Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests?

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Summary

1. Tropical forests are critical for protecting global biodiversity and carbon stores. While forest degradation and fragmentation cause negative impacts on trees, many woody lianas benefit, with associated negative effects on carbon storage. Here we focus on the key question of how abiotic environmental changes resulting from tropical forest fragmentation mediate the allocation of carbon into trees and lianas.

2. We focus on the globally threatened Brazilian Atlantic Forest, in forest fragments spanning 13 to 23,442 ha in area and at fragment edges and interiors. Within each fragment, we established two transects: one at the edge and one in the interior. Each transect consisted of ten 10 x 10 m plots spaced at 20 m intervals. Within each plot we sampled living trees with diameter ≥4.8 cm at 1.3 m above ground, living lianas with diameter ≥1.6 cm at 10 cm above ground, and several microclimatic and soil variables.

3. Fragmentation changed a broad suite of abiotic environmental conditions recognized as being associated with forest carbon stocks: edges and smaller fragments were hotter, windier, and less humid, with more fertile and less acid soils at edges. Tree carbon stocks were thus higher in forest interiors than at edges, and were positively related to fragment size in interiors, but were not impacted by fragment size at edges.

4. Trees and lianas showed different responses to fragmentation: in interiors of small fragments, tree carbon stocks declined whereas liana carbon stocks increased; and at edges, tree carbon stocks were not affected by fragment size, whereas liana carbon stocks were highest in smaller fragments. These patterns were strongly related to changes in abiotic environmental conditions.

5. We conclude that the abiotic changes across the fragmentation gradient, rather than liana proliferation, were more likely to reduce tree carbon stocks. Cutting of lianas is frequently
promoted for restoring forest carbon in human-modified tropical forests. However, this approach may not be effective for restoring forest carbon stocks in fragmented forests.

**Keywords**: Carbon cycle; Biomass; Microclimate; Air Temperature; Desiccation; Soil fertility; REDD+.
Introduction

The loss, fragmentation and disturbance of tropical forests represent a major threat to biodiversity (Laurance et al. 2006; Gibbs et al. 2010; Solar et al. 2015) and globally important ecosystem services, including carbon storage and climate regulation (Magnago et al. 2014, 2015a; Lewis et al. 2015). For example, tropical forests contribute to over a third of the net primary productivity in global terrestrial ecosystems (Field 1998), and the largest tropical forest countries harbour 45% of the terrestrial global carbon stocks (Bonan 2008). Tropical forest deforestation and disturbance contributes to 6-17% of the global anthropogenic CO₂ emissions, which is second only to the burning of fossil fuels (van der Werf et al. 2009). In countries such as Brazil, CO₂ emissions from forest losses and disturbance account for 22% of total emissions (Tollefson 2013). Understanding how land-use change affects the carbon stocks in tropical forest fragments is critical, especially given the potential to implement carbon-based payments for ecosystem services and biodiversity conservation (e.g. the United Nations Reducing Emissions from Deforestation and Forest Degradation [REDD+] program) (Berenguer et al. 2014; Magnago et al. 2015a).

Outside of tropical peatlands, the vast majority of carbon held within tropical forests is stored in mature trees (Chave et al. 2005; Berenguer et al. 2014), yet this is also the stock that is most vulnerable to anthropogenic disturbance (Laurance et al. 2000; Berenguer et al. 2014). In fragmented landscapes, alterations to the microclimate at forest edges include increased wind speeds, higher temperatures via canopy openness, and lower humidity (Laurance et al. 2002; Magnago et al. 2015b). These impacts alter tree functional attributes (hardwood to softwood species) and drive high rates of tree mortality (Laurance et al. 2000; Briant, Gond & Laurance 2010; Magnago et al. 2014, 2015a; b), reducing tree carbon stocks (Laurance et al. 2006; Berenguer et al. 2014).
While such environmental changes reduce carbon stocks in trees, there is a growing body of evidence suggesting that many woody lianas benefit from forest disturbance and fragmentation (Laurance et al. 2001; Schnitzer & Bongers 2002). Several complementary mechanisms can explain the competitive advantage of lianas over trees in certain environmental conditions, including a greater capability to access deep-water facilitating resistance to drought events, the ability to cause mechanical damage to trees which opens up gaps, and rapid colonization and proliferation with high light intensity or soils with increased fertility due to nutrient deposition (Laurance et al. 2002, 2014; Schnitzer & Bongers 2002; Restom & Nepstad 2004; Magrach et al. 2014). Lianas may also benefit from the increase in global atmospheric CO$_2$, which can cause a greater increase in rates of fecundity, recruitment and growth for lianas than tree species (Schnitzer & Bongers 2011; Laurance et al. 2014).

