth, and survival in gaps, increasing the amount of time that it takes gaps to recover a tall canopy (Schnitzer et al. 2008, Schnitzer and Carson 2010). In many cases, lianas arrest tree regeneration, leaving gaps in a recalcitrant, low canopy state for decades (Schnitzer et al. 2000). These liana-dominated, low-canopy sites can expand outward over time (Foster et al. 2008), presumably when neighboring trees fall or are pulled into the gap by lianas (Young and Hubbell 1991). Lianas also reduce biomass accumulation in the intact forest, where they have an additional negative effect on forest-level biomass accumulation (e.g., Grauel and Putz 2004, van der Heijden and Phillips 2009, Tobin et al. 2012). Consequently, using more realistic estimates of forest turnover and considering both gap and intact forest, the effects of lianas on carbon accumulation are likely to be far greater than our relatively conservative estimate.

Whether liana belowground biomass compensates for their aboveground effects is unknown, but we think that it is unlikely. Lianas maximize their root system for water and nutrient foraging, uptake, and transport rather than anchoring, and thus lianas likely have long, porous, highly efficient, low-density roots that are able to adequately provide sufficient amounts of water to their stems (e.g., Tyree and Ewers 1996). In contrast, tree roots are likely to reflect the lower porosity and higher wood density of their stems because of the lower per-area water demand from the stem, as well as the important role of tree roots in anchoring the trunk (Tyree and Ewers 1996). Thus, the same constraints on liana and tree stems may apply to their roots. The belowground contribution of lianas and trees to forest biomass increment and storage may be an important component of the carbon cycle, but is currently poorly understood (van der Heijden et al. 2013, Powers in press).

Within forest variation of the liana effect on forest biomass

The strength of the liana effect on carbon accumulation within a given forest will vary with a number of factors, including liana density, tree biomass, and the rates of forest turnover and gap-phase regeneration. In the current study, lianas imposed the greatest reduction in carbon accumulation in gaps that had the highest initial tree biomass compared to gaps with lower initial tree biomass (Figure 4, Appendix D). Initial tree biomass and gap size were positively correlated, and therefore lianas will likely have the greatest effect on carbon accumulation in large gaps where the biomass of regenerating trees is high. Lianas will also likely have a large effect on carbon accumulation in young secondary forests, where liana and tree densities can be exceedingly high (DeWalt et al. 2000, Letcher in press).

The ongoing increase in liana density, biomass, and productivity in many neotropical forests (reviewed by Schnitzer and Bongers 2011, Schnitzer in press) could result in further loss of carbon accumulation in those forests. For example, tree biomass on Barro Colorado Island, Panama has decreased substantially over the past 30 years (Chave et al. 2008), whereas lianas abundance, productivity, and their level of canopy tree infestation in this forest have all increased over this same period (Wright et al. 2004, Ingwell et al. 2010, Schnitzer et al 2012). While it is premature to conclude that lianas are the predominant factor responsible for tree biomass decreases on BCI, our data, along with other experimental studies on the negative effects of lianas on trees (Grauel and Putz 2004, Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008, Schnitzer and Carson 2010), suggest that this is a viable hypothesis. Data from this current study and from the general negative relationship between liana density and basal area and tree carbon uptake and storage found in other forests (e.g., van der Heijden and Phillips 2009, Durán and Gianoli 2013, van der Heijden et al. 2013) indicate that lianas can have a huge detrimental effect on biomass uptake in tropical forests, which can severely limit the capacity of tropical forests to accumulate carbon. Increases in liana abundance will likely further reduce forest-level biomass and carbon accumulation and storage.

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APPENDIX A. Gap size and initial tree and liana biomass in the liana-removal and control gaps on Gigante Peninsula, Barro Colorado Nature Monument, Panama.

APPENDIX B. The ΔAICc values for the best fitting fixed and random effects mixed models.

APPENDIX C. Observed versus predicted model tree aboveground biomass accumulation in the control and removal gaps during the 8-year study period on Gigante Peninsula, Barro Colorado Nature Monument, Panama.

