

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

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25 **Summary**

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

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

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

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

46 **5.** We conclude that the abiotic changes across the fragmentation gradient, rather than liana  
47 proliferation, were more likely to reduce tree carbon stocks. Cutting of lianas is frequently

48 promoted for restoring forest carbon in human-modified tropical forests. However, this approach  
49 may not be effective for restoring forest carbon stocks in fragmented forests.

50

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

53

54 **Introduction**

55           The loss, fragmentation and disturbance of tropical forests represent a major threat to  
56 biodiversity (Laurance *et al.* 2006; Gibbs *et al.* 2010; Solar *et al.* 2015) and globally important  
57 ecosystem services, including carbon storage and climate regulation (Magnago *et al.* 2014,  
58 2015a; Lewis *et al.* 2015). For example, tropical forests contribute to over a third of the net  
59 primary productivity in global terrestrial ecosystems (Field 1998), and the largest tropical forest  
60 countries harbour 45% of the terrestrial global carbon stocks (Bonan 2008). Tropical forest  
61 deforestation and disturbance contributes to 6-17% of the global anthropogenic CO<sub>2</sub> emissions,  
62 which is second only to the burning of fossil fuels (van der Werf *et al.* 2009). In countries such  
63 as Brazil, CO<sub>2</sub> emissions from forest losses and disturbance account for 22% of total emissions  
64 (Tollefson 2013). Understanding how land-use change affects the carbon stocks in tropical forest  
65 fragments is critical, especially given the potential to implement carbon-based payments for  
66 ecosystem services and biodiversity conservation (e.g. the United Nations Reducing Emissions  
67 from Deforestation and Forest Degradation [REDD+] program) (Berenguer *et al.* 2014; Magnago  
68 *et al.* 2015a).

69           Outside of tropical peatlands, the vast majority of carbon held within tropical forests is  
70 stored in mature trees (Chave *et al.* 2005; Berenguer *et al.* 2014), yet this is also the stock that is  
71 most vulnerable to anthropogenic disturbance (Laurance *et al.* 2000; Berenguer *et al.* 2014). In  
72 fragmented landscapes, alterations to the microclimate at forest edges include increased wind  
73 speeds, higher temperatures via canopy openness, and lower humidity (Laurance *et al.* 2002;  
74 Magnago *et al.* 2015b). These impacts alter tree functional attributes (hardwood to softwood  
75 species) and drive high rates of tree mortality (Laurance *et al.* 2000; Briant, Gond & Laurance  
76 2010; Magnago *et al.* 2014, 2015a; b), reducing tree carbon stocks (Laurance *et al.* 2006;  
77 Berenguer *et al.* 2014).

78           While such environmental changes reduce carbon stocks in trees, there is a growing body  
79 of evidence suggesting that many woody lianas benefit from forest disturbance and  
80 fragmentation (Laurance *et al.* 2001; Schnitzer & Bongers 2002). Several complementary  
81 mechanisms can explain the competitive advantage of lianas over trees in certain environmental  
82 conditions, including a greater capability to access deep-water facilitating resistance to drought  
83 events, the ability to cause mechanical damage to trees which opens up gaps, and rapid  
84 colonization and proliferation with high light intensity or soils with increased fertility due to  
85 nutrient deposition (Laurance *et al.* 2002, 2014; Schnitzer & Bongers 2002; Restom & Nepstad  
86 2004; Magrach *et al.* 2014). Lianas may also benefit from the increase in global atmospheric  
87 CO<sub>2</sub>, which can cause a greater increase in rates of fecundity, recruitment and growth for lianas  
88 than tree species (Schnitzer & Bongers 2011; Laurance *et al.* 2014).

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

98           We address these important knowledge gaps in the globally threatened Brazilian Atlantic  
99 Forest, where we examined how abiotic environmental changes resulting from tropical forest  
100 fragmentation mediate the allocation of carbon into trees and lianas. Previous studies in tropical

101 forests have shown how edge effects usually change the abiotic environment of fragments  
102 (Laurance *et al.* 2002; Magnago *et al.* 2015b) and that these changes can affect forest structure,  
103 reducing tree carbon stocks and increasing the dominance of lianas (Laurance *et al.* 2014;  
104 Magrach *et al.* 2014; Magnago *et al.* 2015ab). We therefore measured tree carbon stocks, liana  
105 abundances and carbon stocks, soil nutrients and acidity, and microclimatic conditions to answer  
106 three main questions: (i) are microclimatic and soil conditions controlled by the fragmentation  
107 gradient (fragment size and edge-interior location)?; (ii) do environmental changes following  
108 fragmentation reduce trees carbon stock and increase lianas abundances and carbon stocks?; and  
109 (iii) does liana prevalence affect tree carbon stocks?

