

₁ Habitat edges affect tree diversity more than biomass
₂ regeneration in a wet neotropical secondary forest

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₉ **Keywords:** secondary forest; regeneration; timber plantation associated biodiversity; edge
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¹⁵ **Abstract**

¹⁶ About half of all forests are tropical and secondary, making tropical forest regeneration
¹⁷ integral to future forests. Tree stand biomass and taxonomic richness can recover in a few
¹⁸ decades, but relative abundances may lag indefinitely. Since most forests are within a km of
¹⁹ a habitat edge, edge effects likely affect community composition regeneration, mediated by
²⁰ shade tolerance and dispersal traits, along with management history. This study addressed
²¹ how wet tropical secondary forest regeneration was affected by distance to habitat edge, and
²² hypothesized that old timber plantations facilitate regeneration by favoring shade tolerant
²³ or late successional taxa, and adjacent forest edges mediate community composition. An
²⁴ abandoned neotropical timber plantation adjacent to primary forest was censused for trees
²⁵ along a 300 m edge distance gradient, and analysis matched taxa to traits using relevant
²⁶ literature.

²⁷ As distance from primary forest edge increased, stem and wood density tended to increase
²⁸ significantly, with ca 10% variation explained, while biomass and canopy light tended to stay
²⁹ the same. Stand tree richness also tended to increase significantly, but diversity decreased
³⁰ steeply and non-linearly, and taxonomic composition varied notably. Finally, tree taxa as-
³¹ sociated with both early and late successional stages decreased significantly, but biomass by
³² dispersal mode did not tend to change. Overall this study supports that stand composi-
³³ tion is less resilient and more subject to edge effects than biomass and richness, suggesting
³⁴ that global forests will likely be distinctly new assemblages in the future, with timber and
³⁵ biodiversity trade-offs occurring based on local and regional management activity.

³⁶ Abstracto

³⁷ Más de la mitad de bosques son tropicales y secundarios, indicando que la regeneración de
³⁸ bosques tropicales es integral al futuro de bosques, globalmente. Biomasa arboreal y riqueza
³⁹ taxonómica pueden recuperarse en algunas décadas, pero abundancias relativas pueden durar
⁴⁰ más de un siglo. Dado que la mayoría de bosques quedan entre un km de su orilla, efec-
⁴¹ tos de borde probablemente afectan la regeneración de composición de comunidad, mediado
⁴² por tolerancia a sombra y características de disperso, y también historia de manejo. Este
⁴³ estudio investigó cómo la regeneración de bosque secundario tropical húmedo fue afectado
⁴⁴ por distancia a borde de hábitat, e hipotetizó que plantaciones de madera viejas facilitan
⁴⁵ regeneración porque favorecen a taxa tolerantes a sombra o de sucesión tarde, y que oril-
⁴⁶ las de bosque adyacente median cambios a composición de comunidad. Una plantación de
⁴⁷ madera neotropical adyacente a bosque primario fue censada por árboles siguiendo un tran-
⁴⁸ secto de 300 m midiendo un gradiente de distancia de orilla, y análisis combinó taxa con
⁴⁹ características ecológicas usando literatura relevante.

⁵⁰ Mientras distancia de bosque primario aumentó, densidad de madera y tallos tendieron a
⁵¹ aumentar significativamente, con 10% variación explicado, mientras tanto biomasa y luz de
⁵² dócel tendió a quedarse igual. Riquesa taxonómica de árboles también tendió a aumentar
⁵³ significativamente, pero diversidad bajó profundamente y no-linealmente, y composición tax-
⁵⁴ onomica varió notablemente. Finalmente, biomasa de taxa de árboles asociados con etapas
⁵⁵ de sucesión ambos temprano y tarde bajaron significativamente, pero biomasa por modo de
⁵⁶ disperso no tendió a cambiar. Entre todo este estudio apoya que composición taxonómica es
⁵⁷ menos resiliente y más sujeto a efectos de borde negativos que biomasa y riqueza taxonómica,
⁵⁸ sugeriendo que bosques globales probablemente serán ensamblajes nuevamente distintos en el
⁵⁹ futuro, con compensaciones entre producción de madera y biodiversidad que ocurren basado
⁶⁰ en manejo local y regional.