APPENDIX D. Aboveground biomass accumulation (kg m^{-2}) over an 8-year period (1998-2006) in gaps on Gigante Peninsula, Barro Colorado Nature Monument, Panama.

Figures

Figure 1. Mean relative biomass accumulation (growth and mortality measured as a percentage of the previous census) over an 8-year period (1998-2006) in treefall gaps with lianas removed (dark bars) and in control gaps with lianas present on Gigante Peninsula, Barro Colorado Nature Monument, Panama. The dark bars represent mean annual biomass accumulation in the absence of lianas (liana removal gaps), the grey bars represent annual biomass accumulation of trees in control gaps, and the white bars the sum of trees and liana in control gaps. Error bars represent one standard error. Significant differences between the treatments are indicated by asterisks: * P≤0.10, ** P≤0.05. Adding liana biomass increment to tree biomass increment in the control plots did significantly change the results.

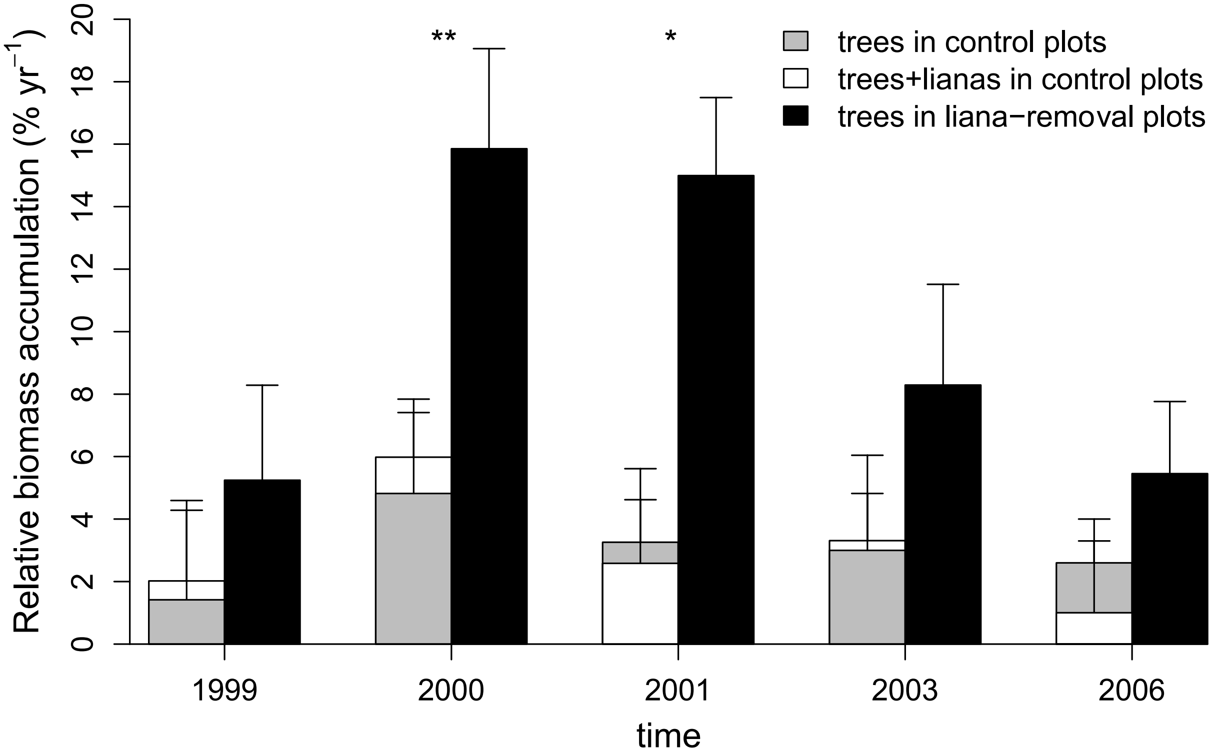
Figure 2. Aboveground biomass accumulation (kg m^{-2}) in treefall gaps over an 8-year period (1998-2006) on Gigante Peninsula, Barro Colorado Nature Monument, Panama. The dashed black line represents tree biomass accumulation from growth and mortality in gaps without lianas, the solid black line represents tree biomass accumulation from growth and mortality in control gaps with lianas present, and the solid grey line represents the additive aboveground biomass accumulation of lianas and trees (growth and mortality) in the control gaps. Dashed lines in smaller font represent the 90% confidence intervals for each of the aboveground biomass increment lines.

