

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

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₇ **Keywords:** secondary forest; regeneration; timber plantation associated biodiversity; edge
₈ effect; aboveground biomass; shade

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¹³ **Abstract**

¹⁴ About half of all forests are tropical and secondary, making tropical forest regeneration
¹⁵ integral to future forests. Tree stand biomass and taxonomic richness can recover in a few
¹⁶ decades, but relative abundances may lag indefinitely. Since most forests are within a km of
¹⁷ a habitat edge, edge effects likely affect community composition regeneration, mediated by
¹⁸ shade tolerance and dispersal traits, along with management history. This study addressed
¹⁹ how wet tropical secondary forest regeneration was affected by distance to habitat edge, and
²⁰ hypothesized that old timber plantations facilitate regeneration by favoring shade tolerant
²¹ or late successional taxa, and adjacent forest edges mediate community composition. An
²² abandoned neotropical timber plantation adjacent to primary forest was censused for trees
²³ along a 300 m edge distance gradient, and analysis matched taxa to traits using relevant
²⁴ literature.

²⁵ As distance from primary forest edge increased, stem and wood density tended to increase
²⁶ significantly, with ca 10% variation explained, while biomass and canopy light tended to stay
²⁷ the same. Stand tree richness also tended to increase significantly, but diversity decreased
²⁸ steeply and non-linearly, and taxonomic composition varied notably. Finally, tree taxa as-
²⁹ sociated with both early and late successional stages decreased significantly, but biomass by
³⁰ dispersal mode did not tend to change. Overall this study supports that stand composi-
³¹ tion is less resilient and more subject to edge effects than biomass and richness, suggesting
³² that global forests will likely be distinctly new assemblages in the future, with timber and
³³ biodiversity trade-offs occurring based on local and regional management activity.

³⁴ Abstracto

³⁵ Más de la mitad de bosques son tropicales y secundarios, indicando que la regeneración de
³⁶ bosques tropicales es integral al futuro de bosques, globalmente. Biomasa y riqueza tax-
³⁷ onómica pueden recuperarse en algunas décadas, pero abundancias relativas pueden durar
³⁸ más de un siglo. Dado que la mayoría de bosques quedan entre un km de su orilla, efec-
³⁹ tos de borde probablemente afectan la regeneración de composición de comunidad, mediado
⁴⁰ por tolerancia a sombra y características de disperso, y también historia de manejo. Este
⁴¹ estudio investigó cómo la regeneración de bosque secundario tropical húmedo fue afectado
⁴² por distancia a borde de hábitat, e hipotetizó que plantaciones de madera viejas facilitan
⁴³ regeneración porque favorecen a taxa tolerantes a sombra o de sucesión tarde, y que oril-
⁴⁴ las de bosque adyacente median cambios a composición de comunidad. Una plantación de
⁴⁵ madera neotropical adyacente a bosque primario fue censada por árboles siguiendo un tran-
⁴⁶ secto de 300 m midiendo un gradiente de distancia de orilla, y análisis combinó taxa con
⁴⁷ características ecológicas usando literatura relevante.

⁴⁸ Mientras distancia de bosque primario aumentó, densidad de madera y tallos tendieron a
⁴⁹ aumentar significativamente, con 10% variación explicado, mientras tanto biomasa y luz de
⁵⁰ dócel tendió a quedarse igual. Riquesa taxonómica de árboles también tendió a aumentar
⁵¹ significativamente, pero diversidad bajó profundamente y no-linealmente, y composición tax-
⁵² onomica varió notablemente. Finalmente, biomasa de taxa de árboles asociados con etapas
⁵³ de sucesión ambos temprano y tarde bajaron significativamente, pero biomasa por modo de
⁵⁴ disperso no tendió a cambiar. Entre todo este estudio apoya que composición taxonómica es
⁵⁵ menos resiliente y más sujeto a efectos de borde negativos que biomasa y riqueza taxonómica,
⁵⁶ sugeriendo que bosques globales probablemente serán ensamblajes nuevamente distintos en el
⁵⁷ futuro, con compensaciones entre producción de madera y biodiversidad que ocurren basado
⁵⁸ en manejo local y regional.