61 1 Introduction

62 Forest and landscape restoration is a key international conservation and climate change adap-
63 tation strategy (*De Pinto et al., 2020*), and while tropical forests specifically store most land
64 biomass (*Pan et al., 2013*), most are now secondary (*FAO, 2020*) and regenerating degraded
65 functions (*Hubau et al., 2020*) amid increasing climate stressors (*Anderegg et al., 2022*) yet
66 insufficient policy support (*Chazdon, 2018*) via skewed priorities (*Pyron and Mooers, 2022*).
67 Secondary forests can regenerate relatively quickly compared to old-growth forests in some
68 ways, but in other ways remain distinct. Neotropical secondary forests can grow quickly
69 enough to accumulate biomass >10x faster than old-growth forests (*Finegan, 1996; Poorter*
70 *et al., 2016*), and substantially offset carbon emissions, with estimates ranging from ~10%
71 from Amazonian deforestation (*Smith et al., 2020*) to a decade of fossil fuel emissions from all
72 of Latin American and the Caribbean (*Chazdon et al., 2016*). They also recover taxonomic
73 richness and biomass quite quickly, as well as tree height, averaging 80% of old-growth forest
74 levels in just 20 years, especially in wetter regions (*Rozendaal et al., 2019*). The recovery of
75 species richness alone is beneficial in that it also tends to correlate with the recovery of some
76 ecosystem services (*Guariguata and Ostertag, 2001; Stanturf et al., 2014*) like biomass and
77 carbon storage (*Liu et al., 2018*). However, secondary neotropical forests diverge widely in
78 taxonomic composition (*Norden et al., 2015*), potentially taking over a century to recover
79 (*Poorter et al., 2021*) with added variability (*Atkinson et al., 2022*). Despite being one of
80 the slowest ecosystem properties to recover, restoring recovering community composition is
81 often important for preserving rare taxa (*Carlo and Morales, 2016*), which can be keystone
82 to locally-adapted food webs, including birds (*Maas et al., 2016*). Understanding secondary
83 forest regeneration is key for global biodiversity conservation at the global scale, yet local
84 management remains the strongest driver of tropical forest carbon stores (*Pyles et al., 2022*).
85 Secondary forest regeneration is often affected by edge effects, or changes near an ecosystem
86 boundary, as well as land-use history, especially in heterogeneously-managed landscapes

