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3 **Limited influence from edges and topography on vegetation structure and**
4 **diversity in Atlantic Forest**

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17

18 **Abstract**

19 Although Atlantic Forest is diverse and heavily fragmented, little is known about the impact of

20 edges created from fragmentation on forest structure and plant diversity. Our investigation of

21 vegetation at agricultural edges aimed to determine edge width, to compare effects of edge

22 influence and topography and to assess patterns of diversity. We collected data on forest

23 structure, plant groups, plant families and vertical vegetation structure in 2 x 2 m contiguous

24 plots along 250 m transects across the edges of 24 fragments approx. 70 km west of São Paulo,
25 Brazil. We used randomization tests to estimate the magnitude and distance of edge influence,
26 generalized linear mixed models to assess the effect of topography, and wavelet analysis to
27 evaluate spatial patterns. Although there was evidence of edge degradation (lower diversity and
28 cover of most plant groups compared to interior forest) and edge sealing (abrupt changes at the
29 edge particularly for leafy vertical diversity), edge influence did not extend very far with a
30 distance of edge influence or less than 20 m for most variables. Less extensive edge influence
31 compared to other tropical forests was not explained by topography (slope) but could be due to
32 more extensive fragmentation and land use history. The use of multiple approaches to studying
33 forest edges provided complementary information to improve our understanding of the structure
34 of anthropogenic edges in Atlantic Forest. Signs of edge degradation suggest that edge influence
35 should be considered in conservation planning even though edges are narrow.

36

37 **Key words** Edge influence, Forest structure, Spatial pattern, Topographic influence, Wavelet
38 analysis

39

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42 **Introduction**

43 Effects of forest fragmentation on vegetation at edges of forest remnants have been studied in
44 ecosystems worldwide. At created forest edges, greater temperature extremes, increased light
45 exposure, lower humidity and higher wind speeds than forest interiors influence vegetation
46 through structural damage, production of deadwood and increased growth or regeneration (Chen
47 et al. 1995; Laurance et al. 1998a; Didham and Lawton 1999; Harper et al. 2005). Despite
48 numerous studies on vegetation at edges, site-specific results (Franklin et al. 2021) necessitate
49 further investigation to understand impacts of fragmentation in a particular region. One
50 characteristic that varies substantially is the distance of edge influence (DEI, the extent to which
51 a difference in vegetation can be detected compared to interior forest), which is particularly
52 important for conservation as it can be used for mapping and planning. Although many studies
53 have reported low estimates of DEI of 20 m or less for plant variables (Harper et al. 2005;
54 Franklin et al. 2021), larger estimates of up to 100 and even 300 m have been reported from the
55 Brazilian Amazon forest (Laurance et al. 1998a).

56 Variable results from edge studies suggest that other factors affect edge influence such as
57 topography, which may overshadow or interact with edge influence on vegetation (Chapman and
58 McEwan 2013; Lippok et al. 2014; Jucker et al. 2018). Topography alters forest characteristics;
59 small differences in relative elevation can affect forest structure, composition and diversity
60 through changes in hydrology and soil characteristics (Allié et al. 2015; Jucker et al. 2018).
61 Valleys have taller canopies, more trees, greater basal area, and greater tree species and
62 structural diversity compared to ridges and steep slopes because of greater productivity (Homeier
63 et al. 2009; Detto et al. 2013; Fortunel et al. 2018; Jucker et al. 2018). Edge influence on

64 vegetation (the difference between the edge and interior) was found to be more pronounced on
65 slopes than hill tops (Guerra et al. 2013).

66 Structural diversity is a useful metric to compare edge studies as it has been shown to be
67 a better predictor than species diversity when related to ecosystem functions such as productivity
68 (Proulx and Parrott 2008). Vertical foliage distribution and horizontal structural complexity are
69 important for bird habitat (Zellweger et al. 2013). Conserving a high level of diverse plant types
70 and structural elements in forest remnants creates a broad range of habitats that host wildlife,
71 plants and other species (Farah et al. 2017; Silveira dos Santos et al. 2022). However, structural
72 diversity has not been comprehensively evaluated or related specifically to edge influence.

73 High habitat diversity is particularly apparent in Atlantic Forest, a biodiversity hotspot
74 that surpasses most of the Amazon rainforest in plant species diversity per unit area (Myers et al.
75 2000; Forzza et al. 2012; Joly et al. 2014; Janisova et al. 2016). However, due to urban
76 development, cattle ranching and plantations, only 16% of the original forest remains (Riberio et
77 al. 2009). Understanding the impact of edge influence on structural diversity in Atlantic Forest is
78 important for developing management, conservation, and restoration strategies. Our objectives
79 were (i) to determine the DEI on vegetation in Atlantic Forest, (ii) to compare the effects of edge
80 influence vs. topography on vegetation structure, (iii) to determine whether the effect of slope
81 varies depending on distance from the edge and (iv) to assess patterns of different measures of
82 diversity (structural, taxonomic) across forest edges. We assessed responses of vegetation
83 structure including structural diversity and abundance of different plant groups. Despite high
84 levels of diversity and impacts of fragmentation, we know of no studies that have quantified DEI
85 on vegetation in the Atlantic Forest. We hypothesized that DEI would be extensive as in other
86 tropical forests, but might be moderated by topography.

87

88

89 **Methods**

90 Study area

91 We conducted our study in the southeastern part of the Atlantic Forest surrounding the
92 Cantariera-Mantiqueira corridor, approximately 70 km from the city of São Paulo (Fig. 1). Our
93 study area consists of a fragmented landscape of primary and secondary forest surrounded by
94 pastureland, agriculture, forestry (i.e., Eucalyptus plantations) and rural and urban settlements.
95 Seasonal forest is in different succession stages due to fire history. The climate is humid
96 subtropical with hot (25°C to 35°C) humid summers and milder winters (10°C to 20°C).
97 Elevation varies between 700 and 1700 m above sea level.

98

99 Data collection

100 Two datasets were collected in July-August (winter) and October-December (spring) in
101 2015; each one sampled 12 forest edges for a total of 24 edges. The non-forest side of the edge
102 consisted of livestock pastures with cattle ranching; most edges were fenced.