59 **1 Introduction**

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

85 (*Melo et al., 2013; Perfecto et al., 2009*). About 70% of all forests have been estimated
86 to be within a km of their edge (*Haddad et al., 2015*), resulting in tropical forests having
87 been estimated to lose ~22% aboveground carbon along heavily-managed edges >100m, in
88 part due to shortening trees and lighter leaf mass (*Ordway and Asner, 2020*). Edge effects
89 also have the potential to shape community composition, based on the local dispersal kernel
90 patterns of existing taxa (*Wandrag et al., 2017*), which while complicated (*Muller-Landau
91 and Hardesty, 2009*), can also correlate with simpler plant traits like height and seed mass
92 (*Tamme et al., 2014; Thomson et al., 2011*).

93 Properties of the existing tree community also depend on land-use history and previous
94 management (*Omeja et al., 2012*) including plantation use for timber production, which
95 historically has favored tree taxa that tend to pioneering, or be faster-growing, have lower
96 wood densities, and be less shade-tolerant (*Tabarelli et al., 2008*). Legacy effects from
97 management like intensive timber planting could in theory delay or result in non-linear
98 changes between successional stages (*Albrich et al., 2020; Gough et al., 2021*), which would
99 make future management more uncertain, unlike more sustainable thinning practices and
100 agroforestry (*Lefland et al., 2018*). Overall, while edge effects near degraded habitat edges
101 are often negative, meta-population (*Levins, 1979*) and -community (*Leibold et al., 2004;
102 Warren et al., 2015*) theories highlight dispersal as a key process for offsetting extinction debt
103 and thus maintaining biodiversity. Near primary forest, dispersal may facilitate secondary
104 forest regeneration, and help explain relatively high biodiversity compared to adjacent stands
105 that can be found in agroforests (*Oliveira-Neto et al., 2017*), forests affected by logging (*Clark
106 and Covey, 2012; Edwards et al., 2014*), and timber plantations (*Pryde et al., 2015*).

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

112 canopy light availability would increase, while stand biomass and diversity would decrease.

113 2 Methods

114 2.1 Study site

115 This study was done in a neotropical lowland rainforest on the Osa Peninsula at the Greg
116 Gund Conservation Center (approx. 8.3778176, -83.2935426) near the Piro Biological Station
117 run by Osa Conservation. (See *Taylor et al. (2015)* for a broader ecosystem description of the
118 region.) The study site was a regrowing 20 ha timber plantation of *Bombacopsis quinata*
119 abandoned in ~1990 after the vulnerably dry-adapted species from the Guanacaste region
120 (*Hulshof and Powers, 2020; Pérez Cordero and Kanninen, 2002*) grew poorly in very wet
121 conditions. This focal secondary forest area was roughly triangular, surrounded by primary
122 forest on the two S and NW sides (Fig 1) and a wide service road on the third NE border,
123 with primary forest beyond it. This census was done in 2013 during the rainy season months
124 between June and August.

125 2.2 Census design

126 Edge effects were studied by dividing the secondary forest area into six 50 m strata spanning
127 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to the
128 E (Fig 1), using available GIS software (*ArcGIS 10*, esri.com, and *QGIS 2*, qgis.org). Each
129 stratum was randomly filled with a number of 21 x 21 m square census plots oriented N
130 that was proportional to its area—specifically with 11, eight, five, three, two, and one plot(s),
131 respectively, as distance away from primary forest increased. The total area of the 30 census
132 plots equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to
133 similar studies (*Onyekwelu and Olabiwonnu, 2016*).