Liana proliferation would negatively affect the carbon storage potential of forests (Laurance et al. 2001; Schnitzer & Bongers 2002; Durán et al. 2015) as they contribute relatively little to the overall forest carbon stock (Chave et al. 2008; van der Heijden & Phillips 2009; Durán & Gianoli 2013) because they prioritise hydraulic efficiency rather than wood density or stem diameter relative to leaf area (Poorter et al. 2010). Furthermore, investment in leaves rather than woody stems results in a more rapid return of carbon to the atmosphere (van der Heijden, Powers & Schnitzer 2015). However, it remains unclear how trees and lianas are affected by the interaction between fragment area and edge effects, or to what extent any changes are mediated by alterations in soil and microclimatic conditions.

We address these important knowledge gaps in the globally threatened Brazilian Atlantic Forest, where we examined how abiotic environmental changes resulting from tropical forest fragmentation mediate the allocation of carbon into trees and lianas. Previous studies in tropical
forests have shown how edge effects usually change the abiotic environment of fragments (Laurance et al. 2002; Magnago et al. 2015b) and that these changes can affect forest structure, reducing tree carbon stocks and increasing the dominance of lianas (Laurance et al. 2014; Magrach et al. 2014; Magnago et al. 2015ab). We therefore measured tree carbon stocks, liana abundances and carbon stocks, soil nutrients and acidity, and microclimatic conditions to answer three main questions: (i) are microclimatic and soil conditions controlled by the fragmentation gradient (fragment size and edge-interior location)?; (ii) do environmental changes following fragmentation reduce trees carbon stock and increase lianas abundances and carbon stocks?; and (iii) does liana prevalence affect tree carbon stocks?

Material and Methods

Study area

This study was based in the state of Espírito Santo, in South-East Brazil. Within the region, we focused on the municipalities of Sooretama, Linhares and Jaguaré (18°54′–19°15′S and 39°54′–40°15′W, 28–65 m.a.s.l) (Fig. S1; Magnago et al. 2014), which contain a landscape matrix composed mainly of pastures, Eucalyptus spp., coffee and papaya plantations (Rolim et al. 2005), plus many forest fragments, including two larger than 20,000 ha (see Text S1 for more details). The climate is tropical wet (Köppen classification), with mean annual precipitation of 1403 mm and a dry season from May to September when precipitation is 33 mm per month (Peixoto & Gentry 1990).
Tree and liana sampling

Fieldwork was conducted from January 2011 to January 2012. We created permanent plots along transects within nine fragments ranging from 13 to 1318 ha in area (mean = 334 ha) and within two control fragments larger than 20,000 ha in Reserva Natural Vale (RNV) and Reserva Biológica de Sooretama (REBIO) (Table S1; Magnago et al. 2014). We established one edge and one interior transect within each of our nine fragments, with transects consisting of ten 10 × 10 m plots spaced at 20 m intervals. We also established six transects within control fragments: one edge and one interior transect in RNV, and two edge and two interior transects in REBIO, with a mean distance of 17.1 (± 10.4) km between transects. Based on mapping of IBGE (1987), all transects were on Yellow Ultisol soils. The spatially auto-correlated plots were aggregated into a single 0.1 ha transect for all of our analyses. Although larger sample areas reduce error in diversity and forest structure metrics (Baraloto et al. 2012), 0.1 ha is frequently used for assessing tropical forest carbon stocks (Saatchi et al. 2011; Stegen et al. 2011; Magnago et al. 2015a).

A major review of 33 abiotic and biotic edge parameters showed that 10 parameters extended less than 25 m from forest edge, while all but one factor (wind speed) extended less than 300 m (Laurance et al. 2002). Hence, we established edge transects ~5 m inside the fragment and parallel to the forest edge to capture all edge parameters, and interior transects with distance ≥300 m from the nearest edge (although the smallest fragments did not permit a longer minimum distance from edge).

Within each plot, we sampled every living tree with a diameter at breast height (DBH) ≥4.8 cm at 1.3 m height. We identified the botanical material using collections at the CVRD Herbarium of the Reserva Natural Vale and VIES Herbarium of the Federal University of
Espírito Santo, and with assistance from experts in the identification of specific plant families (e.g. Myrtaceae and Sapotaceae). Botanical material collected in the fertile stage was deposited at the CVRD Herbarium. Within the plots, we also measured every liana ≥1.6 cm diameter at 10 cm above ground (Diameter at Soil Height [DSH]). We only sampled individuals with ≥50% of their roots inside the plot (see Phillips et al. 2009).