103 At each edge, we sampled vegetation in contiguous 2 x 2 m plots along a 250-m transect
104 perpendicular to the edge extending 50 m into the pasture and 200 m into the forest for a total of
105 125 plots for each of the 24 transects. We defined the edge as the limit of continuous forest
106 canopy. In each plot, we estimated cover of different plant groups including trees, saplings,
107 shrubs (July dataset only), tree ferns/palms, ferns, lianas, vines, snags, graminoids, epiphytes,
108 moss and litter. Cover categories were <10%, 10-20%, 20-50%, 50-80% and >80% (July
109 dataset), and <10%, 10-30%, 30-60%, 60-80% and >80% (October dataset); mid-points were

110 used for analysis. For the October dataset, we sampled the number of trees by diameter classes
111 (<3 cm, 3-10 cm, 10-30 cm and >30 cm diameter at breast height) and estimated cover for each
112 plant family. We assessed vertical structure by visualizing a column above each plot divided into
113 2 x 2 x 2 m cubes and estimated the abundance (July dataset) or determined the presence /
114 absence (October dataset) of woody (lianas, branches, tree trunks) and leafy (leaves, fleshy
115 vines) material within each cube.

116 Every 8 meters, we recorded altitude, elevation and coordinates using GPS, and the
117 change in relative elevation with a clinometer. We estimated canopy cover every 8 m for the
118 October dataset by taking a photo of the canopy over the plot at 1.4 m using an iPhone camera
119 and visually estimating the percentage of canopy cover.

120

121 Analysis

122 We calculated functional diversity in each plot using the Shannon diversity index: $H' = -$
123 $\sum [p_i * \ln(p_i)]$ where p_i was the proportion of each of plant group. Functional richness was the
124 number of plant groups in each plot. The Shannon index was also used to calculate the diversity
125 of plant families. For leafy and woody vertical diversity of branches and leaves, we considered
126 each occupied 2 m cube as a pseudospecies such that p_i was the proportion of leafy or woody
127 material within each cube. Leafy and woody vertical richness was the number of cubes occupied
128 by leafy or woody material for each plot. Canopy height was determined as the highest 2 m cube
129 occupied by leafy or woody material.

130 We estimated the magnitude of edge influence (MEI) and DEI for functional, family,
131 leafy and woody richness and diversity, individual plant groups, individual plant families
132 (frequency >10%) and density of trees in diameter classes using the randomization test of edge

133 influence (RTEI) Add-In in Microsoft Excel (Harper and Macdonald 2011). The MEI measures
134 the strength of edge influence: $MEI = (x_d - x_i)/(x_d + x_i)$ where x_d = average of the variable x at
135 distance d from the edge and x_i = average of the variable x in interior forest (Harper et al. 2005).
136 We considered 150 to 200 m (26 reference distances) to be interior forest.

137 DEI measures how far from the edge a response variable significantly differs from
138 interior forest by testing the significance of values for each distance using randomization tests.
139 We used RTEI with blocking using the following steps (Harper and Macdonald 2011). (1) For
140 each transect, we randomly selected an ‘edge’ value from the data set consisting of the value at a
141 given distance from the edge and all interior forest values. (2) Randomized differences were
142 calculated between the average of the randomly selected ‘edge’ values for all transects and the
143 average of all the remaining ‘interior’ values. (3) These first two steps were repeated for a total
144 of 5000 permutations to create a distribution of randomized differences. (4) The percentile of the
145 observed difference between the edge and the interior within the distribution of the randomized
146 differences was compared to the p-value, for which we used $p = 0.05$ for a two-tailed test. DEI
147 was then estimated as the set of three or more consecutive distances (or segments of three or
148 distances separated by one or two distances) over which the average response was significant.

149 To assess the influence of distance from edge, slope, and season (wet/dry for the
150 July/October datasets) on structural diversity and the cover of plant groups, we performed spatial
151 generalized linear mixed models (GLMMs). GLMMs are flexible in accounting for spatial
152 autocorrelation as they fit overall fixed effects with linear predictors containing random effects
153 and spatially autocorrelated within-group errors (Dormann et al. 2007). Slope, the difference in
154 elevation across each 8 m segment, was transformed to squared slope to account for its quadratic
155 relationship with the response variables. We used the `glmmPQL` function (Dormann et al. 2007)

156 from the packages MASS (Venables and Ripley 2002) and nlme (Pinheiro et al. 2015) in R 3.2.2.
157 (R Core Team 2015). We used a Gaussian distribution for structural diversity and a negative
158 binomial distribution for the cover of plant groups. We only included significant interactions
159 between distance from edge and squared slope. We applied the models for the entire transect and
160 for the first 25 m from the edge to detect finer scale changes.

161 We used wavelet analysis in PASSAGE 2.0 (Rosenberg and Anderson 2011) to assess
162 patterns of functional, family, leafy vertical and woody vertical richness across forest edges, and
163 patterns of woody and leafy richness and diversity for the July dataset. We used the Haar wavelet
164 template and wavelet position variance (with 10% maximum scale) to identify transitions in
165 vegetation structure along transects (Dale and Mah 1998; Kembel and Dale 2006). We assessed
166 the significance of abrupt transitions using randomization tests of position variance with 999
167 permutations and a 95% confidence interval. We considered abrupt changes as two or more
168 distances with significant wavelet variance (excluding single distances).

169

170 **Results**

171 Although some aspects of vegetation structure were significantly affected by the forest
172 edge, edge influence did not extend very far into the forest. Canopy cover and height increased
173 from low values in the non-forested area to around 75% cover and 11 m in height within the
174 forest (Fig. 2). Four different measures of richness followed the same trend (Fig. 3) and patterns
175 of diversity were similar (not shown). The richness of plant groups and families increased
176 abruptly at the edge from about one or two per plot, respectively, in the non-forested area to five
177 per plot within the forest. Patterns of vertical richness (both woody and leafy material) appeared

178 more gradual from the edge to interior forest, increasing from one layer of leafy material and
179 virtually no woody material to about five layers of each in the forest.

180 The MEI of 24 out of 28 variables was negative with lower values at the edge compared
181 to interior forest, with the exceptions of graminoids, moss, Asteraceae and Poaceae, which had
182 greater values at the edge (Table 1). The DEI ranged from being limited to the non-forested area
183 (including only negative distances such that values at the edge were not significantly different
184 from interior forest) to distances generally up to 20 m; a few exceptions included maximum
185 DEIs of 88, 72 and 58 m for canopy height, and woody and leafy vertical richness, respectively.
186 Edge influence on richness and diversity of plant groups extended 10 m into the forest. Although
187 negative edge influence on vertical diversity (woody and leafy) extended 12-20 m into the forest,
188 lower vertical richness compared to interior forest was found up to approx. 60 m from the edge.
189 Richness and diversity of families had lower absolute values of MEI of -0.20 to -0.28 and DEI of
190 0 m compared to other measures of diversity. Edge influence was greatest for medium sized 3-10
191 cm diameter trees compared to other size categories; the density of the largest trees was not
192 significantly different at the edge compared to interior forest. The MEI and DEI for individual
193 structural components varied; notably vine cover was significantly lower at the edge but
194 significantly higher 34-38 m from the edge compared to interior forest. Edge influence on
195 individual families was generally limited to the non-forest area (values at the edge were not
196 significantly different from interior forest); however, DEI extended to 8 m for Rubiaceae and the
197 cover of Asteraceae was significantly greater 14-20 m from the edge compared to interior forest.