110

## 111 **Material and Methods**

### 112 *Study area*

113 This study was based in the state of Espírito Santo, in South-East Brazil. Within the  
114 region, we focused on the municipalities of Sooretama, Linhares and Jaguaré (18°54'–19°15'S  
115 and 39°54'–40°15'W, 28–65 m.a.s.l) (Fig. S1; Magnago *et al.* 2014), which contain a landscape  
116 matrix composed mainly of pastures, *Eucalyptus* spp., coffee and papaya plantations (Rolim *et*  
117 *al.* 2005), plus many forest fragments, including two larger than 20,000 ha (see Text S1 for more  
118 details). The climate is tropical wet (Köppen classification), with mean annual precipitation of  
119 1403 mm and a dry season from May to September when precipitation is 33 mm per month  
120 (Peixoto & Gentry 1990).

121

122 *Tree and liana sampling*

123 Fieldwork was conducted from January 2011 to January 2012. We created permanent plots along  
124 transects within nine fragments ranging from 13 to 1318 ha in area (mean = 334 ha) and within  
125 two control fragments larger than 20,000 ha in Reserva Natural Vale (RNV) and Reserva  
126 Biológica de Sooretama (REBIO) (Table S1; Magnago *et al.* 2014). We established one edge and  
127 one interior transect within each of our nine fragments, with transects consisting of ten 10 × 10 m  
128 plots spaced at 20 m intervals. We also established six transects within control fragments: one  
129 edge and one interior transect in RNV, and two edge and two interior transects in REBIO, with a  
130 mean distance of 17.1 (± 10.4) km between transects. Based on mapping of IBGE (1987), all  
131 transects were on Yellow Ultisol soils. The spatially auto-correlated plots were aggregated into a  
132 single 0.1 ha transect for all of our analyses. Although larger sample areas reduce error in  
133 diversity and forest structure metrics (Baraloto *et al.* 2012), 0.1 ha is frequently used for  
134 assessing tropical forest carbon stocks (Saatchi *et al.* 2011; Stegen *et al.* 2011; Magnago *et al.*  
135 2015a).

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

142 Within each plot, we sampled every living tree with a diameter at breast height (DBH)  
143 ≥4.8 cm at 1.3 m height. We identified the botanical material using collections at the CVRD  
144 Herbarium of the Reserva Natural Vale and VIES Herbarium of the Federal University of

145 Espírito Santo, and with assistance from experts in the identification of specific plant families  
146 (e.g. Myrtaceae and Sapotaceae). Botanical material collected in the fertile stage was deposited  
147 at the CVRD Herbarium. Within the plots, we also measured every liana  $\geq 1.6$  cm diameter at  
148 10 cm above ground (Diameter at Soil Height [DSH]). We only sampled individuals with  $\geq 50\%$   
149 of their roots inside the plot (see Phillips *et al.* 2009).

150

### 151 *Trees and lianas carbon estimation*

152 Following previous studies in the region (Magnago *et al.* 2015a), we used Chave *et al.*'s  
153 (2005) equation to estimate the Above Ground Biomass of Trees (AGBt):

154

$$155 \quad \text{AGBt} = \rho \cdot \exp(-1.499 + 2.148 \ln(\text{DBH}) + 0.207(\ln(\text{DBH}))^2 - 0.0281(\ln(\text{DBH}))^3)$$

156

157 where  $\rho$  = wood density ( $\text{g}/\text{cm}^3$ ).

158

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

$$161 \quad \text{AGBl} = \exp(-1.484 + 2.657 \ln(\text{DSH}))$$

162

163 We assume that 50% of AGB of each tree and liana individual is represented by carbon  
164 (Malhi *et al.* 2004; Chave *et al.* 2005). Tree species data for wood density on dry weight ( $\text{g}/\text{cm}^3$ )  
165 were obtained from *The Global Wood Density (GWD) database*, subsection *Tropical South*  
166 *America* (<http://hdl.handle.net/10255/dryad.235>; (Chave *et al.* 2009; Zanne *et al.* 2009). We  
167 made two following adjustments (following Flores & Coomes 2011; Hawes *et al.* 2012): (i) for



168 tree morphospecies only identified to the family or genus level, we used the average wood  
169 density of the minor taxonomic group; (ii) for species not in the GWD database, we used the  
170 average wood density for the species' genus.

171

### 172 *Sampling microclimatic and soil variables*

173 In each plot, we sampled the microclimatic variables of maximum air temperature (°C),  
174 maximum wind speed (km/h) and relative humidity (%) using two Kestrel Weather and  
175 Environmental Meters (model 4500, Nielsen-Kellerman Company, USA). These measures are  
176 known to respond to fragmentation and edge effects (Chen *et al.* 1999; Didham & Lawton 1999;  
177 Laurance *et al.* 2002). The data for the two control fragments were obtained from Magnago *et al.*  
178 (2015b). To standardize microclimatic data collection among the sample plots, all measures were  
179 recorded once per plot during a 15-minute period (between 08:00-11:00 and then 14:00-17:00)  
180 and at 1.5 m above ground. Because microclimatic parameters show natural variation (e.g.,  
181 warmer days have higher humidity and stronger winds than other days), we also recorded  
182 microclimatic data approximately 10 m from the edge in the matrix adjacent to each fragment.  
183 Each fragment's microclimatic data is then expressed as the percentage change from the matrix  
184 values (Table S1).