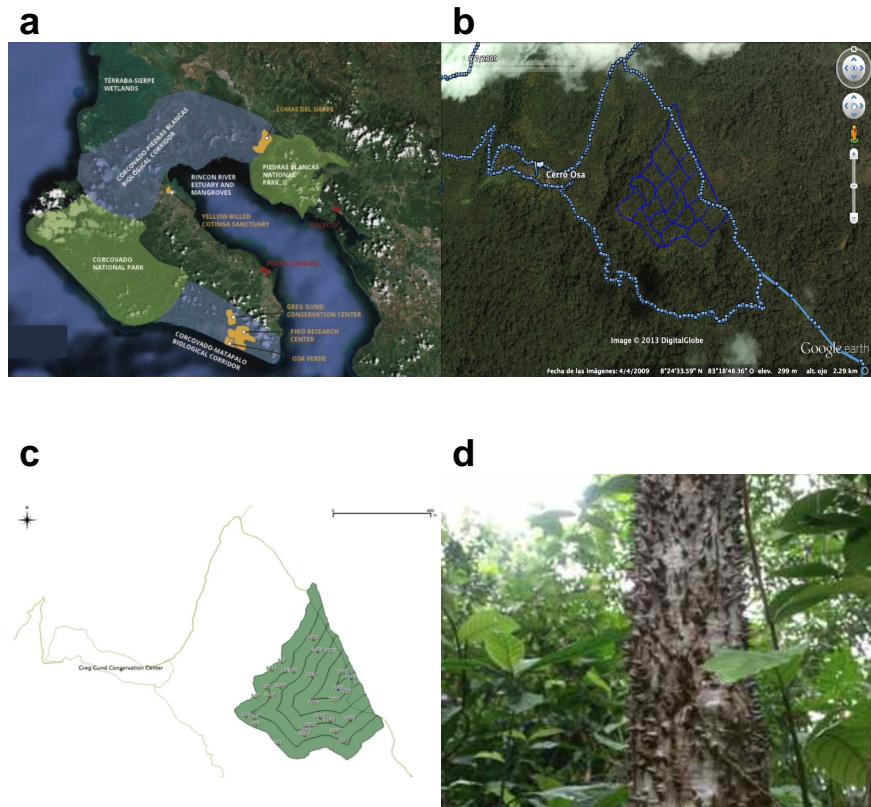


Figure 1: Map of (a) conservation areas and (b) study site (c) showing plot design among distance strata, and focal plantation timber taxon (c) *Bombacopsis quinata* on Osa Peninsula, Costa Rica. Map image data © 2009 Google, © 2022 Osa Conservation. Photo credit: Nicholas Medina.

¹³⁴ **2.3 Plot measurements**

¹³⁵ Light reaching the forest floor was measured at the center of each plot at chest height using
¹³⁶ a densiometer (*Forestry Suppliers, Inc.*), as an average of four readings taken facing each
¹³⁷ cardinal direction.

¹³⁸ The slope of the forest floor was measured using a rangefinder (*Bushnell, Forestry Suppliers,*
¹³⁹ *Inc*) to measure the distance the diagonal between two plot corners and triangulate the
¹⁴⁰ observation angle.

¹⁴¹ The diameter of all stems >10 cm wide were recorded in each census plot, totaling over
¹⁴² 1,000 trees. Following common forestry guidelines, in cases where a tree split into 2 or
¹⁴³ more stems below breast height, each stem was measured separately; in cases where a stem
¹⁴⁴ split only above breast height, it was measured as a single stem. Tree height was recorded
¹⁴⁵ by measuring distances to both the crown and the stem at chest height (~2.7 m) using a
¹⁴⁶ rangefinder (*Bushnell, Forestry Suppliers, Inc.*) and triangulating the missing side length.
¹⁴⁷ Taxa were identified with localized knowledge and field guides matching common names to
¹⁴⁸ Latin binomials, and trait information was gathered from the literature.