198 In terms of relationships with topography, functional diversity significantly increased
199 with distance from edge across for both sets of distances (25, 200 m) but there was no significant
200 correlation with slope (Table 2). Diversity during the wet season was about 20% less than in the

201 dry season, regardless of distance from edge or slope (regression coefficient of -0.19). Distance
202 affected most structural groups, which usually increased in cover with distance from edge. Slope
203 only had an effect on tree ferns / palms and snags; the cover of both significantly decreased with
204 slope at the 200 m scale with regression coefficients of -0.015 and -0.010, respectively. Trees,
205 vines, snags, epiphytes and litter had significantly greater cover in the wet season. There was a
206 significant interaction between distance and slope for ferns and epiphytes at the 25 m scale
207 (regression coefficients = 0.02 and 0.036 for ferns and epiphytes, respectively); the influence of
208 distance on fern and epiphyte cover was significantly greater on more abrupt slopes and there
209 was less influence of slope on fern and epiphyte cover at greater distances from the edge.

210 Results of the wavelet analysis showed more abrupt changes in richness within a few
211 metres of the forest edge, but the proportion of transects with this pattern depended on the type
212 of richness (Fig. 4). About a third of the transects had abrupt transitions in the richness of plant
213 groups, families and layers of woody material at or near the forest edge compared to only a fifth
214 of transects with abrupt transitions in the number of layers of leafy material. There were more
215 abrupt changes in the number of layers of woody and leafy material throughout the transects, but
216 very few for functional or family richness. We observed an interesting difference between woody
217 and leafy material richness vs. diversity (Fig. 5). Although up to 40 to 60% of transects had
218 abrupt transitions at the edge for diversity, fewer than 20% of transects had an abrupt transition
219 in richness at the edge.

220

221 **Discussion**

222 Although edge influence on structural and taxonomic diversity in Atlantic Forest was not
223 very extensive, forest edges had a distinct structure characterized by low canopy cover and

224 height, low density of all sizes of trees, and greater abundance of graminoids. Lower canopy
225 cover and height at the edge than the interior was probably due to strong winds and tree mortality
226 common at forest edges (Oosterhoorn and Kappelle 2000) including at tropical pasture edges
227 (Laurance et al. 1998a). Other studies on agricultural edges in tropical forests also reported low
228 canopy tree abundance (e.g., Kapos et al. 1997; Laurance et al. 1997; Viana et al. 1997;
229 Williams-Linera et al. 1998; Oosterhoorn and Kappelle 2000) and shorter tree height (Camargo
230 and Kapos 1995). A synthesis by Franklin et al. (2021) found that most studies of
231 anthropogenically created edges found lower tree abundance but higher abundance of snags and
232 tree regeneration; edge responses for graminoids and forbs were mixed. At our agricultural
233 edges, graminoids may have spread to the forest edge and out-competed regenerating trees
234 leading to lower rather than higher cover and density of saplings and trees. Other studies of
235 tropical agricultural edges found lower recruitment or understorey tree density (Turton et al.
236 1997; Viana et al. 1997; Benitez-Malvido 1998; Oosterhoorn and Kappelle 2000). Although the
237 edges we studied were maintained, they had not developed a side canopy of greater vegetation
238 growth typical of other edges (e.g., Matlack 1993). Often anthropogenic edges exhibit edge
239 sealing, whereby dense vegetation develops at sharp edges maintained by human activity (Harper
240 et al. 2005). Instead, our results indicate that these are degraded forest edges dominated by
241 graminoids with lower cover of most vegetation.

242 Negative edge influence (lower values at the edge) for all indices of diversity contrasts
243 with most research findings of greater plant species richness and diversity at anthropogenic
244 edges (Franklin et al. 2021). However, other tropical edge studies have found lower richness or
245 diversity (e.g., Olupot 2009; Mendonca et al. 2015) and a recent global review found that lower
246 species richness is common at tropical edges (Willmer et al. 2022). In tropical forests, fewer

247 families and plant groups are adapted to open canopied conditions found at the edge with
248 increased light and wind; this is reflected in our results as more families and plant groups had
249 negative rather than positive MEI. Lower woody and leafy vertical diversity can be explained by
250 a shorter canopy at the edge that narrows the range from the ground for leafy and woody
251 structure stratification (Marques et al. 2015; Dial et al. 2011). The shorter DEI of woody
252 compared to leafy structures may show that edge effects are more pronounced and intense on
253 regenerative leafy vegetation rather than slow growing woody material. Weaker MEI and longer
254 DEI evident for vertical diversity and especially richness may be evidence of edge expansion
255 (Harper et al. 2005). However, most other types of diversity exhibited a steeper gradient of
256 higher values at the edge and short DEI, which is characteristic of edge sealing (Harper et al.
257 2005). There may be a lag before edge degradation affects family and functional diversity or
258 these diversity measures may be more resistant to edge influence.

259 Edge characteristics of lower structural and taxonomic diversity may be signs of
260 degradation of maintained forest edges in Atlantic Forest, but they did not extend very far.
261 Overall, edge influence on vegetation limited to 20 m or less was narrow compared to other
262 tropical forests. Franklin et al. (2021) found that estimates of DEI for anthropogenic edges were
263 greater in tropical forests compared to boreal and temperate forests but varied considerably from
264 0 to 10 m in Mexico, Panama and the Amazon (Williams-Linera et al. 1990, 1998; Sizer and
265 Tanner 1999) to 100 to 210 m in Africa and the Amazon (Young et al. 1995; Laurance et al.
266 1998a, 1998b). Our results suggest that edge influence does not extend as far into Atlantic Forest
267 fragments as compared to other tropical forests, but with such disparate results other factors are
268 likely involved.

269 Because edge influence is reported to be much more extensive in the relatively flat
270 lowland Amazon tropical forests, we considered whether topography might alleviate edge
271 influence in the hilly remnants of Atlantic Forest. In response to our second objective, we found
272 that distance from edge had more of an effect on vegetation structure than slope, which only had
273 a significant effect on the cover of tree ferns / palms and snags. We expected more of a slope
274 effect since topographical characteristics can affect the spatial distribution of vegetation and alter
275 canopy structure and forest dynamics (Oliveria-Filho et al. 1998; Jucker et al. 2018). Steeper
276 slopes usually have more canopy gaps (Ediriweera et al. 2008) and greater structural complexity
277 (Jucker et al. 2018) because of greater exposure to wind, fog, and solar radiation (Werner et al.
278 2012), limiting nutrients and water availability (Werner and Homeier 2015; Jucker et al. 2018),
279 and variable light distribution (Getzin and Wiegand 2007). However, Muscarella et al. (2020)
280 found that topographic heterogeneity only weakly affected tropical forest species and functional
281 diversity. Snag cover was the only variable in our study affected by slope and not by edge
282 influence; this suggests that tree mortality is due to factors other than greater wind at edges or
283 that wind patterns may be more impacted by topography than edge creation.