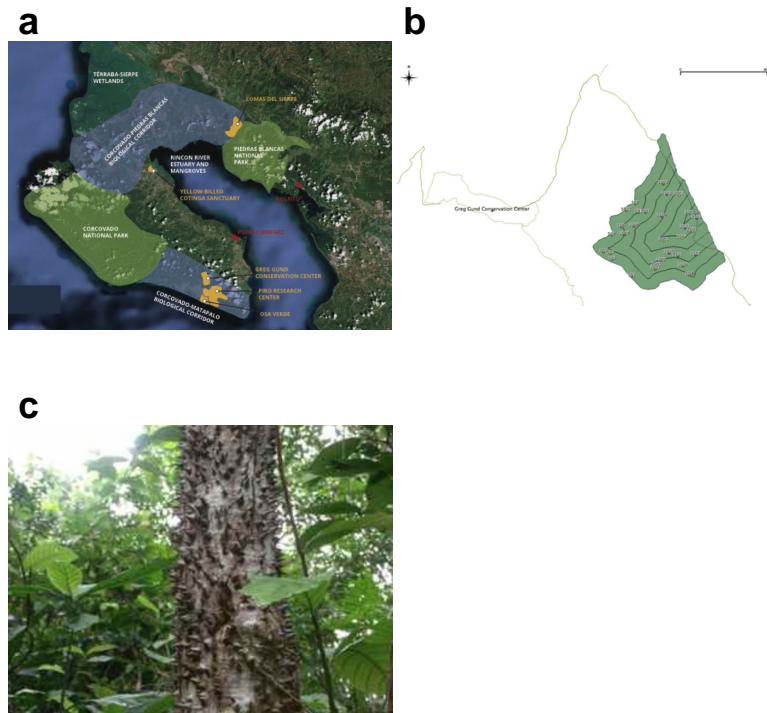
87 (*Melo et al., 2013; Perfecto et al., 2009*). About 70% of all forests have been estimated
88 to be within a km of their edge (*Haddad et al., 2015*), resulting in tropical forests having
89 been estimated to lose ~22% aboveground carbon along heavily-managed edges >100m, in
90 part due to shortening trees and lighter leaf mass (*Ordway and Asner, 2020*). Edge effects
91 also have the potential to shape community composition, based on the local dispersal kernel
92 patterns of existing taxa (*Wandrag et al., 2017*), which while complicated (*Muller-Landau
93 and Hardesty, 2009*), can also correlate with simpler plant traits like height and seed mass
94 (*Tamme et al., 2014; Thomson et al., 2011*). The traits of existing taxa also depend on land-
95 use history and previous management (*Omeja et al., 2012*), which historically has favored
96 tree taxa that tend to pioneering, or be faster-growing, have lower wood densities, and be
97 less shade-tolerant (*Tabarelli et al., 2008*). Legacy effects from management like intensive
98 timber planting could in theory delay or result in non-linear changes between successional
99 stages (*Albrich et al., 2020; Gough et al., 2021*), which would make future management more
100 uncertain, unlike more sustainable thinning practices and agroforestry (*Lefland et al., 2018*).
101 Overall, while edge effects near degraded habitat edges are often negative, meta-population
102 (*Levins, 1979*) and -community (*Leibold et al., 2004; Warren et al., 2015*) theories highlight
103 dispersal as a key process for offsetting extinction debt and thus maintaining biodiversity.
104 Near primary forest, dispersal may facilitate secondary forest regeneration, and help explain
105 relatively high biodiversity compared to adjacent stands that can be found in agroforests
106 (*Oliveira-Neto et al., 2017*), forests affected by logging (*Clark and Covey, 2012; Edwards et
107 al., 2014*), and timber plantations (*Pryde et al., 2015*).

108 This study reports tree regeneration patterns of an abandoned wet neotropical timber plan-
109 tation, highlighting edge effects from an adjacent primary forest. We hypothesized that
110 remaining timber trees would mediate forest regrowth by maintaining shade that would sup-
111 press less shade-tolerant pioneer tree taxa and allow for more tree diversity closer to the
112 primary forest edge. Accordingly, we predicted that further from the primary forest edge,
113 canopy light availability would increase, while stand biomass and diversity would decrease.

¹¹⁴ **2 Methods**

¹¹⁵ **2.1 Study site**

¹¹⁶ This study was done in a neotropical lowland rainforest on the Osa Peninsula at the Greg
¹¹⁷ Gund Conservation Center (approx. 8.3778176, -83.2935426) near the Piro Biological Station
¹¹⁸ run by Osa Conservation. (See *Taylor et al. (2015)* for a broader ecosystem description of the
¹¹⁹ region.) The study site was a regrowing 20 ha timber plantation of *Bombacopsis quinata*
¹²⁰ abandoned in ~1990 after the dry-adapted species from the Guanacaste region (*Hulshof and*
¹²¹ *Powers, 2020; Pérez Cordero and Kanninen, 2002*) grew poorly in very wet conditions. This
¹²² focal secondary forest area was roughly triangular, surrounded by primary forest on the two
¹²³ S and NW sides (Fig ??) and a wide service road on the third NE border, with primary
¹²⁴ forest beyond it. This census was done in 2013 during the rainy season months between June
¹²⁵ and August.