Trees and lianas carbon estimation

Following previous studies in the region (Magnago et al. 2015a), we used Chave et al.'s (2005) equation to estimate the Above Ground Biomass of Trees (AGBt):

\[
AGBt = \rho \exp(-1.499 + 2.148 \ln(DBH) + 0.207(\ln(DBH))^2 - 0.0281(\ln(DBH))^3)
\]

where \(\rho\) = wood density (g/cm\(^3\)).

For estimating live Liana Above Ground Biomass (AGBl) we used Schnitzer et al.'s (2006) equation:

\[
AGBl = \exp(-1.484 + 2.657 \ln(DSH))
\]

We assume that 50% of AGB of each tree and liana individual is represented by carbon (Malhi et al. 2004; Chave et al. 2005). Tree species data for wood density on dry weight (g/cm\(^3\)) were obtained from The Global Wood Density (GWD) database, subsection Tropical South America (http://hdl.handle.net/10255/dryad.235; (Chave et al. 2009; Zanne et al. 2009). We made two following adjustments (following Flores & Coomes 2011; Hawes et al. 2012): (i) for
tree morphospecies only identified to the family or genus level, we used the average wood
density of the minor taxonomic group; (ii) for species not in the GWD database, we used the
average wood density for the species’ genus.

**Sampling microclimatic and soil variables**

In each plot, we sampled the microclimatic variables of maximum air temperature (°C),
maximum wind speed (km/h) and relative humidity (%) using two Kestrel Weather and
Environmental Meters (model 4500, Nielsen-Kellerman Company, USA). These measures are
known to respond to fragmentation and edge effects (Chen *et al.* 1999; Didham & Lawton 1999;
Laurance *et al.* 2002). The data for the two control fragments were obtained from Magnago *et al.*
(2015b). To standardize microclimatic data collection among the sample plots, all measures were
recorded once per plot during a 15-minute period (between 08:00-11:00 and then 14:00-17:00)
and at 1.5 m above ground. Because microclimatic parameters show natural variation (e.g.,
warmer days have higher humidity and stronger winds than other days), we also recorded
microclimatic data approximately 10 m from the edge in the matrix adjacent to each fragment.
Each fragment’s microclimatic data is then expressed as the percentage change from the matrix
values (Table S1).

For soil variables we collected three replicate samples of the topsoil (0-10 cm depth) in
each 10 × 10 m plot. These were mixed to form one composite sample per plot, which were then
analyzed in the Soil Analysis Laboratory, Federal University of Viçosa (UFV). We selected the
following variables as measures of soil fertility (Hazelton & Murphy 2007; Ronquim 2010): Sum
of Bases (calculated by the sum of Ca+Mg+K+Na), Effective Cation Exchange Capacity,
organic matter content, available phosphorus and pH in H2O (Table S1).
Data Analysis

General modelling framework

All statistical analyses and model selections were constructed by applying Generalized Linear Mixed Models (GLMM) using each fragment as a random factor (Bolker et al. 2009). We used a Negative Binomial error distribution with log link function for response variable of count data (abundance), since these data showed overdispersion, preventing the use of Poisson error. A Gaussian error distribution was used for continuous response variables. However, when response variable was a ratio, we applied a log-normal distribution. These analyses were performed using the “glmer.nb” function for Negative Binomial models and “lmer” function for Gaussian and log-normal models in the “lme4” package. All models were validated using the relation between standardized residuals with standardized normal quantiles, using the function “qqmath” in “lme4”.

To determine the best model, we used an information theoretical approach based on the Akaike Information Criterion of Second Order (AICc), which is indicated for small sample sizes, and the best model was indicated by the AICc lower value (Burnham & Huyvaert 2011). We used the “dredge” function from the “MuMIN” package to test all possible combinations of the variables included in the full model, including the null model. The approach of using AICc combined with a low number of parameters (two fixed explanatory variables and the interaction between them) in the GLMM full model avoided overfitted models and reduced the chances of type I error (Burnham & Anderson 2002 and Zuur et al. 2009). For all best models, we used residuals maps to assess whether spatial autocorrelation was determining model outcomes (Dormann et al. 2007; Zuur et al. 2009). All analyses were performed in the R environment, version 2.15.3 (R Development Core Team. 2012).
Are microclimatic and soil conditions controlled by the fragmentation gradient?