284 The lack of interaction between slope and distance from edge for most variables means
285 that in response to our third objective, edge influence did not vary with slope as we expected
286 (Oliveira-Filho et al. 1998; Guerra et al. 2013). Edge influence on vegetation structure has been
287 found to be more pronounced on slopes than hill tops in the Atlantic Forest, but topographic
288 effects did not override edge influence (Guerra et al. 2013). Both Pereira et al. (2007) and Guerra
289 et al. (2013) contend that topography must be considered as a potential modulating factor to
290 understand the effects of fragmentation in the complex Atlantic Forest mountainous landscape.
291 However, in our study, slope did not seem to impact edge influence and had less of an impact

292 than distance from edge or season. The exception was less edge influence on steeper slopes for
293 ferns and epiphytes, which was opposite to the interaction found by Guerra et al. (2013).

294 Therefore, other factors are likely responsible for less extensive edge influence in
295 Atlantic Forest including topographic position, proximity to the coast, secondary disturbance
296 within the forest and edge maintenance. Although we measured slope we did not quantify
297 topographic position such as whether edges occurred on hill tops or valley bottoms. Topographic
298 position could have more of an impact on vegetation structure than edge influence as organic
299 matter, nutrients and seeds move downslope creating a gradient in vegetation that might mask
300 the edge to interior forest gradient. In valleys, greater productivity and turnover result in taller
301 trees, more gaps, vertical stratification and higher tree species diversity (Werner and Homeier
302 2015; Fortunel et al. 2018; Homeier et al. 2010; Detto et al. 2013; Jucker et al. 2018).

303 Fragmentation may have created edge-like conditions throughout the Atlantic Forest, and
304 impacted the forests within vegetation remnants (Ribeiro et al. 2009; Farah et al. 2017). In these
305 heavily fragmented landscapes, the surrounding anthropogenic matrix shapes the fauna and flora
306 responses within forest remnants, such as has been observed in birds (Barros et al. 2019), dung
307 beetles (Martello et al. 2016), bees and wasps (Medeiros et al. 2021), ants (Martello et al. 2022)
308 and seed predation (Mendes et al. 2016) within Atlantic Forest. Land use history can also affect
309 processes such as tree recruitment and growth in fragments of Atlantic Forest (Torres et al.
310 2023). These factors likely create widespread variability in vegetation structure and composition
311 within interior forest that overshadows variability due to edge influence.

312 Less extensive edge influence in these forests is also apparent from our results of abrupt
313 changes in diversity within ~ 5 m of the edge, revealing a pattern of a steep gradient at the edge
314 that does not extend further into the forest. Additional abrupt transitions throughout individual

315 transects also reveal heterogeneity throughout the forest remnants. Inherent heterogeneity in
316 structural and transitional diversity may contribute to shorter DEI that is measured within the
317 context of the variation in interior forest. Our results suggest that abrupt changes in diversity can
318 be detected at maintained agricultural edges, whereas there was little to no evidence of abrupt
319 changes in vegetation due to fine scale heterogeneity in vegetation structure at natural inherent
320 wetland edges (Brownstein et al. 2013; Harper et al. 2021) and insect outbreak edges maintained
321 by moose browsing (Franklin and Harper 2016).

322 Wavelet analysis allowed us to differentiate edge influence on vegetation characteristics
323 to reveal different edge structure compared to interior forest. Structure variables (functional
324 richness, woody material) had more significant changes at the edge compared to plant families
325 and leafy material. Therefore, it appears that there is a more abrupt transition in woody structure
326 at the forest edge compared to a more gradual gradient in taxonomic diversity and leafy
327 structure. This is compatible with the hypothesis that secondary responses (species composition,
328 leafy material) extend further into the forest than primary responses (structure) (Harper et al.
329 2005). We note that our DEI results do not corroborate this conclusion (e.g., for trees), which
330 suggests that spatial pattern analysis provides additional insight into the effects of edge
331 influence. Another interesting result is that an abrupt transition at the edge was notable only for
332 vertical diversity but not for richness. Changes in richness were more gradual from the edge to
333 the interior, which matches the gradual change in canopy height. Along the same gradient, the
334 amount of leafy and woody material must have filled in the layers at the edge, thus creating
335 somewhat of a side canopy, albeit a shorter one than in interior forest. Therefore the wavelet
336 results of our vertical structure sampling does provide some evidence of a side canopy that was
337 not detectable from our other results.

338

339

340 **Conclusions and conservation implications**

341 Forest edges in the agricultural forest mosaic of Atlantic Forest near São Paulo are abrupt
342 transitions from short grass-dominated pasture to tall closed canopied forests with high
343 taxonomic and structural diversity. Edges themselves were characterized by low diversity, but
344 DEI was short for most structural variables and diversity measures. Our results did not provide
345 any evidence that topography (slope) may explain the lack of extensive edge influence; however,
346 topographic position may play a role.

347 We found evidence of edge degradation, reduced recruitment and a shorter canopy at the
348 edge. Although some variables such as tree and sapling cover suggested that edge sealing had not
349 taken place, there was evidence of a side canopy of more diverse leafy vertical structure. We
350 arrived at our understanding of edge structure only by using different analyses for the same data
351 set: DEI and wavelet analysis to examine patterns in more detail at a fine scale. Adding
352 multivariate analysis also allowed us to differentiate effects of topography and edge influence.
353 Having all three approaches provided complementary information to our analysis of taxonomic
354 and structural diversity at anthropogenic edges in Atlantic Forest.

355 Contrary to our hypothesis, DEI was not very extensive in Atlantic Forest but it is
356 important to note that even a DEI of 20 m or less can be substantial in heavily fragmented
357 landscapes (Riutta et al. 2014; Franklin et al. 2021) such as Atlantic Forest. Comparisons of
358 results from other studies on anthropogenic edges in tropical forests make it clear that DEI is not
359 similar and must be determined for each region. Further research is needed to determine which
360 factors affect DEI even for the same edge types within the same biome. For Atlantic Forest, signs

361 of edge degradation suggest that edge influence should be considered in conservation planning
362 even though edges are narrow, and the abrupt gradient in vegetation structure may be a factor in
363 explaining wildlife responses to edge creation.