Figure 3. Cumulative aboveground biomass increment from woody plant growth (A) and loss from tree mortality (B) in treefall gaps on Gigante Peninsula, Barro Colorado Nature Monument, Panama. The dashed black line represents tree aboveground biomass increment in liana-free gaps, the solid black line represents tree aboveground biomass increment in control gaps where lianas were present, and the grey line represents the additive aboveground biomass increment of lianas and trees in control plots. Dashed lines in smaller font represent the 90% confidence

intervals for each of the aboveground biomass increment lines. Note that the y-axes are different, giving cumulative aboveground mortality (B) the appearance of a larger contribution than it actually has.

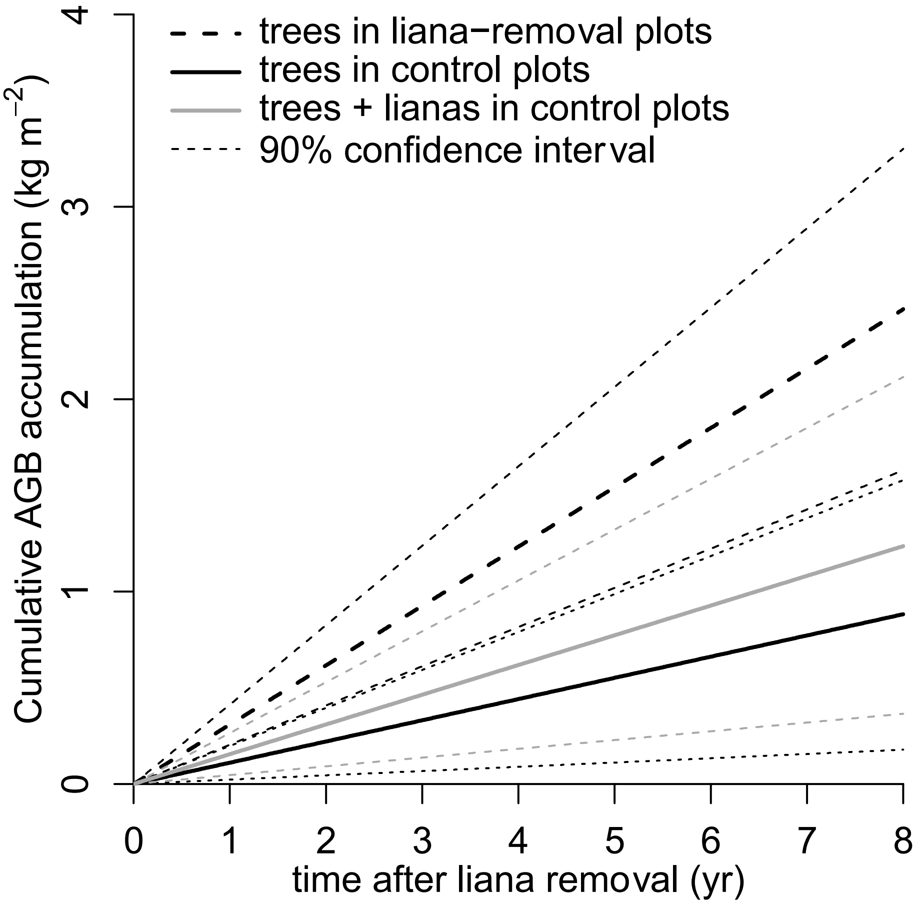
Figure 4. The effect of lianas on mean annual biomass accumulation (kg m^{-2}) in gaps that differ in initial tree aboveground biomass on Gigante Peninsula, Barro Colorado Nature Monument, Panama. Lianas had a substantially greater effect on aboveground biomass accumulation in large gaps with high initial biomass compared to small gaps with low initial biomass.