For each microclimatic and soil response variable (all continuous) we evaluated the GLMM framework considering two explanatory variables: (i) fragment size (continuous) and (ii) edge-interior location (categorical), plus the interaction between them. We then constructed a PCA with all soil and microclimatic variables together. The final PCA1 included only the variables with significant Spearman’s correlation values with the PCA1 axes and included Sum of Bases, Effective Cation Exchange Capacity, maximum air temperature, maximum wind speed and relative humidity (Figure S2A). Therefore, the final PCA1 did not select organic matter, phosphorus and pH. The significance of each axis of the PCA1 was obtained by 999 Monte Carlo’s permutation tests. As only axis 1 was significant (p=0.001) (see Figure S2A), we used it as our composite metric of abiotic changes (Abiotic Change Axis 1, hereafter). We analysed the response of Abiotic Change Axis 1 using the GLMM framework to evaluate the effect of fragment size, edge-interior location, and the interaction between fragment size and edge-interior location. To develop a more complete gradient of environmental changes, we repeated the PCA1 procedures also including fragment size (Figure S2B). The Spearman’s correlation values of all variables used in PCA2 are shown in Figure S3. Again, only axis 1 was significant (p=0.001) (Figure S2B), which we then used as our composite metric of all microclimatic and soil changes and fragment size reductions (Fragmentation Axis 1, hereafter; Figure S3).

Does fragmentation alter trees and lianas carbon stocks?

We used GLMMs to examine the impact of fragmentation on trees and lianas carbon stocks and also on liana abundance. First we ran each GLMM using two explanatory variables:
(i) fragment size and (ii) edge-interior location, plus the interaction between them. We then repeated this GLMM replacing fragment size with Fragmentation Axis 1.

We evaluated the effect of fragmentation on the relative dominance of lianas (see Phillips et al. 2002) using a GLMM to examine the ratio between lianas and trees (for both abundance and carbon stock metrics). Again, our first GLMM used two explanatory variables: (i) fragment size and (ii) edge-interior location, plus the interaction between them. We then repeated this replacing fragment size with Fragmentation Axis 1.

Does liana prevalence affect trees carbon stock?

We used GLMMs to examine whether there was a negative association between tree carbon stocks (response variable) and liana abundance or liana carbon stock (explanatory variables; (Durán & Gianoli 2013). As there was a strong Spearman’s correlation between liana abundance and their carbon stock (r=0.8; p<0.0001), we did not include these two variables within the same full model and instead ran full models separately and then compared the best models for each variable (see Table S7).

Results

Are microclimatic and soil conditions controlled by the fragmentation gradient?

Overall, our composite Abiotic Axis 1 was strongly predicted by fragment size (GLMM; t=-5.350, p<0.0001, Figure S4A) and edge-interior location (GLMM; t=6.546, p<0.0001, Figure S4B). This was reflected by the changes in the specific microclimatic variables, although there was some variation in their individual responses. Air temperature was significantly higher in small fragments (GLMM; t=-3.06, p=0.01; Figure 1A) and near forest edges (GLMM; t=3.56,
p<0.01; Figure 1B). In contrast, air humidity showed a significant interaction between fragment size and edge-interior location (GLMM; t=-3.05, p=0.01; Figure 1C), with a higher accrual of air humidity with increasing fragment size in the interior than at the edge. Wind speed showed a significant interaction with fragment size and edge-interior location (GLMM; t=2.28, p<0.05; Figure 1E), with a significant negative influence of fragments size for plots located in interiors (F=8.79, p=0.01; Figure 1E), but no effect for those located near edges (F=0.2, p=0.66; Figure 1E).

For soil, the best model showed that edges had significantly higher Effective Cation Exchange Capacity and were thus more fertile when compared with the interior (GLMM; t=2.971; p<0.01; Figure 2A). Also, there was a slightly non-significant negative effect of fragment size on Effective Cation Exchange Capacity (GLMM; t=-1.983, p=0.06; Figure 2B). Soils from transects located in forest edges showed higher values of Sum of Bases (GLMM; t=3.64, p<0.01; Figure 3C) and lower acidity (GLMM; t=2.55, p<0.05; Figure 2D) than interiors. The best models also suggested a slight (but non-significant) influence of fragment edges on available phosphorous (GLMM; t=2.033, p=0.06; Figure 2E) and organic matter contents (GLMM; t=-2.02, p=0.07; Figure 2F).