364

365

366 **Author contributions** J.D., R.S.C.A. and R.Y. collected the data. K.A.H. and N.D.Q. analyzed
367 the data. K.A.H. and M.C.R. set up and supervised the project. K.A.H. wrote the manuscript with
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369

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378

379 **Data availability** Data are available on the Borealis repository (Harper 2022) at the following
380 DOI: <https://doi.org/10.5683/SP3/YO7LE9> as part of a data paper (Harper et al. 2023).

381

382 **Conflict of interest** The authors have no competing interest to disclose.

383

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570 **Tables and Figures**

571 Table 1. Magnitude and distance of edge influence (MEI and DEI) for vegetation responses
 572 within Atlantic Forest, Brazil. For sample size, n = number of transects. Edge influence was not
 573 significant for epiphytes, tree ferns / palms and the following plant families: Anacardiaceae,
 574 Euphorbiaceae, Fabaceae, Malvaceae, Maranthaceae, Meliaceae, Piperaceae.

Response	n	MEI	DEI (m)
Canopy cover	12	-0.97	-48 to 18
Canopy height	24	-0.38	-48 to 34, 46 to 64, 84 to 88
Plant group richness	24	-0.44	-48 to 10
Plant group diversity	24	-0.54	-48 to 10
Vertical woody richness	24	-0.41	-48 to 32, 54 to 62
Vertical woody diversity	12	-0.35	-48 to 12
Vertical leafy richness	24	-0.31	-48 to 40, 54 to 58
Vertical leafy diversity	12	-0.41	-48 to 20
Family richness	12	-0.20	-48 to 0
Family diversity	12	-0.28	-48 to 0
Tree density < 3 cm diameter	12	-0.88	-48 to 10
Tree density 3-10 cm diameter	12	-1.00	-48 to 16
Tree density > 10 cm diameter	12	-0.54	-48 to -2
Trees	24	-0.51	-48 to 2, 12 to 16
Saplings	24	-0.88	-48 to 0
Ferns	24	-0.53	-38 to -34, -24 to -16
Lianas	24	-1.00	-48 to 2

Vines	24	-1.00	-48 to 0, 34 to 38*
Snags	24	-1.00	-48 to -4
Graminoids	24	0.34	-48 to 2
Moss	24	0.16	-48 to -4, 14 to 18
Litter	24	-0.35	-48 to 2, 10 to 14
Asteraceae	12	0.79	14 to 20
Melanomastaceae	12	-1.00	-48 to -14
Myrtaceae	12	-0.63	-48 to -8
Poaceae	12	0.17	-48 to -14
Rubiaceae	12	-0.88	-48 to 8
Sapindaceae	12	-0.39	-48 to -16

575 * DEI of -48 to 0 m is for negative edge influence whereas 34 to 38 m is for positive edge
576 influence (greater values compared to interior forest).

577

Table 2. Estimates of regression coefficients \pm standard error with p-value (in brackets) of each explanatory variable (distance, squared slope, and season (dry/wet)) for 25 and 200 m from the edge for spatial generalized linear mixed models for functional diversity and cover of different plant groups (n = 600 for the 200 m analysis and n = 75 for the 25 m analysis). Bold values represent significant results. All intercepts had p-values of < 0.0001 .

	Intercept	Distance	Slope	Distance:Slope	Wet season
Plant group diversity 200 m	1.0 \pm 0.0	0.00068 \pm 0.00028 (0.016)	-0.0011 \pm 0.0006 (0.065)	NS	-0.19 \pm 0.04 (0.0002)
Plant group diversity 25 m	0.75 \pm 0.08	0.016 \pm 0.003 (< 0.0001)	-0.0011 \pm 0.0010 (0.25)	NS	-0.20 \pm 0.08 (0.022)
Trees 200 m	-3.5 \pm 0.1	0.00088 \pm 0.00060 (0.15)	-0.0035 \pm 0.0022 (0.12)	NS	0.36 \pm 0.11 (0.0036)
Trees 25 m	-4.2 \pm 0.3	0.029 \pm 0.008 (0.0008)	-0.011 \pm 0.006 (0.072)	NS	0.45 \pm 0.33 (0.19)
Tree ferns / palms 200 m	-5.0 \pm 0.3	-0.00043 \pm 0.00136 (0.75)	-0.015 \pm 0.008 (0.045)	NS	-0.65 \pm 0.36 (0.087)
Tree ferns / palms 25 m	-5.7 \pm 0.6	0.015 \pm 0.025 (0.56)	-0.014 \pm 0.015 (0.36)	NS	-0.027 \pm 0.494 (0.96)

Ferns 200 m	-4.8 ± 0.3	-0.0036 ± 0.0016 (0.024)	0.0026 ± 0.0029 (0.37)	NS	0.060 ± 0.398 (0.88)
Ferns 25 m	-3.7 ± 0.4	-0.053 ± 0.026 (0.046)	-0.023 ± 0.014 (0.12)	0.0020 ± 0.0009 (0.032)	-0.41 ± 0.43 (0.35)
Liana 200 m	-3.0 ± 0.2	0.0024 ± 0.0010 (0.019)	0.0017 ± 0.0025 (0.49)	NS	0.32 ± 0.18 (0.089)
Lianas 25 m	-3.6 ± 0.6	0.034 ± 0.017 (0.046)	0.0024 ± 0.0043 (0.58)	NS	0.40 ± 0.54 (0.46)
Vines 200 m	-4.2 ± 0.2	0.00067 ± 0.00112 (0.55)	-0.00065 ± 0.00360 (0.86)	NS	1.7 ± 0.2 (< 0.0001)
Vines 25 m	-4.8 ± 0.5	0.034 ± 0.013 (0.011)	0.0046 ± 0.0039 (0.25)	NS	1.5 ± 0.4 (0.0019)
Snags 200 m	-4.0 ± 0.2	-0.0031 ± 0.0010 (0.0014)	-0.010 ± 0.004 (0.012)	NS	-0.21 ± 0.17 (0.23)
Snags 25 m	-4.0 ± 0.3	0.0011 ± 0.0147 (0.94)	-0.0055 ± 0.0063 (0.39)	NS	-0.81 ± 0.31 (0.017)
Graminoids 200 m	-2.2 ± 0.3	-0.0025 ± 0.0011 (0.017)	-0.0025 ± 0.0025 (0.32)	NS	0.65 ± 0.35 (0.080)
Graminoids 25 m	-1.9 ± 0.3	-0.0083 ± 0.0074 (0.27)	-0.0077 ± 0.0047 (0.11)	NS	0.60 ± 0.32 (0.076)
Epiphytes 200 m	-6.7 ± 0.5	0.0044 ± 0.0021 (0.040)	-0.0023 ± 0.0093 (0.81)	NS	1.3 ± 0.5 (0.014)
Epiphytes 25 m	-8.2 ± 0.8	0.022 ± 0.015 (0.16)	-0.061 ± 0.036 (0.096)	0.0036 ± 0.0014 (0.0096)	-0.26 ± 1.08 (0.81)

