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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 10×10 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

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

53

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 CO_2 emissions, which is second only to the burning of fossil fuels (van der Werf et al. 2009). In countries such as Brazil, CO_2 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).

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_2, 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 ($18^{\circ}54'$–$19^{\circ}15'$S

115   and $39^{\circ}54$–$40^{\circ}15'$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 ($\pm$ 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 $\geq$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    $\geq$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 ≥1.6 cm diameter at

148   10 cm above ground (Diameter at Soil Height [DSH]). We only sampled individuals with ≥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         $$ABGt = \rho. \exp(-1.499 + 2.148 \ln(DBH) + 0.207(\ln(DBH))^2 - 0.0281(\ln(DBH))^3)$$

156

157   where ρ = wood density (g/cm^3).

158

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

160   equation:

161         $$AGBl = \exp(-1.484 + 2.657 \ln(DSH))$$

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 (g/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_2O (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 "MᴜMIɴ" 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

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:

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% (±1.8%) of the

280 total carbon (i.e., trees + lianas carbon stocks) in interiors and 87.1% (±7.9%) at edges. Total

281 carbon in interior transects (61.8 ±25.8 Mg) was nearly three-fold that at edges (22.8 ±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

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

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 adaptions 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   Magrach 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

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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
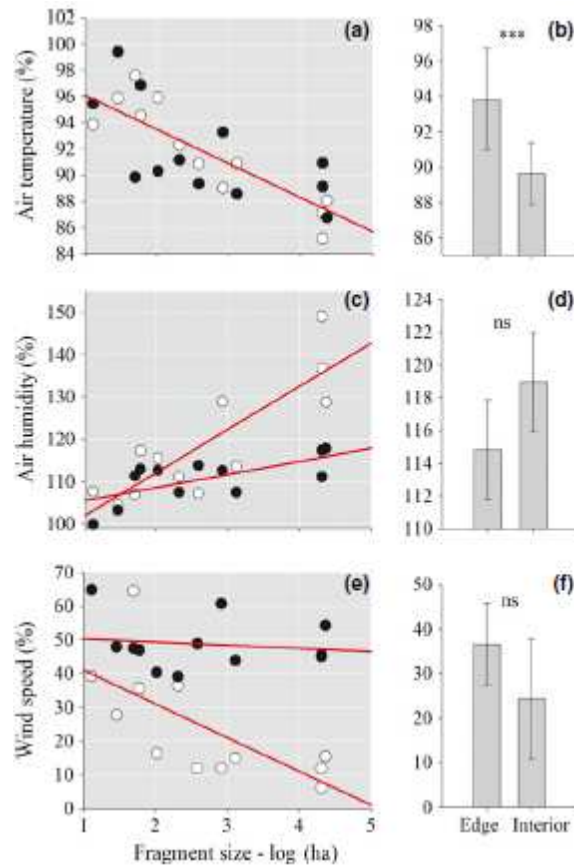692 relation to lianas abundances, lianas carbon stocks and edge-interior location.