**Does fragmentation alter tree’s and liana’s carbon stocks?**

We sampled 4,140 trees and 8,236 lianas. As expected, across all transects, much more carbon was stored by trees than lianas (Table S1). On average, trees stored 97.7% (±1.8%) of the total carbon (i.e., trees + lianas carbon stocks) in interiors and 87.1% (±7.9%) at edges. Total carbon in interior transects (61.8 ±25.8 Mg) was nearly three-fold that at edges (22.8 ±11.6 Mg).
Considering only tree’s carbon stock, there was a 69% reduction from 60.7 Mg in interiors to 18.7 Mg at edges.

Trees and lianas responded very differently to fragmentation. Following the fragment size gradient (interior plus edge), tree carbon stocks ranged from 115.7 Mg/transect in the largest (>23,000ha) to 46.4 Mg/transect in the smallest (13 ha) fragment, representing a 60% reduction. In contrast, liana carbon stocks increased by 200%, from 1.6 Mg/transect in the largest to 4.79 Mg/transect in the smallest fragment.

Tree carbon stocks - There was a significant interaction effect of fragment size and edge-interior location (GLMM; t= -4.435; p=0.001; Figure 3A): decreasing fragment size had a significant negative effect on trees carbon stock in interiors (F = 17.4; P = 0.002; Figure 3A), but no significant effect at edges (F = 1.3; P = 0.3; Figure 3A). The best model also showed significant reductions of tree carbon stocks at edges versus interiors (GLMM; t= -11.6; p<0.0001; Figure 3B). Very similar results were obtained when we replaced fragment size with Fragmentation Axis 1. There was a significant interaction effect between Fragmentation Axis 1 and edge-interior location (GLMM; t= -4.9; p=0.0003; Figure 3C), and increasing environmental impacts had a significant negative effect on tree carbon stocks in interiors (F = 13.82; P = 0.004; Figure 3C), but no significant effect at edges (F = 0.096; P = 0.7; Figure 3C). The best model also showed significant reductions of tree carbon stocks at edges versus interiors (GLMM; t= -6.045; p<0.0001; Figure 3D).

Liana carbon stocks - There was a significant interaction effect of fragment size and edge-interior location on liana carbon stocks (GLMM; t= -3.14, p=0.01; Figure 3E). However, in contrast with trees, decreasing fragment size had a positive effect on liana carbon stocks in forest interiors (F = 6.47; P = 0.03; Figure 3E), but had a more strongly positive effect at edges
The best models also revealed significantly higher liana carbon stocks at fragment edges than interiors (GLMM; t= 5.38; p= 0.0002; Figure 3F). Again, similar results were obtained when we replaced fragment size with Fragmentation Axis 1. There was a significant interaction effect of Fragmentation Axis 1 and edge-interior location on liana carbon stocks (GLMM; t= -2.664, p=0.014; Figure 3G), as increasing environmental impacts had a slightly non-significant positive effect in forest interiors (F = 4.1: P = 0.07; Figure 3G), but a strongly positive effect at edges (F = 16.8: P = 0.002; Figure 3G). Also, the best models showed no significant change in liana carbon stocks between edges and interior habitats (GLMM; t= 1.5; p= 0.15; Figure 3H).

Liana abundance - Liana abundance increased in smaller fragments (GLMM; t= -4.221, p<0.0001; Figure S5A) and at fragment edges (GLMM; t= 18.259, p<0.0001; Figure S5B), but there was no significant interaction between fragment size and edge-interior location. The models using Fragmentation Axis 1 showed similar results, with the best model revealing significant increases in lianas with harsher environmental conditions (GLMM; t= -3.91, p<0.0001; Figure S6A) and at fragment edges (GLMM; t= 6.58, p<0.0001; Figure S6B).

Relative prevalence of trees and lianas - For carbon stocks, the best GLMM models of the ratio of lianas to trees showed higher dominance of lianas in smaller fragments (GLMM; t= -6.353, p<0.0001; Figure 3I) and at fragment edges (GLMM; t= 9.982, p<0.0001; Figure 3J). Similar relationships were found when replacing fragment size with Fragmentation Axis 1, with a higher dominance of lianas in harsher conditions (GLMM; t= -4.232, p<0.001; Figure 3L) and at fragment edges (GLMM; t=4.186, p<0.001; Figure 3M).

For abundance, there was a higher dominance of lianas relative to trees in smaller fragments (GLMM; t= -5.189, p<0.001; Figure 3N) and at fragment edges (GLMM; t= 18.091,
Again, similar relationships emerged when replacing fragment size with Fragmentation Axis 1, with relatively higher abundance of lianas in harsher environmental conditions (GLMM; $t= -4.739, p<0.001$; Figure 3P) and at fragment edges (GLMM; $t= 6.259, p<0.0001$; Figure 3Q).