Figure 1



Relative biomass accumulation (% yr^{-1})
0
2
4
6
8
10
12
14
16
18
20
**
*
trees in control plots
trees+lianas in control plots
trees in liana−removal plots
1999
2000
2001
2003
2006
time

Figure 2



trees in liana−removal plots
trees in control plots
trees + lianas in control plots
90% confidence interval
Cumulative AGB accumulation (kg m^{-2})
0
1
2
3
4
0
1
2
3
4
5
6
7
8
time after liana removal (yr)

Figure 3

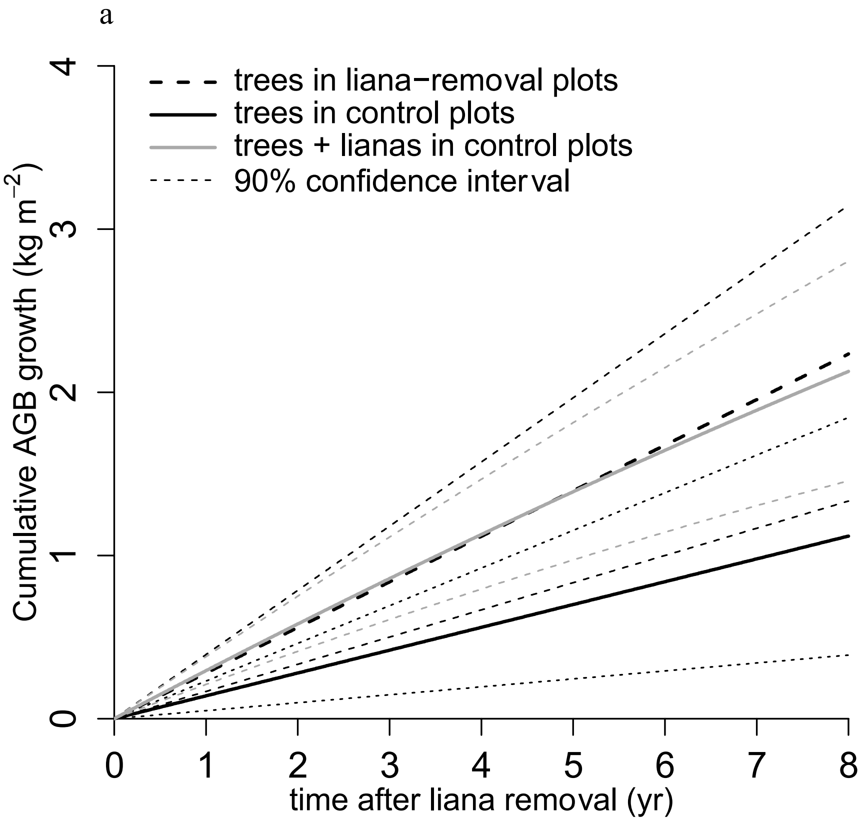
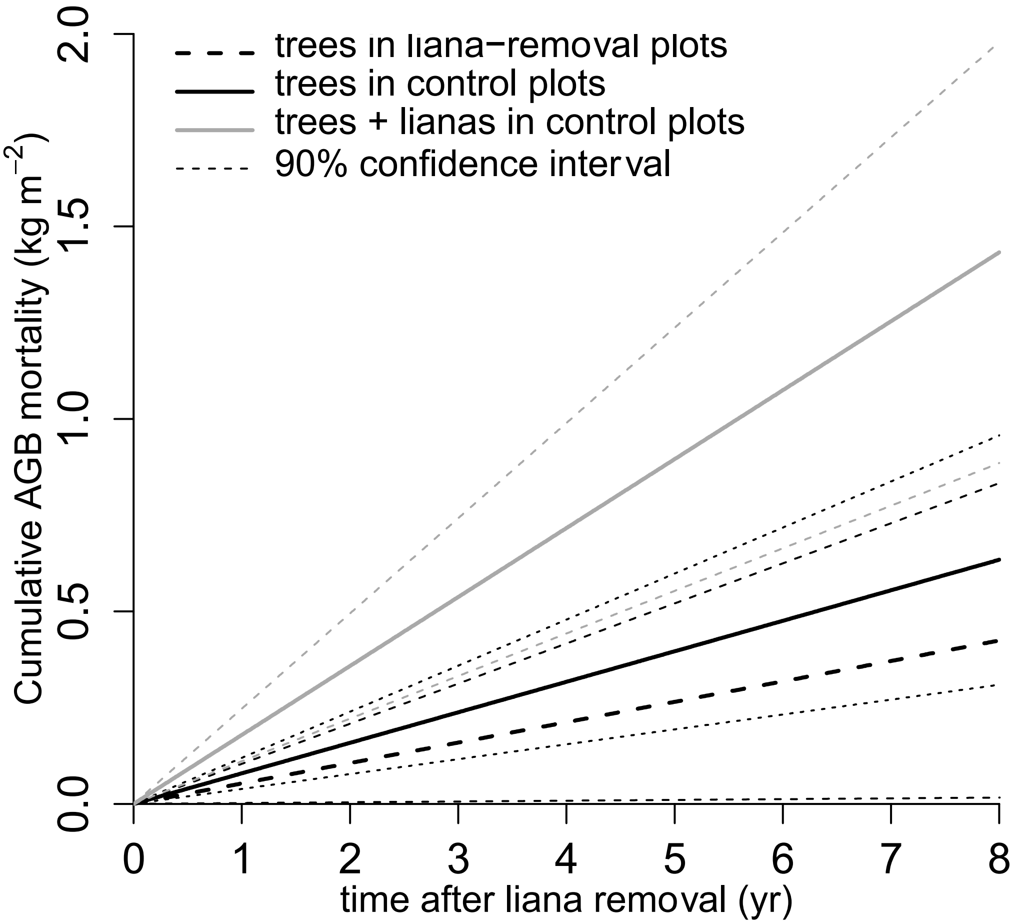
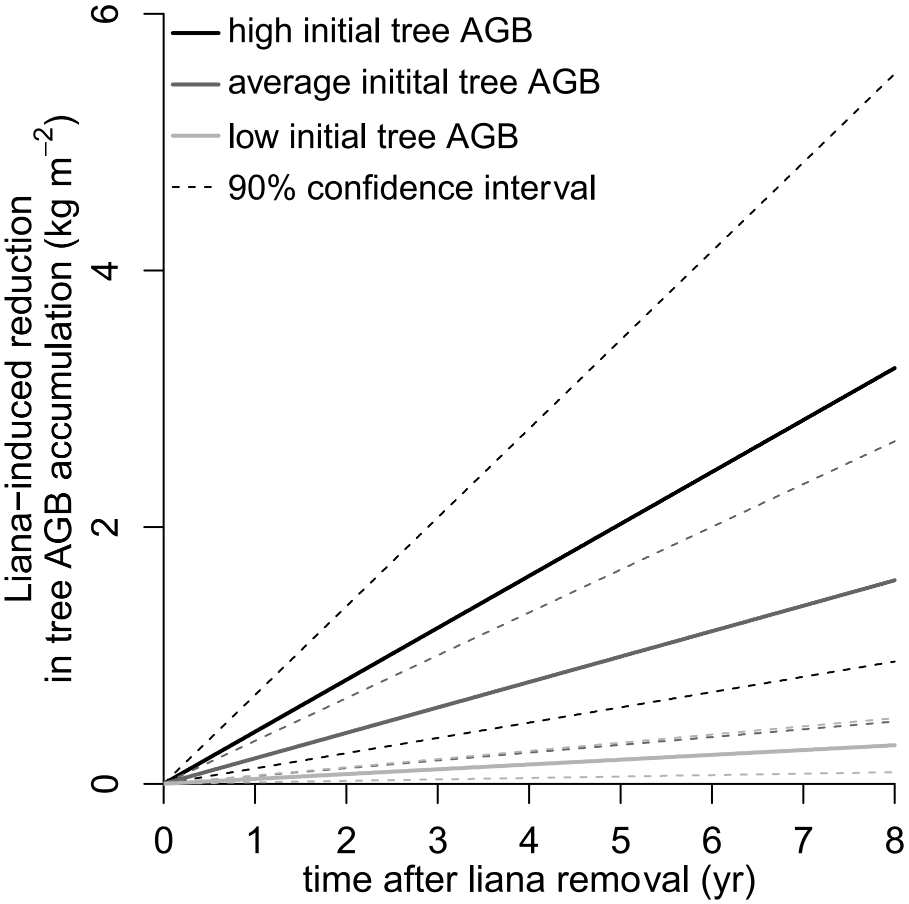