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¹²⁷ **2.2 Census design**

¹²⁸ Edge effects were studied by dividing the secondary forest area into six 50 m strata spanning
¹²⁹ 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to the
¹³⁰ E (Fig ??), using available GIS software (*ArcGIS 10*, esri.com, and *QGIS 2*, qgis.org). Each
¹³¹ stratum was randomly filled with a number of 21 x 21 m square census plots oriented N
¹³² that was proportional to its area—specifically with 11, eight, five, three, two, and one plot(s),
¹³³ respectively, as distance away from primary forest increased. The total area of the 30 census
¹³⁴ plots equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to
¹³⁵ similar studies (*Onyekwelu and Olabiwonnu, 2016*).

¹³⁶ **2.3 Plot measurements**

¹³⁷ Light reaching the forest floor was measured at the center of each plot at chest height using
¹³⁸ a densiometer (*Forestry Suppliers, Inc.*), as an average of four readings taken facing each
¹³⁹ cardinal direction.

¹⁴⁰ The slope of the forest floor was measured using a rangefinder (*Bushnell, Forestry Suppliers,*
¹⁴¹ *Inc*) to measure the distance the diagonal between two plot corners and triangulate the
¹⁴² observation angle.

¹⁴³ The diameter of all stems >10 cm wide were recorded in each census plot, totaling over
¹⁴⁴ 1,000 trees. Following common forestry guidelines, in cases where a tree split into 2 or
¹⁴⁵ more stems below breast height, each stem was measured separately; in cases where a stem
¹⁴⁶ split only above breast height, it was measured as a single stem. Tree height was recorded
¹⁴⁷ by measuring distances to both the crown and the stem at chest height (~2.7 m) using a
¹⁴⁸ rangefinder (*Bushnell, Forestry Suppliers, Inc.*) and triangulating the missing side length.
¹⁴⁹ Taxa were identified with localized knowledge and field guides matching common names to
¹⁵⁰ Latin binomials, and trait information was gathered from the literature.

151 Aboveground biomass (AGB) was estimated per stem using the allometric equation by *Chave*
152 *et al.* (2015). The equation specifically for wet tropical forests was used, which has performed
153 slightly better compared to both pantropical and previous other models by (*Alvarez et al.*,
154 2012; *Chave et al.*; 2005; *Ngomanda et al.*, 2014). The equation version with height was
155 used since height was accessibly measurable and has shown improved local accuracy (*Domke*
156 *et al.*, 2012; *Khan et al.*, 2020). Wood density (or specific gravity) values when available also
157 improve biomass estimates even more than height (*Van Breugel et al.*, 2011). The equation
158 used was:

$$AGB = 0.0673(pD^2H)^{0.976}$$

159 with diameter D in cm, height H in m, and wood density or specific gravity p in $g\text{ cm}^{-3}$.
160 DBHs and heights were measured in the field and wood densities were extracted from avail-
161 able literature. Where information was limited, values at the genus level were used and
162 unrepresented taxa were assumed to be 0.58 following World Agroforestry Database guide-
163 lines (worldagroforestry.org). Original values found and recorded were later updated to
164 modern values using the pipeline developed in the *BIOMASS* 2.1.8 R software package by
165 *Réjou-Méchain et al.* (2017), which notably replaced unknown wood density values with
166 plot-level averages instead during stem biomass calculations.

167 Traits including successional stage and main dispersal mode were matched to species with
168 *Werden et al.* (2020) data, and wood tissue carbon matched to genera with the GLOWCAD
169 database (*Doraisami et al.*, 2022) given high alignment at species levels (*Chave et al.*, 2006).