Does liana prevalence affect tree carbon stocks?

Although both measures of liana prevalence were negatively associated with tree carbon stocks (Table S7), liana abundance was a much stronger predictor than liana carbon stocks (model comparisons showed Delta AICc of 7). The single best model revealed a significant effect of liana abundance due to the interaction between edge-interior location on tree carbon stocks (GLMM: $t=-4.7$, $p<0.0001$; Figure 4): only forest interiors had a strong association between higher liana abundance and lower tree carbon stocks ($F = 6.4$: $P = 0.03$; Figure 4), whereas there was no significant association at edges ($F = 0.23$: $P = 0.64$; Figure 4). We found no clear pattern of spatial autocorrelation in any of our model residuals (Supplementary Material 2).

Discussion

Fragmentation and edge effects are reducing the potential of forests to store carbon pan-tropically (Laurance et al. 2002; Durán et al. 2013; Magnago et al. 2015ab). Here we showed that fragmentation processes change a broad suite of abiotic environmental conditions, which could benefit lianas over trees, and that trees and lianas reveal contrasting responses to fragmentation area and edge effects. We examine these results in detail by first assessing our research questions before investigating their management implications for tropical forests.
Abiotic drivers of trees and lianas

Fragment size and edge location capture almost all of the variation in the abiotic variables we recorded. These variables were associated with significant reductions in trees carbon stock, but only within fragment interiors (Laurance et al. 2001, 2006). Many studies suggest that forest succession at edges alters forest structure to protect the fragment interiors from the hotter and drier matrix (Laurance et al. 2006). Our study adds to this by suggesting that structural changes at edges occur regardless of fragment size.

Many of the abiotic variables could explain the loss of tree carbon stocks. We observed increased wind speeds in edges (Figures 2 and 4) and it is known that this can extend far (up to 400 m) into forest fragments, causing biomass loss and posterior mortality due to the physical damage in tree canopies (Laurance et al. 1998, 2000, 2002; Magnago et al. 2015b). The decrease of air humidity and increase of air temperatures could also have contributed to the overall reduction in tree carbon stocks: droughts and extreme high temperatures are related with carbon reduction due to enhanced tree mortality and changed tree species composition at regional scales (Rolim et al. 2005; Laurance et al. 2006; Allen et al. 2010). In addition, these microclimatic changes can promote the replacement of slow growing hardwood species with fast growing softwood species, which have lower carbon storage capacity (Laurance et al. 2006).

Abiotic drivers of liana dominance

Liana’s abundance and carbon stock was generally higher within small fragments and at edges, where the soils were more fertile and the microclimate was hotter and drier (Schnitzer & Bongers 2002; Laurance et al. 2014; Durán et al. 2015). There are four good reasons why lianas
are more successful than trees in these conditions. First, their flexible stems mean they are not affected by elevated wind speeds. Second, their stomatal control and deep roots mean they can survive high temperatures and low humidity whilst maintaining productivity during dry events (Chen et al. 2015);

Third, lianas could benefit from increased soil fertility stimulated by: (i) the burning of biomass in the matrix, which rapidly supplies nutrients and increases pH at forest edges (Moreira et al. 2009); and (ii) the wind-blown input of soluble nutrients from artificial fertilizers applied in nearby agricultural plantations (Selle 2007; Moreira et al. 2009). Finally, liana growth could be further enhanced by plant-soil feedbacks (Kulmatiski et al. 2008; van der Putten et al. 2013), as the high rates of tree mortality and turnover in fragment edges, plus the high levels of leaf production by lianas and pioneer trees (Laurance et al. 2002; van der Heijden et al. 2015), can return greater amounts of nutrients to the top soil.

*Interactions between trees and lianas*

Could some of the patterns we observed be driven by competition between the plant forms and the interaction with disturbance? For example, lianas can be stronger competitors with trees in more stressful and disturbed regimes due to their better-developed root system and higher root extension rate (Schnitzer & Bongers 2002, 2011; Restom & Nepstad 2004). These adaptations allow lianas to exploit soil resources, such as nutrients and deep-water (Schnitzer & Bongers 2002, 2011). Although our snapshot study cannot demonstrate causation, it does provide some insights into the likelihood of liana-tree competition and highlights some areas for new research. In particular, if lianas and trees do compete, our results indicate that this either only happens in forest interiors, or that there is a threshold level at which lianas no longer have an
effect (Figure 4), because the composition of trees at edges has changed to one with more
defenses against lianas (e.g., fast growth in pioneer species) (van der Heijden & Phillips 2009;
Magrach et al. 2016). Both are plausible, but the fact that trees carbon stock was consistently low
in forest edges strongly suggests that microclimatic variables at edges can affect trees
independently of liana dominance.