185 For soil variables we collected three replicate samples of the topsoil (0-10 cm depth) in  
186 each 10 × 10 m plot. These were mixed to form one composite sample per plot, which were then  
187 analyzed in the Soil Analysis Laboratory, Federal University of Viçosa (UFV). We selected the  
188 following variables as measures of soil fertility (Hazelton & Murphy 2007; Ronquim 2010): Sum  
189 of Bases (calculated by the sum of Ca+Mg+K+Na), Effective Cation Exchange Capacity,  
190 organic matter content, available phosphorus and pH in H<sub>2</sub>O (Table S1).

## 191 **Data Analysis**

### 192 *General modelling framework*

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

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

214

215 *Are microclimatic and soil conditions controlled by the fragmentation gradient?*

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

233

234 *Does fragmentation alter trees and lianas carbon stocks?*

235 We used GLMMs to examine the impact of fragmentation on trees and lianas carbon  
236 stocks and also on liana abundance. First we ran each GLMM using two explanatory variables:

237 (i) fragment size and (ii) edge-interior location, plus the interaction between them. We then  
238 repeated this GLMM replacing fragment size with Fragmentation Axis 1.

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

244

245 *Does liana prevalence affect trees carbon stock?*

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

252

## 253 **Results**

254 *Are microclimatic and soil conditions controlled by the fragmentation gradient?*

255 Overall, our composite Abiotic Axis 1 was strongly predicted by fragment size (GLMM;  
256  $t=-5.350$ ,  $p<0.0001$ , Figure S4A) and edge-interior location (GLMM;  $t=6.546$ ,  $p<0.0001$ , Figure  
257 S4B). This was reflected by the changes in the specific microclimatic variables, although there  
258 was some variation in their individual responses. Air temperature was significantly higher in  
259 small fragments (GLMM;  $t=-3.06$ ,  $p=0.01$ ; Figure 1A) and near forest edges (GLMM;  $t=3.56$ ,

260  $p < 0.01$ ; Figure 1B). In contrast, air humidity showed a significant interaction between fragment  
261 size and edge-interior location (GLMM;  $t = -3.05$ ,  $p = 0.01$ ; Figure 1C), with a higher accrual of air  
262 humidity with increasing fragment size in the interior than at the edge. Wind speed showed a  
263 significant interaction with fragment size and edge-interior location (GLMM;  $t = 2.28$ ,  $p < 0.05$ ;  
264 Figure 1E), with a significant negative influence of fragments size for plots located in interiors  
265 ( $F = 8.79$ ,  $p = 0.01$ ; Figure 1E), but no effect for those located near edges ( $F = 0.2$ ,  $p = 0.66$ ; Figure  
266 1E).

267 For soil, the best model showed that edges had significantly higher Effective Cation  
268 Exchange Capacity and were thus more fertile when compared with the interior (GLMM;  
269  $t = 2.971$ ;  $p < 0.01$ ; Figure 2A). Also, there was a slightly non-significant negative effect of  
270 fragment size on Effective Cation Exchange Capacity (GLMM;  $t = -1.983$ ,  $p = 0.06$ ; Figure  
271 2B). Soils from transects located in forest edges showed higher values of Sum of Bases (GLMM;  
272  $t = 3.64$ ,  $p < 0.01$ ; Figure 3C) and lower acidity (GLMM;  $t = 2.55$ ,  $p < 0.05$ ; Figure 2D) than interiors.  
273 The best models also suggested a slight (but non-significant) influence of fragment edges on  
274 available phosphorous (GLMM;  $t = 2.033$ ,  $p = 0.06$ ; Figure 2E) and organic matter contents  
275 (GLMM;  $t = -2.02$ ,  $p = 0.07$ ; Figure 2F).

276

277 *Does fragmentation alter tree's and liana's carbon stocks?*

278 We sampled 4,140 trees and 8,236 lianas. As expected, across all transects, much more  
279 carbon was stored by trees than lianas (Table S1). On average, trees stored 97.7% ( $\pm 1.8\%$ ) of the  
280 total carbon (i.e., trees + lianas carbon stocks) in interiors and 87.1% ( $\pm 7.9\%$ ) at edges. Total  
281 carbon in interior transects ( $61.8 \pm 25.8$  Mg) was nearly three-fold that at edges ( $22.8 \pm 11.6$  Mg).