170 2.4 Statistical analyses

171 For all response variables, data were analyzed using plot or distance strata medians and
172 subject to linear regression with distance to forest edge as the only independent variable,
173 after assumption checks of residual normality with Shapiro-Wilk tests and equal variance
174 with Levene tests, using base R version 4.2.0 (2022-04-22) and *rstatix* 0.7.0 package functions

175 (*R Core Team, 2022*).

176 Non-linear regressions were run using the function *poly()* in the base R package *stats* 4.2.0,
177 which was only ultimately recorded for stem density and richness variables, based on signif-
178 icance and explained variance over linear models. All trees censused were included in each
179 analysis including unidentified taxa that represented a single group in taxa-specific analyses.
180 Community analysis and ordination was done as a PERMANOVA with the *adonis()* func-
181 tion from the *vegan* 2.6.2 R package (*Dixon, 2003*). Data and code were organized with R
182 packages *here* (*Müller, 2020*), *bookdown* (*Xie, 2022*), and *grateful* (*Rodríguez-Sánchez et al.,*
183 *2022*), and internal pipeline *oir* (*Medina, 2022*) are stored at github.com/nmedina17/osa.

184 **3 Results**

185 **3.1 Biomass**

186 Aboveground biomass did not tend to change with distance to primary forest edge (Fig 1a),
187 despite significant trends with underlying related variables (Fig 1). Median plot wood density
188 tended to increase marginally significantly ($p=0.598$) with edge distance by $8.2 \times 10^{-5} \pm$
189 1.4×10^{-4} per m explaining R2x100% of variance among median distance strata values (Fig
190 1b). Plot stem density also tended to increase significantly ($p=0.82$) with edge distance but
191 more strongly and non-linearly, by $\sim 65.9 \pm 78.9$ per m (Fig 1c). At this stage in forest
192 regeneration, canopy light availability did not tend to change with distance from forest edge
193 (Fig 1d).

194 **## |**

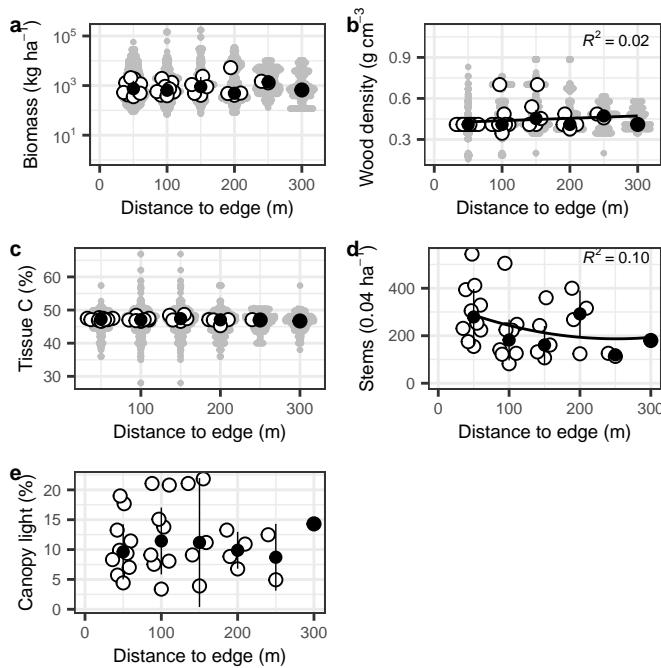


Figure 1: Plot stand properties, namely (a) biomass, (b) wood density, (c) stem density, and (d) canopy light availability. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