a
trees in liana−removal plots
trees in control plots
trees + lianas in control plots
90% confidence interval
Cumulative AGB growth (kg m^{-2})
0
1
2
3
4
0
1
2
3
4
5
6
7
8
time after liana removal (yr)

Figure 3

b


trees in liana−removal plots
trees in control plots
trees + lianas in control plots
90% confidence interval
Cumulative AGB mortality (kg m^{-2})
0.0
0.5
1.0
1.5
2.0
0
1
2
3
4
5
6
7
8
time after liana removal (yr)

602 Figure 4



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APPENDIX A. Gap size and initial tree and liana biomass in the liana-removal and control gaps on Gigante Peninsula, Barro Colorado Nature Monument, Panama.

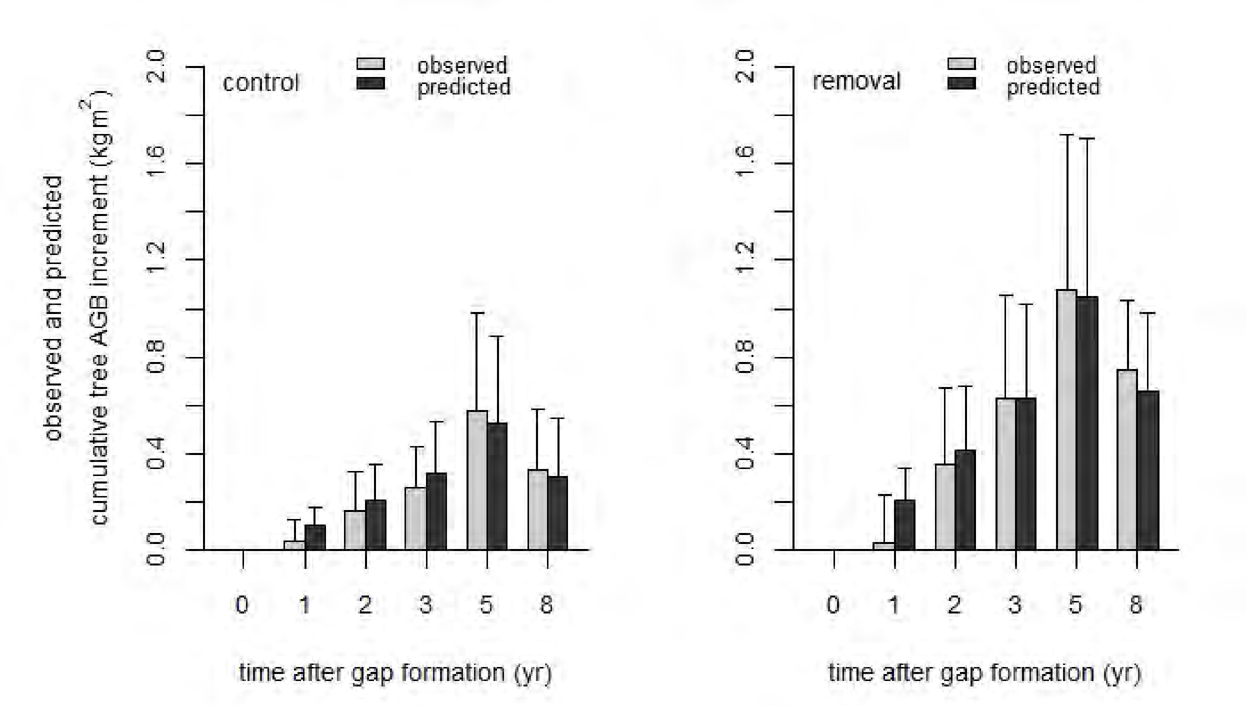
Gap	**Treatment**	**Gap size (m^2)**	**Initial tree biomass (kg m^{-2})**	**Initial liana biomass (kg m^{-2})**
3	C	131.77	3.897	0.898
7	C	57.29	1.329	0.579
9	C	24.41	0.729	4.106
11	C	137.04	10.675	1.808
12	C	52.98	2.565	1.305
13	C	97.44	2.694	2.783
15	C	69.21	1.293	1.422
16	C	127.69	5.502	2.686
18	C	67.14	2.238	1.065
mean±s.e		**85.00±13.39**	**3.865±1.090**	**1.850±0.378**
1	R	77.03	4.819	0.690
4	R	76.05	0.523	5.627
5	R	119.00	3.655	0.832
6	R	230.72	4.330	0.585
8	R	74.09	0.129	0.292
10	R	92.79	0.906	3.115
14	R	96.89	3.456	2.207
17	R	40.93	0.387	1.223
mean±s.e		**115.36±20.16**	**2.276±0.696**	**1.821±0.638**