282 Considering only tree's carbon stock, there was a 69% reduction from 60.7 Mg in interiors to  
283 18.7 Mg at edges.

284 Trees and lianas responded very differently to fragmentation. Following the fragment size  
285 gradient (interior plus edge), tree carbon stocks ranged from 115.7 Mg/transect in the largest (>  
286 23,000ha) to 46.4 Mg/transect in the smallest (13 ha) fragment, representing a 60% reduction. In  
287 contrast, liana carbon stocks increased by 200%, from 1.6 Mg/transect in the largest to 4.79  
288 Mg/transect in the smallest fragment.

289 Tree carbon stocks - There was a significant interaction effect of fragment size and edge-  
290 interior location (GLMM;  $t = -4.435$ ;  $p = 0.001$ ; Figure 3A): decreasing fragment size had a  
291 significant negative effect on trees carbon stock in interiors ( $F = 17.4$ ;  $P = 0.002$ ; Figure 3A), but  
292 no significant effect at edges ( $F = 1.3$ ;  $P = 0.3$ ; Figure 3A). The best model also showed  
293 significant reductions of tree carbon stocks at edges versus interiors (GLMM;  $t = -11.6$ ;  
294  $p < 0.0001$ ; Figure 3B). Very similar results were obtained when we replaced fragment size with  
295 Fragmentation Axis 1. There was a significant interaction effect between Fragmentation Axis 1  
296 and edge-interior location (GLMM;  $t = -4.9$ ;  $p = 0.0003$ ; Figure 3C), and increasing environmental  
297 impacts had a significant negative effect on tree carbon stocks in interiors ( $F = 13.82$ ;  $P = 0.004$ ;  
298 Figure 3C), but no significant effect at edges ( $F = 0.096$ ;  $P = 0.7$ ; Figure 3C). The best model  
299 also showed significant reductions of tree carbon stocks at edges versus interiors (GLMM;  $t = -$   
300  $6.045$ ;  $p < 0.0001$ ; Figure 3D).

301 Liana carbon stocks - There was a significant interaction effect of fragment size and  
302 edge-interior location on liana carbon stocks (GLMM;  $t = -3.14$ ,  $p = 0.01$ ; Figure 3E). However, in  
303 contrast with trees, decreasing fragment size had a positive effect on liana carbon stocks in forest  
304 interiors ( $F = 6.47$ ;  $P = 0.03$ ; Figure 3E), but had a more strongly positive effect at edges

305 (F = 32.1: P = 0.0002; Figure 3E). The best models also revealed significantly higher liana  
306 carbon stocks at fragment edges than interiors (GLMM; t= 5.38; p= 0.0002; Figure 3F). Again,  
307 similar results were obtained when we replaced fragment size with Fragmentation Axis 1. There  
308 was a significant interaction effect of Fragmentation Axis 1 and edge-interior location on liana  
309 carbon stocks (GLMM; t= -2.664, p=0.014; Figure 3G), as increasing environmental impacts had  
310 a slightly non-significant positive effect in forest interiors (F = 4.1: P = 0.07; Figure 3G), but a  
311 strongly positive effect at edges (F = 16.8: P = 0.002; Figure 3G). Also, the best models showed  
312 no significant change in liana carbon stocks between edges and interior habitats (GLMM; t= 1.5;  
313 p= 0.15; Figure 3H).

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

320 Relative prevalence of trees and lianas - For carbon stocks, the best GLMM models of the  
321 ratio of lianas to trees showed higher dominance of lianas in smaller fragments (GLMM; t= -  
322 6.353, p<0.0001; Figure 3I) and at fragment edges (GLMM; t= 9.982, p<0.0001; Figure 3J).  
323 Similar relationships were found when replacing fragment size with Fragmentation Axis 1, with  
324 a higher dominance of lianas in harsher conditions (GLMM; t= -4.232, p<0.001; Figure 3L) and  
325 at fragment edges (GLMM; t=4.186, p<0.001; Figure 3M).

326 For abundance, there was a higher dominance of lianas relative to trees in smaller  
327 fragments (GLMM; t= -5.189, p<0.001; Figure 3N) and at fragment edges (GLMM; t= 18.091,

328 p<0.0001; Figure 3O). Again, similar relationships emerged when replacing fragment size with  
329 Fragmentation Axis 1, with relatively higher abundance of lianas in harsher environmental  
330 conditions (GLMM;  $t = -4.739$ ,  $p < 0.001$ ; Figure 3P) and at fragment edges (GLMM;  $t = 6.259$ ,  
331  $p < 0.0001$ ; Figure 3Q).

332

333 *Does liana prevalence affect tree carbon stocks?*

334 Although both measures of liana prevalence were negatively associated with tree carbon  
335 stocks (Table S7), liana abundance was a much stronger predictor than liana carbon stocks  
336 (model comparisons showed Delta AICc of 7). The single best model revealed a significant  
337 effect of liana abundance due to the interaction between edge-interior location on tree carbon  
338 stocks (GLMM:  $t = -4.7$ ,  $p < 0.0001$ ; Figure 4): only forest interiors had a strong association  
339 between higher liana abundance and lower tree carbon stocks ( $F = 6.4$ ;  $P = 0.03$ ; Figure 4),  
340 whereas there was no significant association at edges ( $F = 0.23$ ;  $P = 0.64$ ; Figure 4). We found  
341 no clear pattern of spatial autocorrelation in any of our model residuals (Supplementary Material  
342 2).