Moss 200 m	-4.8 ± 0.4	0.0067 ± 0.0020 (0.0009)	-0.0066 ± 0.0049 (0.18)	NS	-0.0029 ± 0.4520 (1.0)
Moss 25 m	-4.2 ± 0.4	-0.0054 ± 0.0153 (0.73)	-0.015 ± 0.012 (0.21)	NS	-0.26 ± 0.56 (0.65)
Litter 200 m	-2.1 ± 0.1	0.00051 ± 0.00045 (0.25)	0.0011 ± 0.0009 (0.20)	NS	1.8 ± 0.1 (< 0.0001)
Litter 25 m	-2.2 ± 0.2	0.010 ± 0.004 (0.012)	-0.00046 ± 0.00151 (0.76)	NS	1.7 ± 0.2 (< 0.0001)

Figure captions

Fig. 1. Map of the locations of the 12 transects sampled in July-August (yellow pins) and 12 transects sampled in October-December (white squares) with the inset map showing the location of study area in Brazil.

Fig. 2. Canopy cover (a) and height (b) along the edge to forest interior gradient. Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 12$ transects for canopy cover and 24 transects for canopy height.

Fig. 3. Richness of plant groups (a), families (b) and the number of vertical 2 m cubes with woody (c) and leafy material (d) along the edge to forest interior gradient. Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 24$ transects.

Fig. 4. Proportion of transects with significant abrupt changes along the edge to forest interior gradient for richness of plant groups (a), families (b) and the number of vertical 2 m cubes with woody (c) and leafy material (d). Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 24$ transects except for $n = 12$ transects for (d).

Fig. 5. Proportion of transects with significant abrupt changes along the edge to forest interior gradient for diversity and richness of the number of vertical 2 m cubes with woody (a, b) and leafy material (c, d). Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 12$ transects.

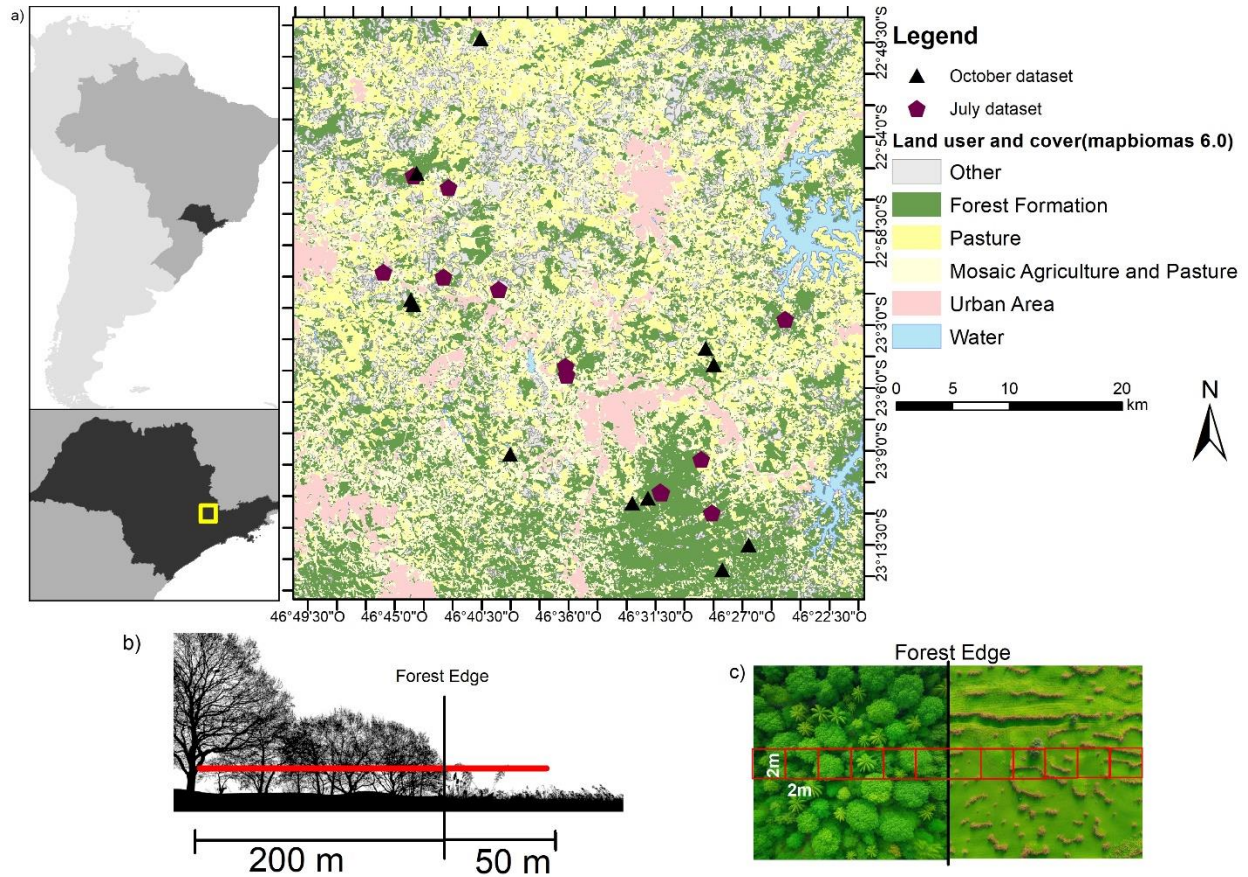


Fig. 1. Map of the study area (a) and diagrams of the sampling design (b, c). In (a), locations are of the 12 transects sampled in July-August (July dataset) and the 12 transects sampled in October-December (October dataset), with the inset map showing the location of study area in Brazil.