Evidence for liana-tree competition was stronger in forest interiors, where there was a
very strong negative relationship between lianas dominance and trees carbon stock (Figure 5).
Again, it is not clear if this association is driven by the contrasting responses of lianas and trees
to abiotic variables that change with forest fragmentation or through direct competition for water,
soil, and light. In practice, these factors are likely to occur simultaneously: for example, due to
wind increases, fragmentation causes mechanical damage to trees (Laurance et al. 2002),
potentially benefitting lianas, which are better adapted to exploit the canopy gaps (Schnitzer et
al. 2014). In turn, this could increase mechanical damage to trees resulting from lianas
themselves, as well as increase competition for soil water – increasing the likelihood for further
tree mortality. Experiments are needed to assess to what extent lianas are driving changes in tree
communities in undisturbed forest interiors, or merely responding to them.

It is important to note that our snapshot study did not assess the effect of drought (Brando
et al. 2014; Rowland et al. 2015), and greater insights into the relevance of competitive
interactions between trees and lianas could be gleaned by undertaking experimental
manipulations across gradients of soil moisture and water availability. In addition, we did not
have wood density values to adjust the carbon equation of lianas. Thus, if liana wood density
changes with habitat disturbance, mainly in forest edges and small fragments where lianas could
be softer than in interiors or larger fragments (as expected for trees; Laurance et al. 2006), then it is possible that lianas carbon stocks are over-estimated in edges and/or smaller fragments.

**Implications for forest management and conclusions**

Liana cutting is widely used as a management technique to enhance tree productivity and restore the functionality of fragments or to reduce collateral damage during selective logging (Edwards, Fisher & Boyd 2010; Kainer, Wadt & Staudhammer 2014). However, the utility of such management will depend on the presence of competition between plant forms. Liana dominance varies among different tropical forests with, for example, reduced liana abundance and biomass across altitudinal gradients in the Atlantic Forest (Alves et al. 2012) and, between forest ecosystems, and across soil fertility and climate gradients (Schinitzer & Bongers 2011). Furthermore, lianas are not normally the first cause of edge-related tree mortality, which is particularly intense in the few years following edge creation (Laurance et al. 1998), in part because microclimatic changes are especially strong near new edges, which are hotter, drier and windier (Laurance et al. 2002). Since most trees along newly formed edges are not physiologically acclimated to these conditions, they simply die standing or via wind throw, especially the big trees (Laurance et al. 2000). In this scenario, lianas only proliferate after the canopy opens due to the initial tree mortality (Schinitzer & Bongers 2011) and appear to be responding to rather than driving change. As such, removing lianas is unlikely to prevent tree mortality.

Liana removal could even jeopardise recovery of forest structure and functionality in the likely scenario that lianas themselves help to buffer forest interiors. Here, abiotic changes would continue to depress trees carbon stock after lianas have been cleared by management, and clearance could even worsen conditions. For example, Rolim et al. (2005) showed that El Niño
drought negatively affects the above-ground biomass of trees species even in forest interiors of a large Lowland Atlantic Forest fragment. Therefore, we are not advocating that lianas dominance cannot cause impacts on trees, but similar studies should be conducted in more tropical forest regions before making general conclusions about how to manage forest to enhance carbon stocks near edges. Our study also shows that, for the Brazilian Atlantic Forest, fragmentation-induced changes of several microclimatic and soil variables can only be reduced by increasing fragment size and reducing edge-interior ratios. This would necessitate a major program of forest restoration (Lamb & Parrotta 2005).

We conclude that tree carbon stocks are negatively impacted by fragmentation via direct links with altered microclimatic and soil conditions. These include low air humidity and high air temperatures, which can increase mortality rate and change species composition, factors likely to alter plant physiology, or increased wind speed, which can cause mechanical damage and mortality (Laurance et al. 2006; Magnago et al. 2015ab). As the vast majority (83%) of the remaining Brazilian Atlantic Forests are found within fragments of less than 50 ha and 46% is located less than 100 m from an edge (Ribeiro et al. 2009), lianas are likely to be an increasingly important feature of this biome. Further research is needed to understand their competitive interactions with trees under changing climatic conditions, their carbon storage potential in disturbed forests, and their ability to facilitate edge closure.