343

## 344 **Discussion**

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



351

352 *Abiotic drivers of trees and lianas*

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

359         Many of the abiotic variables could explain the loss of tree carbon stocks. We observed  
360 increased wind speeds in edges (Figures 2 and 4) and it is known that this can extend far (up to  
361 400 m) into forest fragments, causing biomass loss and posterior mortality due to the physical  
362 damage in tree canopies (Laurance *et al.* 1998, 2000, 2002; Magnago *et al.* 2015b). The  
363 decrease of air humidity and increase of air temperatures could also have contributed to the  
364 overall reduction in tree carbon stocks: droughts and extreme high temperatures are related with  
365 carbon reduction due to enhanced tree mortality and changed tree species composition at  
366 regional scales (Rolim *et al.* 2005; Laurance *et al.* 2006; Allen *et al.* 2010). In addition, these  
367 microclimatic changes can promote the replacement of slow growing hardwood species with fast  
368 growing softwood species, which have lower carbon storage capacity (Laurance *et al.* 2006).

369

370 *Abiotic drivers of liana dominance*

371         Liana's abundance and carbon stock was generally higher within small fragments and at  
372 edges, where the soils were more fertile and the microclimate was hotter and drier (Schnitzer &  
373 Bongers 2002; Laurance *et al.* 2014; Durán *et al.* 2015). There are four good reasons why lianas

374 are more successful than trees in these conditions. First, their flexible stems mean they are not  
375 affected by elevated wind speeds. Second, their stomatal control and deep roots mean they can  
376 survive high temperatures and low humidity whilst maintaining productivity during dry events  
377 (Chen *et al.* 2015);

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

386

### 387 *Interactions between trees and lianas*

388 Could some of the patterns we observed be driven by competition between the plant  
389 forms and the interaction with disturbance? For example, lianas can be stronger competitors with  
390 trees in more stressful and disturbed regimes due to their better-developed root system and  
391 higher root extension rate (Schnitzer & Bongers 2002, 2011; Restom & Nepstad 2004). These  
392 adaptations allow lianas to exploit soil resources, such as nutrients and deep-water (Schnitzer &  
393 Bongers 2002, 2011). Although our snapshot study cannot demonstrate causation, it does provide  
394 some insights into the likelihood of liana-tree competition and highlights some areas for new  
395 research. In particular, if lianas and trees do compete, our results indicate that this either only  
396 happens in forest interiors, or that there is a threshold level at which lianas no longer have an

397 effect (Figure 4), because the composition of trees at edges has changed to one with more  
398 defenses against lianas (e.g., fast growth in pioneer species) (van der Heijden & Phillips 2009;  
399 Magrath *et al.* 2016). Both are plausible, but the fact that trees carbon stock was consistently low  
400 in forest edges strongly suggests that microclimatic variables at edges can affect trees  
401 independently of liana dominance.

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

413 It is important to note that our snapshot study did not assess the effect of drought (Brando  
414 *et al.* 2014; Rowland *et al.* 2015), and greater insights into the relevance of competitive  
415 interactions between trees and lianas could be gleaned by undertaking experimental  
416 manipulations across gradients of soil moisture and water availability. In addition, we did not  
417 have wood density values to adjust the carbon equation of lianas. Thus, if liana wood density  
418 changes with habitat disturbance, mainly in forest edges and small fragments where lianas could

419 be softer than in interiors or larger fragments (as expected for trees; Laurance *et al.* 2006), then it  
420 is possible that lianas carbon stocks are over-estimated in edges and/or smaller fragments.

421 *Implications for forest management and conclusions*

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

438 Liana removal could even jeopardise recovery of forest structure and functionality in the  
439 likely scenario that lianas themselves help to buffer forest interiors. Here, abiotic changes would  
440 continue to depress trees carbon stock after lianas have been cleared by management, and  
441 clearance could even worsen conditions. For example, Rolim *et al.* (2005) showed that El Niño

442 drought negatively affects the above-ground biomass of trees species even in forest interiors of a  
443 large Lowland Atlantic Forest fragment. Therefore, we are not advocating that lianas dominance  
444 cannot cause impacts on trees, but similar studies should be conducted in more tropical forest  
445 regions before making general conclusions about how to manage forest to enhance carbon stocks  
446 near edges. Our study also shows that, for the Brazilian Atlantic Forest, fragmentation-induced  
447 changes of several microclimatic and soil variables can only be reduced by increasing fragment  
448 size and reducing edge-interior ratios. This would necessitate a major program of forest  
449 restoration (Lamb & Parrotta 2005).