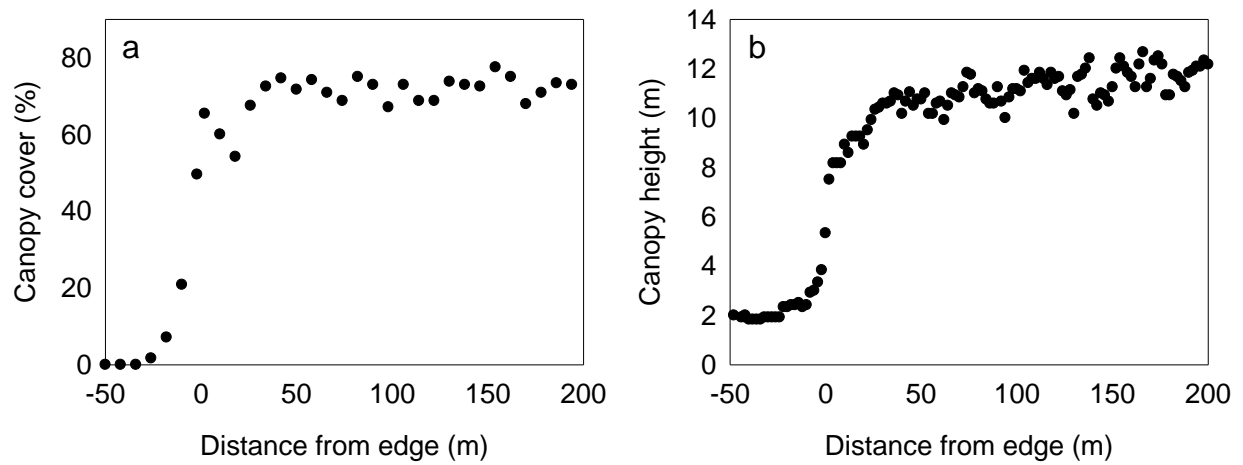


Fig. 2. Canopy cover (a) and height (b) along the edge to forest interior gradient. Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 12$ transects for canopy cover and 24 transects for canopy height.

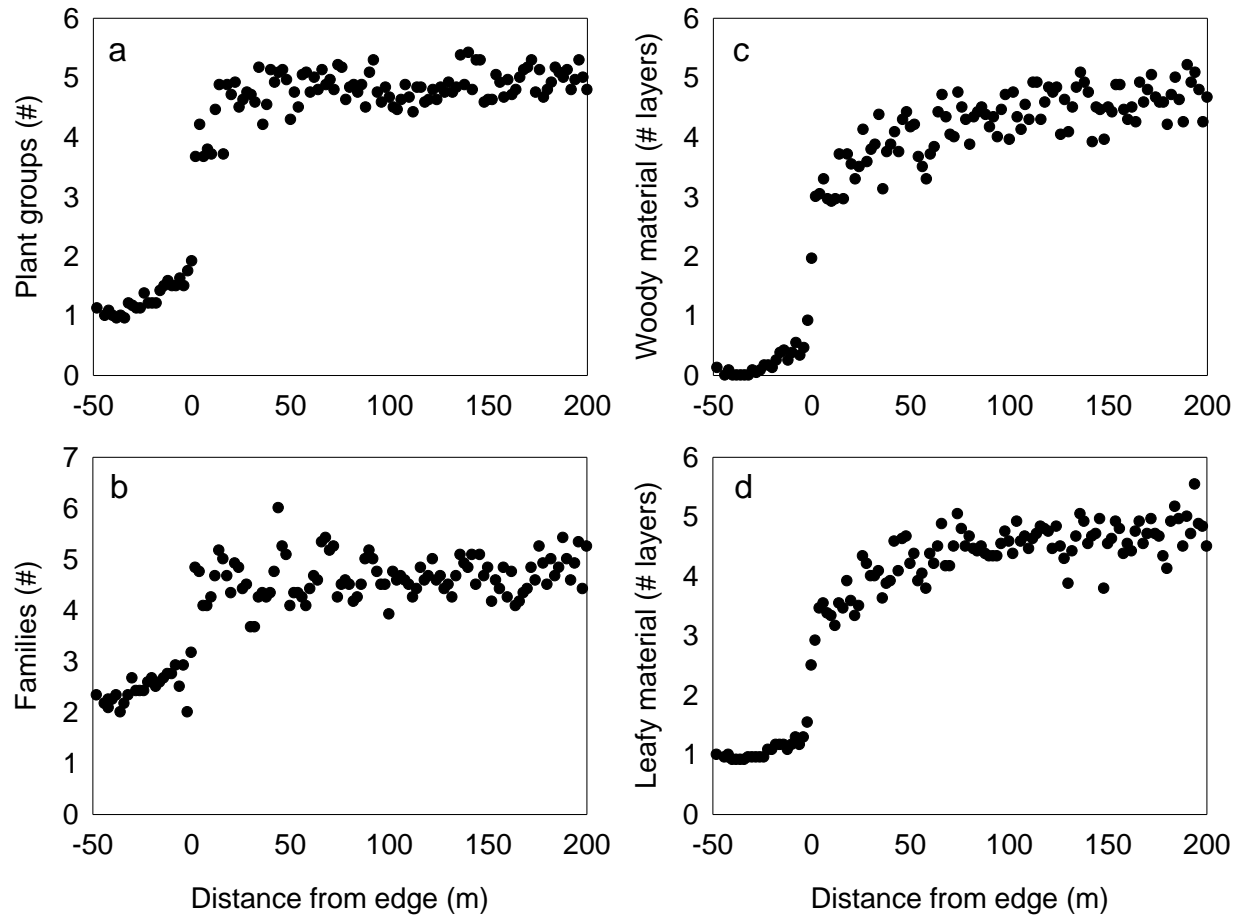


Fig. 3. Richness of plant groups (a), families (b) and the number of vertical 2 m cubes with woody (c) and leafy material (d) along the edge to forest interior gradient. Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 24$ transects.