195 3.2 Composition

196 Overall diversity changed significantly with distance to primary forest edge (Fig 2). Diversity
 197 significantly ($p=0.414$) decreased non-linearly by $\sim 0.1 \pm 0.1$ per m as distance to primary
 198 forest edge increased, which explained $R^2 \times 100\%$ of variance among distance strata medians
 199 (Fig 2a) – while in contrast taxonomic richness increased slightly ($p=0.067$) and linearly
 200 by 0 ± 0 per m and had $R^2 \times 100\%$ variance explained among distance strata (Fig 2b).
 201 Community composition and beta diversity also changed significantly ($p=0.01$) with 25.6%
 202 variance among distance strata explained by distance to primary forest edge, and the first two
 203 principal components explaining 59% and 24% totaling 83% of variance among calculated
 204 plot distances (Fig 2d). Key abundant taxa *Vochysia* and *Ficus* showed different responses
 205 – *Vochysia* nearly tended to decrease with distance to primary forest edge (Fig 2e), while
 206 *Ficus* decreased marginally significantly ($p=0.088$) and linearly by -62.6 ± 25.1 per m with

207 R²x100% variance among distance strata explained (Fig 2f).

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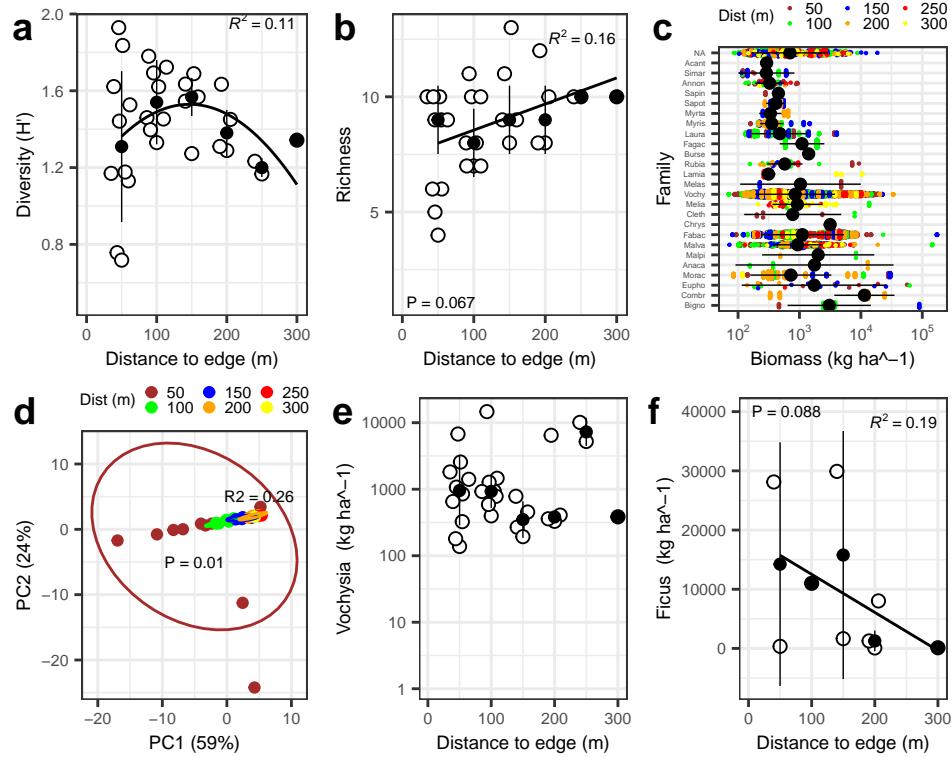


Figure 2: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

209 **3.3 Traits**

210 Overall trait regeneration highlighted successional stage associations over primary dispersal
 211 mode along distance to primary forest (Fig 3). Taxa associated with both early and late
 212 successional stages decreased significantly ($p=0.042$) and curvi-linearly by $\sim -584.9 \pm 167.3$
 213 kg per m with distance to edge explaining $R^2 \times 100\%$ variance among distance strata medians
 214 (Fig 3a). Dispersal modes did not show consistent trends in biomass with increasing distance
 215 to edge (Fig 3b).