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

460

#### 461 **Acknowledgements**

462 We thank Natalia Norden and two anonymous reviewers for comments that greatly improved the  
463 article. We also thank Reserva Natural Vale, Fibria Celulose S.A., Marcos Daniel Institute, and  
464 Pro-Tapir for logistical support, and Reserva Biológica de Sooretama for permission to conduct

465 our research. CNPq – the Brazilian Agency for Science and Technology (grant no. 477780/2009-  
466 1), provided funding. LFSM was supported by Brazilian Studentship and Doctorate Sandwich  
467 Program grants from the Brazilian Federal Agency for Support and Evaluation of Graduate  
468 Education (CAPES) with two grants, Brazilian Studentship and Doctorate Sandwich Program.  
469 A.M. was supported by a Basque Government Postdoctoral Fellowship. JB was supported by  
470 EU H2020 MSCA RISE ODYSSEA (Grant agreement no. 691053). LFSM is currently  
471 supported by a PNPB program of CAPES. The authors declare no conflict of interest.

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669

670 **Supplementary Materials include:**

671 Text S1 - Conservation value of the study region.

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

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

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

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

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

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

679 Table S1 - Identification and variable values of sampled fragments.

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

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

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

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

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

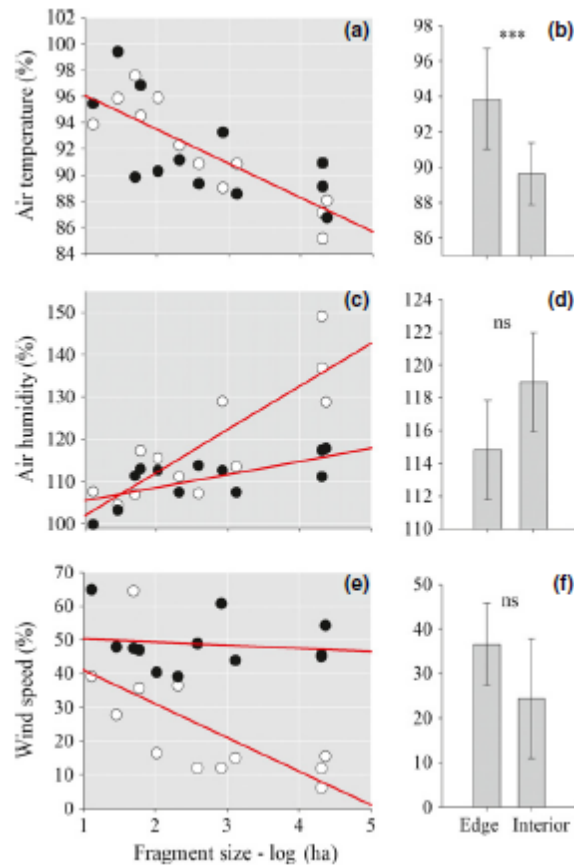
691 Table S7 - Model selection of the Generalized Linear Mixed Models for tree carbon stocks in  
692 relation to lianas abundances, lianas carbon stocks and edge-interior location.

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696 **Figure legends (high-resolution Figures uploaded as separate files)**