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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.
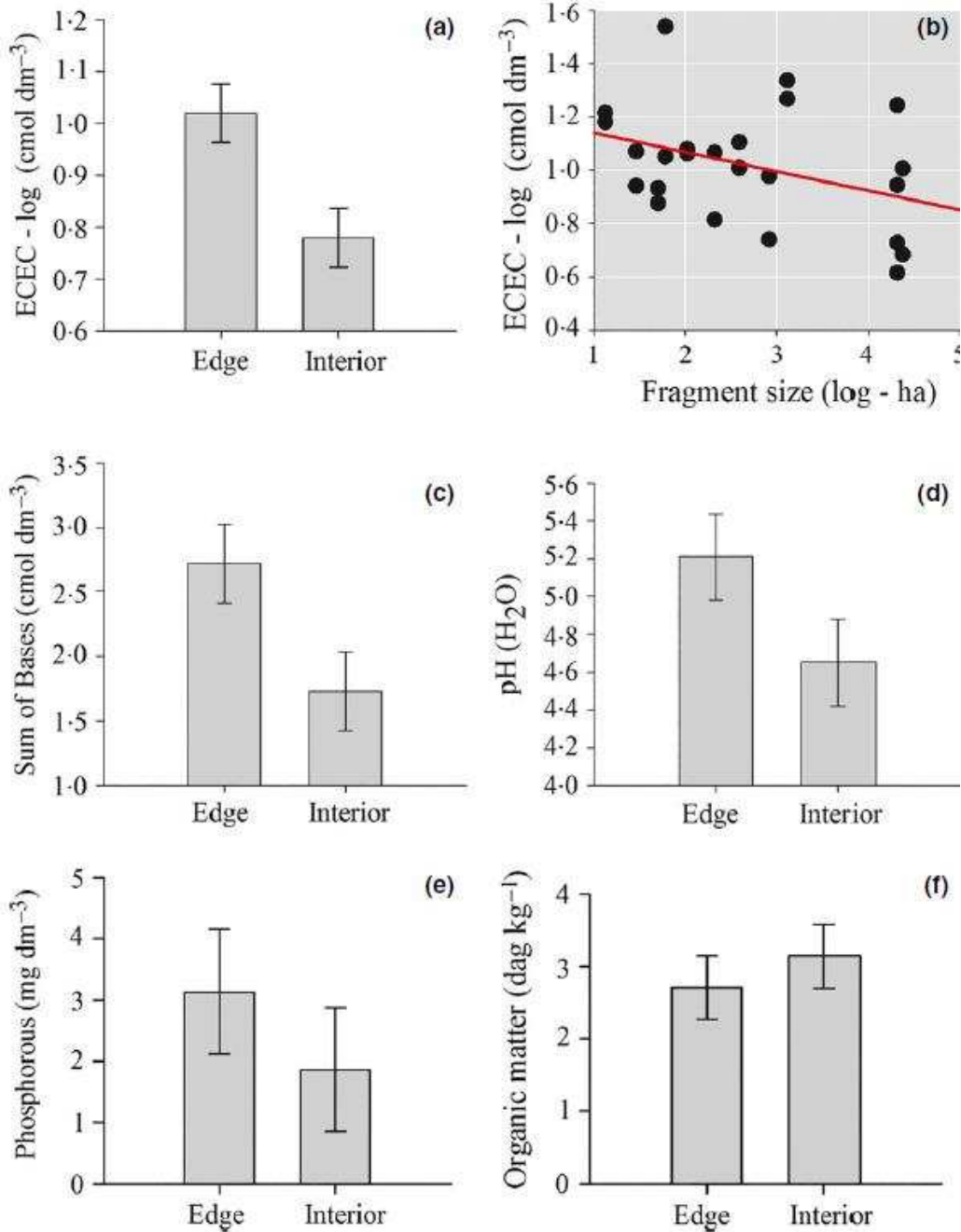
705