Acknowledgements

We thank Natalia Norden and two anonymous reviewers for comments that greatly improved the article. We also thank Reserva Natural Vale, Fibria Celulose S.A., Marcos Daniel Institute, and Pro-Tapir for logistical support, and Reserva Biológica de Sooretama for permission to conduct
our research. CNPq – the Brazilian Agency for Science and Technology (grant no. 477780/2009-1), provided funding. LFSM was supported by Brazilian Studentship and Doctorate Sandwich Program grants from the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES) with two grants, Brazilian Studentship and Doctorate Sandwich Program. A.M. was supported by a Basque Government Postdoctoral Fellowship. JB was supported by EU H2020 MSCA RISE ODYSSEA (Grant agreement no. 691053). LFSM is currently supported by a PNPD program of CAPES. The authors declare no conflict of interest.

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Supplementary Materials include:

Text S1 - Conservation value of the study region.

Figure S1 - Study area and forest fragments sampled in South-eastern Brazil.

Figure S2 - Principal Correlation Analyzes (PCA) of microclimate, soil and fragment size values.

Figure S3 - Correlations between PCA Axis 1 and microclimate, soil and fragment size values.

Figure S4 - Best GLMM model of the PCA Axis 1 with fragment size and edge-interior location.

Figure S5 - Graphs of best model of lianas abundance in relation to fragment size gradients.

Figure S6 - Graphs of best model of lianas abundance in relation to fragmentation abiotic environmental gradients.

Table S1 - Identification and variable values of sampled fragments.

Table S2 - Model selection of the Generalized Linear Mixed Models for all microclimate variables in relation to fragment size and edge-interior location.

Table S3 - Model selection of the Generalized Linear Mixed Models for all soil variables in relation to fragment size and edge-interior location.

Table S4 - Model selection of the Generalized Linear Mixed Models for Fragmentation Axis 1 (PCA2) in relation to fragment size and edge-interior location.

Table S5 - Model selection of the Generalized Linear Mixed Models for carbon stocks of trees and lianas and for ratio of lianas to trees in relation to fragment size and edge-interior location.

Table S6 - Model selection of the Generalized Linear Mixed Models for carbon stocks of trees and lianas and for ratio of lianas to trees in relation to environmental changes (Fragmentation Axis 1, PCA2) and edge-interior location.

Table S7 - Model selection of the Generalized Linear Mixed Models for tree carbon stocks in relation to lianas abundances, lianas carbon stocks and edge-interior location.
Figure 1. Graphs of best models for the effects of fragments size and edge-interior location on microclimatic variables. (A-B) Effects of fragment size and habitats on air temperature; (C-D) Effects of fragment size and habitat on air humidity; (E-F) Effects of fragment size and habitat on wind speed. Black circles = Edge; White circles = Interior. Circles represent values obtained after the summation of raw residuals to the expected values for each variable, being assumed average values for other covariates. Errors bars represent the 95% of confidence intervals. ***=p<0.001; ns=No significant results.
Figure 2. Graphs of best models for the effects of fragments size and edge-interior location on soil attributes. (A) Edge-interior and (B) fragment size effects on soil fertility via Effective Cation Exchange Capacity (ECEC); (C) edge-interior effect on soil fertility via Sum of Bases; (D) edge-interior effect on soil acidity - pH in H₂O; (E) edge-interior effect on phosphorous; (F) edge-interior effect on organic matter. Errors bars represent the 95% of confidence intervals. Circles represent values obtained after the summation of raw residuals with the expected values for each variable, assuming average values for other covariates.
Figure 3. Graphs of best models for the effects of fragments size (A, E, I, N), fragmentation abiotic environmental gradients (Fragmentation Axis 1; C, G, L, P) and edge-interior location (B, D, F, H, J, M, O, Q) on trees carbon stocks (A, B, C, D), lianas carbon stocks (E, F, G, H), ratio of lianas to trees carbon stocks (I, J, L, M), and ratio of lianas to trees individuals (N, O, P, Q). Circles represent values obtained after the summation of raw residuals with the expected values for each variable, assuming average values for other covariates. Black and white circles represent edge and interior location, respectively, when there is a significant effect of the interaction term between fragment size and edge-interior location; when only black circles are shown, there is no significant interaction effect. Errors bars represent the 95% of confidence intervals.
***=p<0.001; ns=No significant results. Negative values for Fragmentation Axis 1 represent more stressful and disturbed conditions, positive values more benign conditions (see Fig. S3).

Figure 4. Graph of best model of trees carbon stocks in relation to lianas individuals. Circles represent values obtained after the summation of raw residuals with the expected values for each variable. Black and white circles represent edge and interior location, respectively, and thus the significant effect of the interaction term between fragment size and edge-interior location.