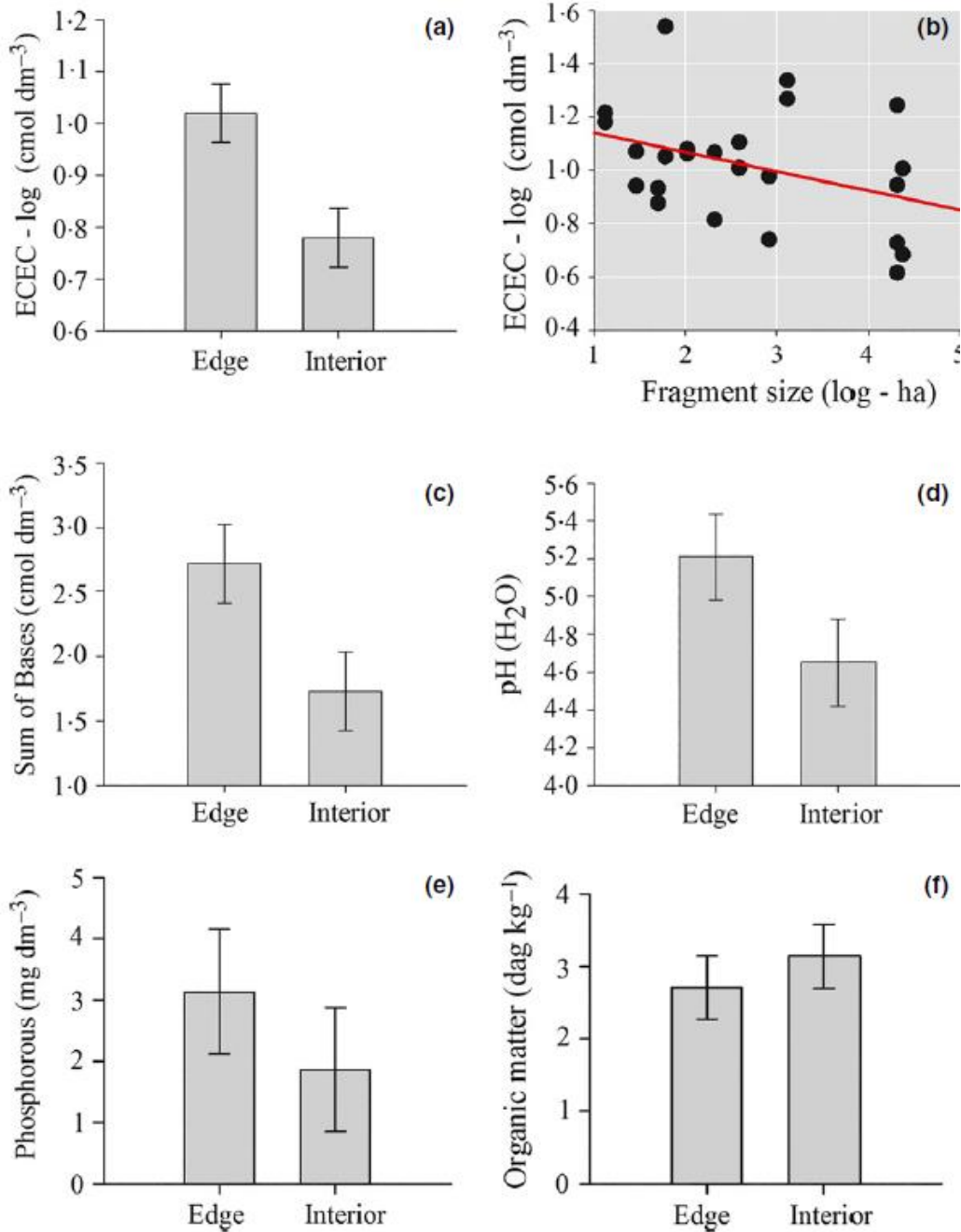


697

698 Figure 1. Graphs of best models for the effects of fragments size and edge-interior location on  
699 microclimatic variables. (A-B) Effects of fragment size and habitats on air temperature; (C-D)  
700 Effects of fragment size and habitat on air humidity; (E-F) Effects of fragment size and habitat  
701 on wind speed. Black circles = Edge; White circles = Interior. Circles represent values obtained  
702 after the summation of raw residuals to the expected values for each variable, being assumed  
703 average values for other covariates. Errors bars represent the 95% of confidence intervals.

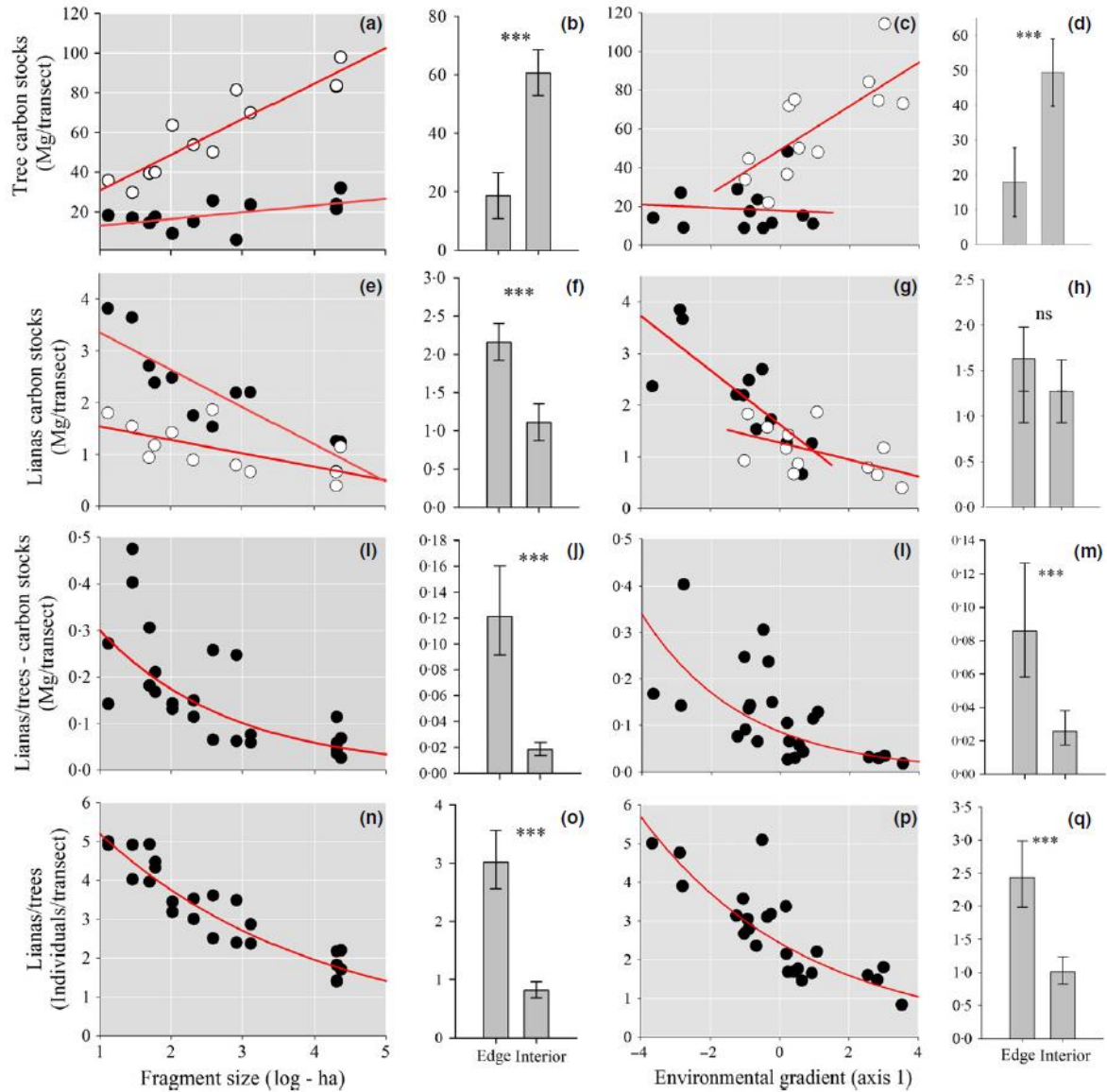
704 \*\*\*= $p < 0.001$ ; ns=No significant results.