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_2O; (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
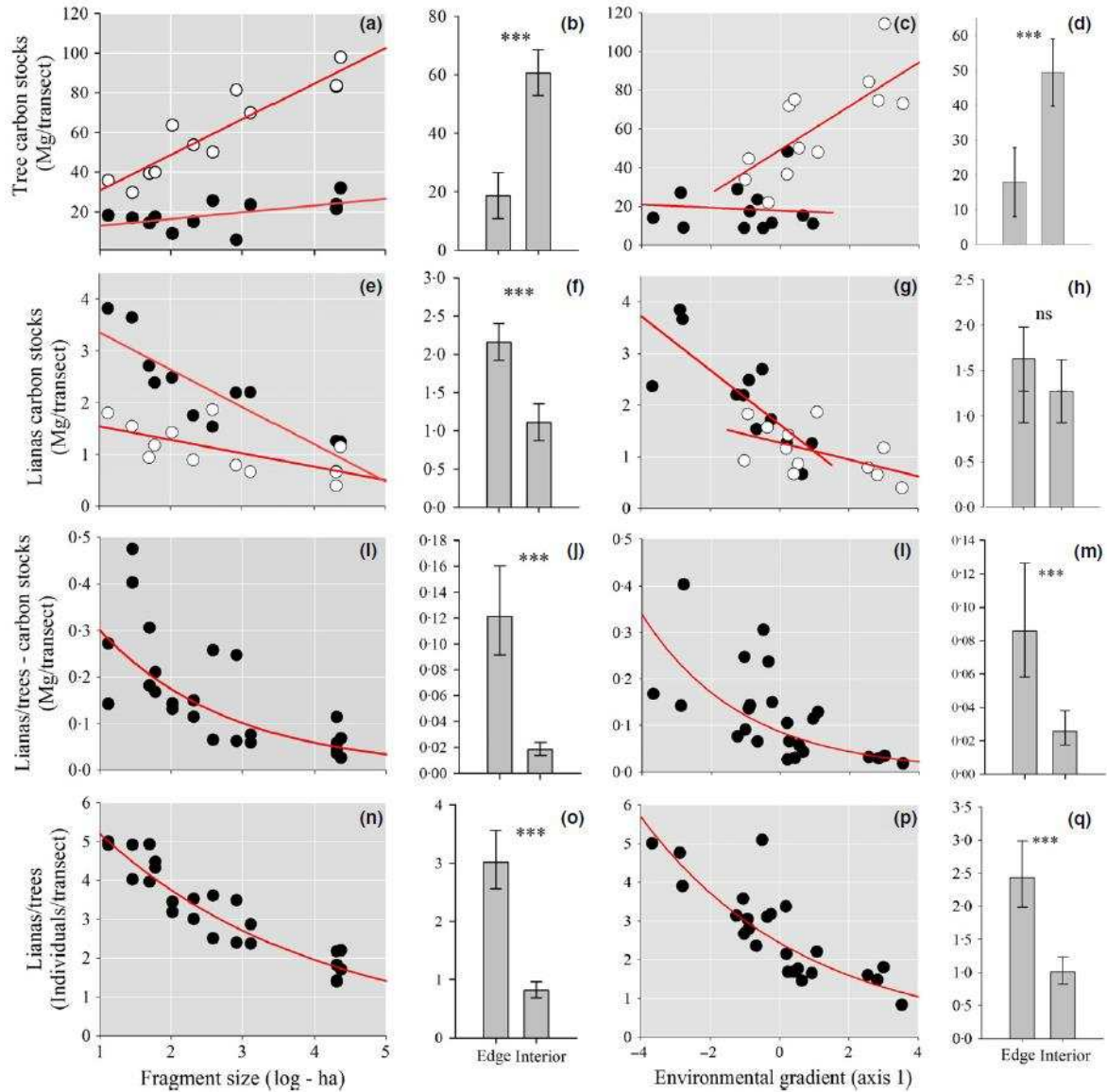
Figure 3. Graphs of best models for the effects of fragments size (A, E, I, N), fragmentation

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

724   more stressful and disturbed conditions, positive values more benign conditions (see Fig. S3).

725
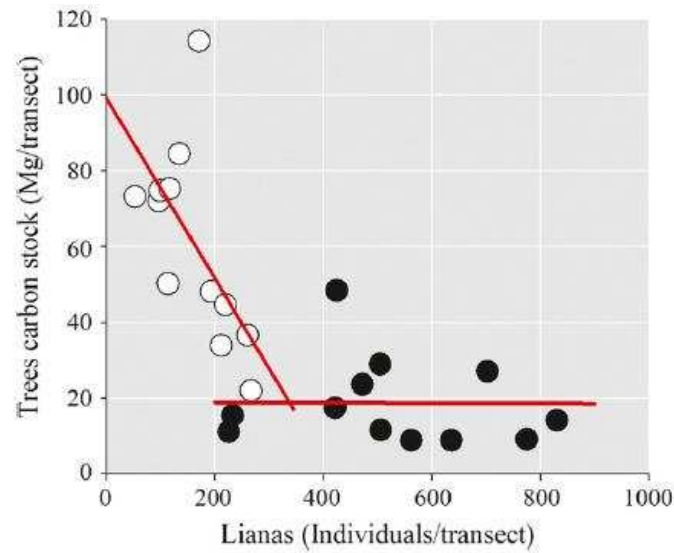
726
727   Figure 4. Graph of best model of trees carbon stocks in relation to lianas individuals. Circles

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.

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