APPENDIX B. The ΔAICc values for the best fitting fixed and random effects mixed models. Models with ΔAICc ≤ 2 were considered competing models and thus we selected the most parsimonious model (i.e. the model with the fewest parameters). The table shows ΔAICc < 2, with the model used in bold. Random effect models were fitted using reduced maximum likelihood (REML), while keeping the fixed effect model constant. Fixed effects models were compared using maximum likelihood (ML), while keeping the random effects model constant. Time = time after gap formation, treat = treatment, treeAGBin = initial tree above-ground biomass, * = interaction effect.

Random effects model	**No. of parameters**	**AICc**	**ΔAICc**
A. Biomass accumulation (growth + recruitment – mortality)			
Trees only			
time * treeAGBin	4	50.59	0.00
Lianas and trees			
time * treeAGBin	4	144.60	0.00
B. Biomass increment (growth only)			
Trees only			
time * treeAGBin	5	-60.33	0.00
Lianas and trees			
time * treeAGBin	6	-13.05	0.00
C. Biomass loss (mortality only)			
Trees only			
time * treeAGBin	4	27.96	0.00
Lianas and trees			
time * treeAGBin	4	115.99	0.00

Fixed effects model	**No. of parameters**	**AICc**	**ΔAICc**
A. Biomass accumulation (growth + recruitment – mortality)			
Trees only			
treat * time * treeAGBin	4	39.08	0.00
Lianas and trees			
treat * time * treeAGBin	**4**	**133.45**	**0.00**
treat * time + treat * time * treeAGBin	6	138.17	0.72
B. Biomass increment (growth only)			
Trees only			
time + treat * time * treeAGBin	**5**	**-79.70**	**0.00**
treat * time + time * treeAGBin + treat * time * treeAGBin	7	-77.53	1.71
Lianas and trees			
time + $time^2$ + treat * time * treeAGBin	6	-43.29	0.00
C. Biomass loss (mortality only)			
Tree only			
treat * time * treeAGBin	**4**	**13.45**	**0.00**
treat * time + treat * treeAGBin	6	13.81	0.36
Lianas and trees			
treat * time * treeAGBin	4	103.02	0.00

APPENDIX C. Observed versus predicted model tree aboveground biomass accumulation in the control and removal gaps during the 8-year study period on Gigante Peninsula, Barro Colorado Nature Monument, Panama. We omitted the year 8 measurements for two gaps because they were completely covered by the crowns of newly fallen trees in that year.



APPENDIX D. Aboveground biomass accumulation (kg m^{-2}) over an 8-year period (1998-2006) in gaps on Gigante Peninsula, Barro Colorado Nature Monument, Panama. Panels represent low tree initial biomass (A), mean tree initial biomass (B), and high tree initial biomass (C). The dashed black line represents trees in gaps without lianas, the solid black line represents only trees in control gaps (with lianas present), and the solid grey line represents the additive aboveground biomass increment of lianas and trees in the control gaps. Dashed lines in smaller font represent the 90% confidence intervals for each of the aboveground biomass increment lines.