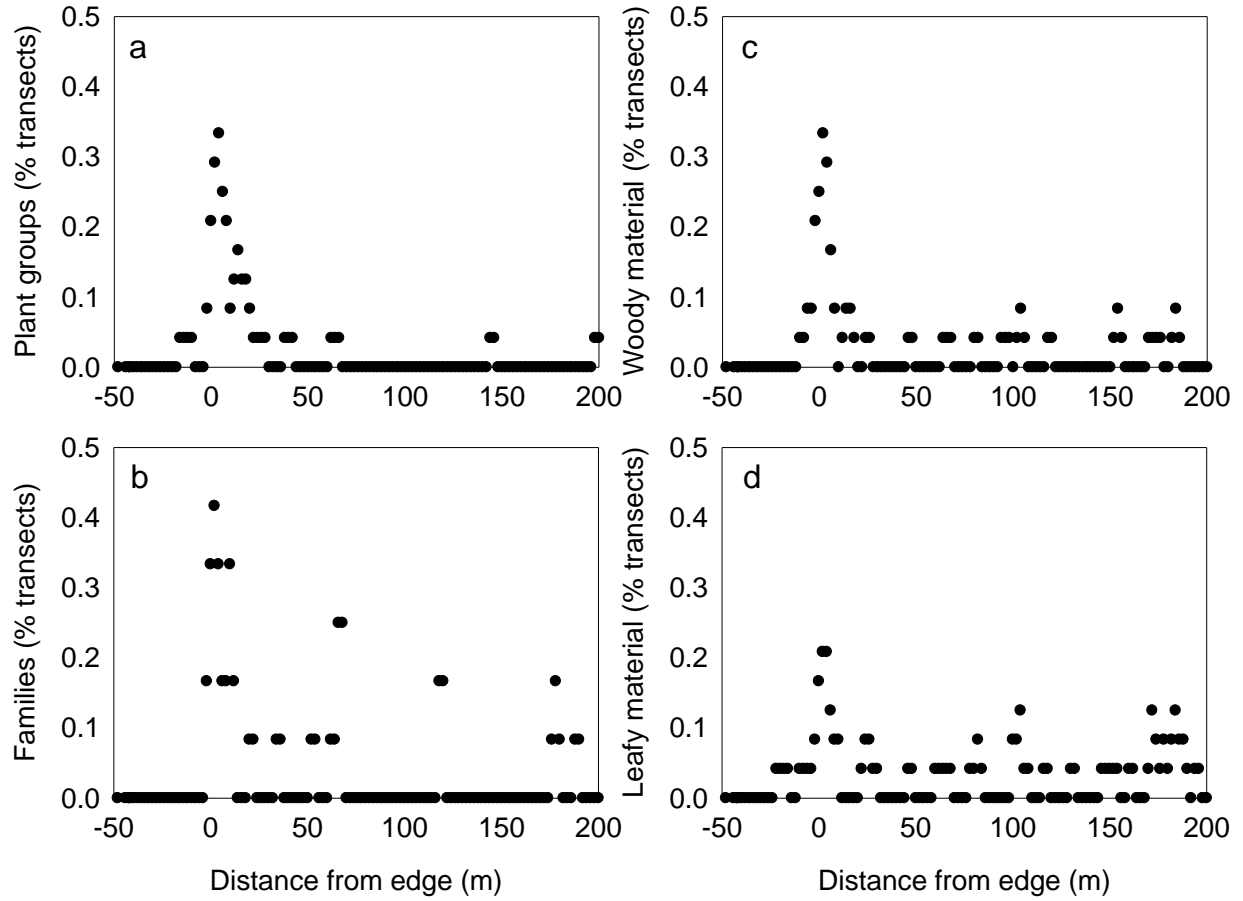


Fig. 4. Proportion of transects with significant abrupt changes along the edge to forest interior gradient for richness of plant groups (a), families (b) and the number of vertical 2 m cubes with woody (c) and leafy material (d). Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 24$ transects except for $n = 12$ transects for (d).

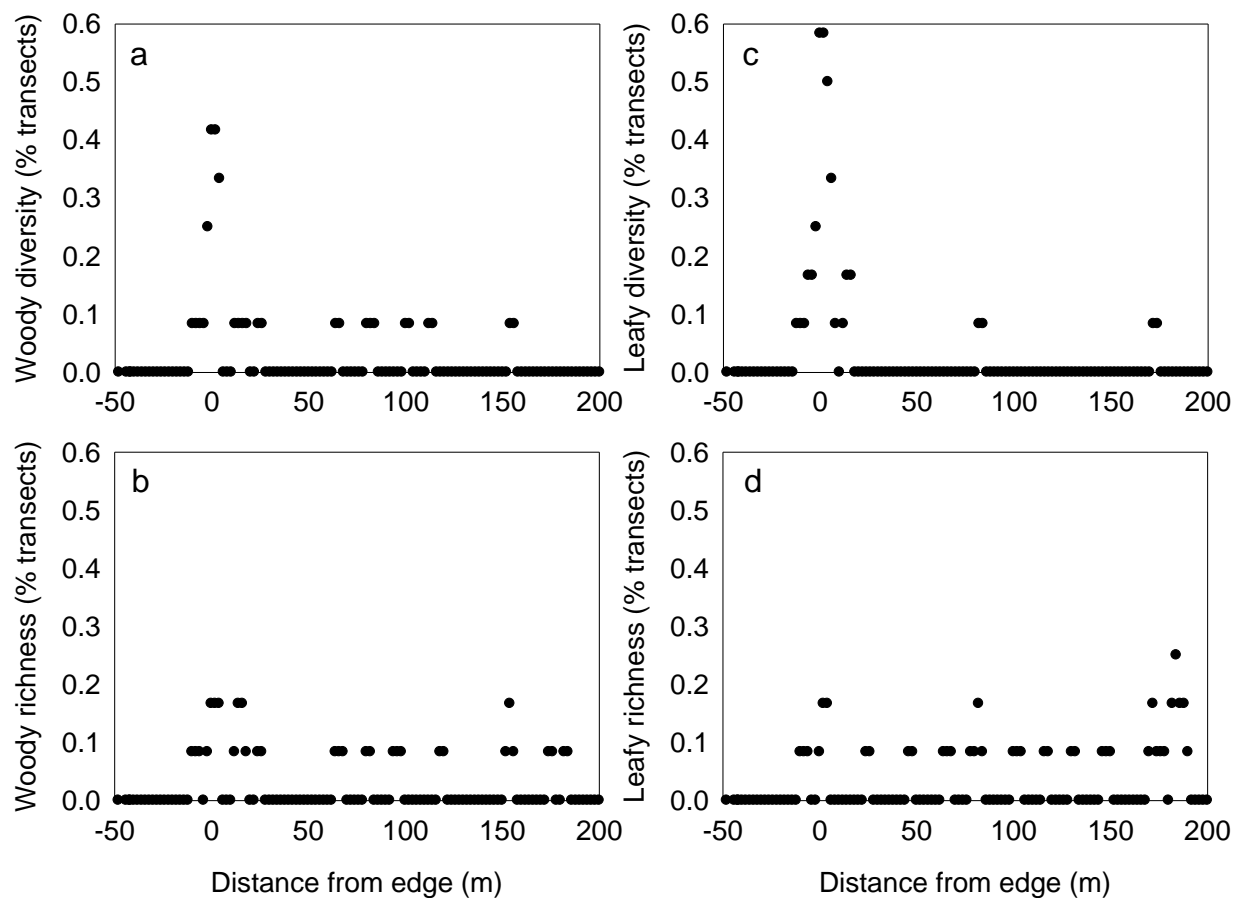


Fig. 5. Proportion of transects with significant abrupt changes along the edge to forest interior gradient for diversity and richness of the number of vertical 2 m cubes with woody (a, b) and leafy material (c, d). Negative distances are in the adjacent non-forested area and 0 m is at the forest edge. Sample size is $n = 12$ transects.