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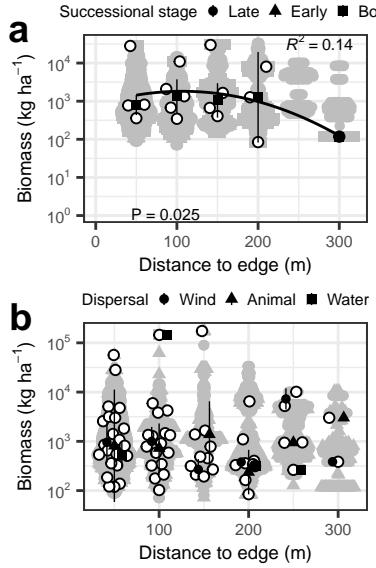


Figure 3: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

219 4 Discussion

220 This study found significant edge effects on secondary forest stand wood and stem density,
 221 tree diversity and community composition, and some functional traits, yet not on overall
 222 aboveground biomass. It was initially hypothesized that community composition would
 223 vary with distance to edge, favoring more shade-tolerant taxa, due to light availability and
 224 dispersal potential, and this evidence supported edge effects on community composition
 225 and biomass of taxa associated with both early- and late-successional stages, but without
 226 detectable roles for light availability or general dispersal mode. Accordingly this suggests
 227 that edge effects do significantly change humid tropical forest community composition, but

228 primarily due to factors other than light competition or dispersal limitation, as well as
229 that aboveground biomass and even low taxonomic richness is resilient after a decade of
230 regeneration.

231 Aboveground biomass storage is a key global ecosystem function and service, but edge effects
232 tend to release about one-third of carbon lost from tropical deforestation (*Brinck et al., 2017*), with more expected in the future (*Mitchard, 2018*). Management has been found
233 to explain most of biomass variation among tropical forest fragments, and wood density
234 ~10% biomass variation (*Pyles et al., 2022*). This study adds that management via edge
235 effects can also mediate ~10% of wood density variation without affecting local biomass,
236 although median stem wood density can describe regional spatial biomass patterns (*Baker*
237 *et al., 2004*). Overall, wood density and richness values may have been pulled down by
238 early-successional clonal trees closest to the primary forest, which tend to have lower wood
239 densities, lowering carbon (*Gonzalez J and Fisher, 1998; Pyles et al., 2022*), and increasing
240 nearby stem density. Lower wood density can also reflect more dynamic forest stands (*Malhi*
241 *et al., 2006*) with higher tree turnover, a consequence of forest fragmentation (*Nascimento*
242 *and Laurance, 2004*) together with other global change drivers (*Laurance et al., 2014*), as
243 well as may reflect possible differences in soil fertility (*Malhi et al., 2004*), all of which
244 represent possible future research directions, beyond strictly neutral dynamics (*Terborgh et*
245 *al., 1995*). Furthermore, light availability at the plot level may not affect biomass storage,
246 but instead individual light gaps may be more important for biomass dynamics (*Chazdon*
247 *and Fetcher, 1984*).

249 Edge effects have been shown to lower both forest biomass and also diversity, and this study
250 adds that the decline can be rapid and non-linear across edge gradients, along with supporting
251 the likelihood of lasting changes to community composition. The rapid diversity loss across
252 the edge gradient may be in part due to finer variations in dispersal patterns among animal
253 taxa, rather than overall dispersal mode more broadly. Similarly, stochastic factors like
254 priority effects after dispersal may also affect offspring establishment and re-growth. While

255 the biomass of the most abundant taxon *Vochysia* was resilient to edge effects, that of
256 the key taxon for frugivores like birds and bats *Ficus* was significantly lowered across the
257 forest edge, pointing to potentially different responses of biomass and food web associated
258 ecosystem services.

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²⁶¹ **Declaration of interests**

²⁶² Authors declare no conflicts of interest.

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²⁷¹ **Author contributions**

²⁷² NM wrote initial draft and later revisions.

²⁷³ **Data statement**

²⁷⁴ Code stored at github.com/nmedina17/osa.

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