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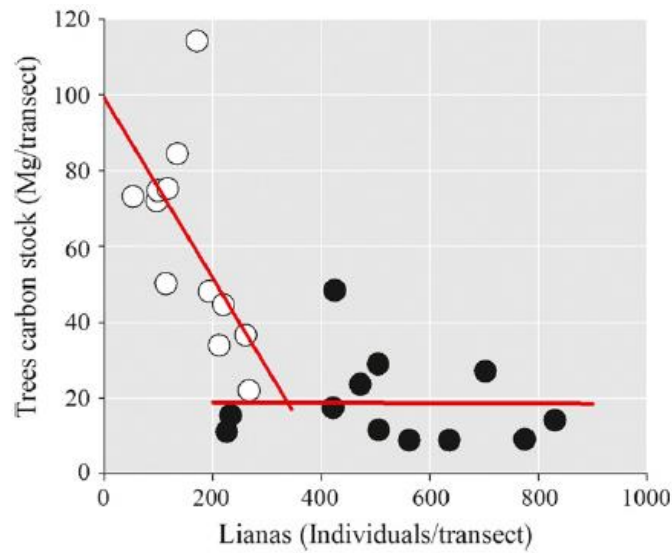
706 Figure 2. Graphs of best models for the effects of fragments size and edge-interior location on  
 707 soil attributes. (A) Edge-interior and (B) fragment size effects on soil fertility via Effective  
 708 Cation Exchange Capacity (ECEC); (C) edge-interior effect on soil fertility via Sum of Bases;  
 709 (D) edge-interior effect on soil acidity - pH in H<sub>2</sub>O; (E) edge-interior effect on phosphorous; (F)  
 710 edge-interior effect on organic matter. Errors bars represent the 95% of confidence intervals.  
 711 Circles represent values obtained after the summation of raw residuals with the expected values  
 712 for each variable, assuming average values for other covariates.



713

714 Figure 3. Graphs of best models for the effects of fragments size (A, E, I, N), fragmentation  
 715 abiotic environmental gradients (Fragmentation Axis 1; C, G, L, P) and edge-interior location (B,  
 716 D, F, H, J, M, O, Q) on trees carbon stocks (A, B, C, D), lianas carbon stocks (E, F, G, H), ratio  
 717 of lianas to trees carbon stocks (I, J, L, M), and ratio of lianas to trees individuals (N, O, P, Q).  
 718 Circles represent values obtained after the summation of raw residuals with the expected values  
 719 for each variable, assuming average values for other covariates. Black and white circles represent  
 720 edge and interior location, respectively, when there is a significant effect of the interaction term  
 721 between fragment size and edge-interior location; when only black circles are shown, there is no  
 722 significant interaction effect. Errors bars represent the 95% of confidence intervals.

723 \*\*\*= $p < 0.001$ ; ns=No significant results. Negative values for Fragmentation Axis 1 represent  
724 more stressful and disturbed conditions, positive values more benign conditions (see Fig. S3).  
725



726  
727 Figure 4. Graph of best model of trees carbon stocks in relation to lianas individuals. Circles  
728 represent values obtained after the summation of raw residuals with the expected values for each  
729 variable. Black and white circles represent edge and interior location, respectively, and thus the  
730 significant effect of the interaction term between fragment size and edge-interior location.  
731