¹⁴⁹ Aboveground biomass (AGB) was estimated per stem using the allometric equation by *Chave*
¹⁵⁰ *et al.* (2015). The equation specifically for wet tropical forests was used, which has performed
¹⁵¹ slightly better compared to both pantropical and previous other models by (*Alvarez et al.*,
¹⁵² 2012; *Chave et al.*; 2005; *Ngomanda et al.*, 2014). The equation version with height was
¹⁵³ used since height was accessibly measurable and has shown improved local accuracy (*Domke*
¹⁵⁴ *et al.*, 2012; *Khan et al.*, 2020). Wood density (or specific gravity) values when available also
¹⁵⁵ improve biomass estimates even more than height (*Van Breugel et al.*, 2011). The equation
¹⁵⁶ used was:

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

¹⁵⁷ with diameter D in cm, height H in m, and wood density or specific gravity p in $g\text{ cm}^{-3}$.

158 DBHs and heights were measured in the field and wood densities were extracted from avail-
159 able literature. Where information was limited, values at the genus level were used and
160 unrepresented taxa were assumed to be *0.58* following World Agroforestry Database guide-
161 lines (worldagroforestry.org). Original values found and recorded were later updated to
162 modern values using the pipeline developed in the *BIOMASS* 2.1.8 R software package by
163 *Réjou-Méchain et al. (2017)*, which notably replaced unknown wood density values with
164 plot-level averages instead during stem biomass calculations.

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

168 2.4 Statistical analyses

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

174 Non-linear regressions were run using the function *poly()* in the base R package *stats* 4.2.0,
175 which was only ultimately recorded for stem density and richness variables, based on signif-
176 icance and explained variance over linear models. All trees censused were included in each
177 analysis including unidentified taxa that represented a single group in taxa-specific analyses.

178 Community analysis and ordination was done as a PERMANOVA with the *adonis()* func-
179 tion from the *vegan* 2.6.2 R package (*Dixon, 2003*). Data and code were organized with R
180 packages *here* (*Müller, 2020*), *bookdown* (*Xie, 2022*), and *grateful* (*Rodríguez-Sánchez et al.,*
181 *2022*), and internal pipeline *oir* (*Medina, 2022a*), and are stored at github.com/nmedina17/osa (*Medina, 2022b*).

₁₈₃ **3 Results**

₁₈₄ **3.1 Biomass**

₁₈₅ Aboveground biomass did not tend to change with distance to primary forest edge (Fig
₁₈₆ 2a), despite significant trends with underlying related variables (Fig 2). Median plot wood
₁₈₇ density tended to increase marginally significantly ($p=0.105$) with edge distance by 0.00019
₁₈₈ per m explaining ~10 % of variance among median distance strata values (Fig 2b), while
₁₈₉ tissue carbon did not change significantly with distance to forest edge (Fig 2c). Plot stem
₁₉₀ density also tended to increase significantly ($p=0.03$) with edge distance but more strongly
₁₉₁ and non-linearly, by $\sim 17.4 \pm 3.4$ per m (Fig 2d). At this stage in forest regeneration, canopy
₁₉₂ light availability did not tend to change with distance from forest edge (Fig 2e). Notably,
₁₉₃ tree diversity decreased marginally significantly ($p=<0.0001$) by ~ 1 per g plot wood density,
₁₉₄ yet only explaining ~4 % of variance (Fig 2f).

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₁₉₆ **3.2 Composition**

₁₉₇ Overall diversity changed significantly with distance to primary forest edge (Fig 3). Diversity
₁₉₈ significantly ($p=0.003$) decreased non-linearly by $\sim 0.5 \pm 0$ per m as distance to primary forest
₁₉₉ edge increased, which explained 73% of variance among distance strata medians (Fig 3a) –
₂₀₀ while in contrast taxonomic richness increased slightly ($p=0.067$) and linearly by 0 ± 0 per
₂₀₁ m and had 16% variance explained among distance strata (Fig 3b). Community composition
₂₀₂ and beta diversity also changed significantly ($p=0.01$) with 11.4% variance among distance
₂₀₃ strata explained by distance to primary forest edge, and the first two principal components
₂₀₄ explaining 47% and 23% totaling 70% of variance among calculated plot distances (Fig
₂₀₅ 3d). Key abundant taxa *Vochysia* and *Ficus* showed different responses – *Vochysia* nearly

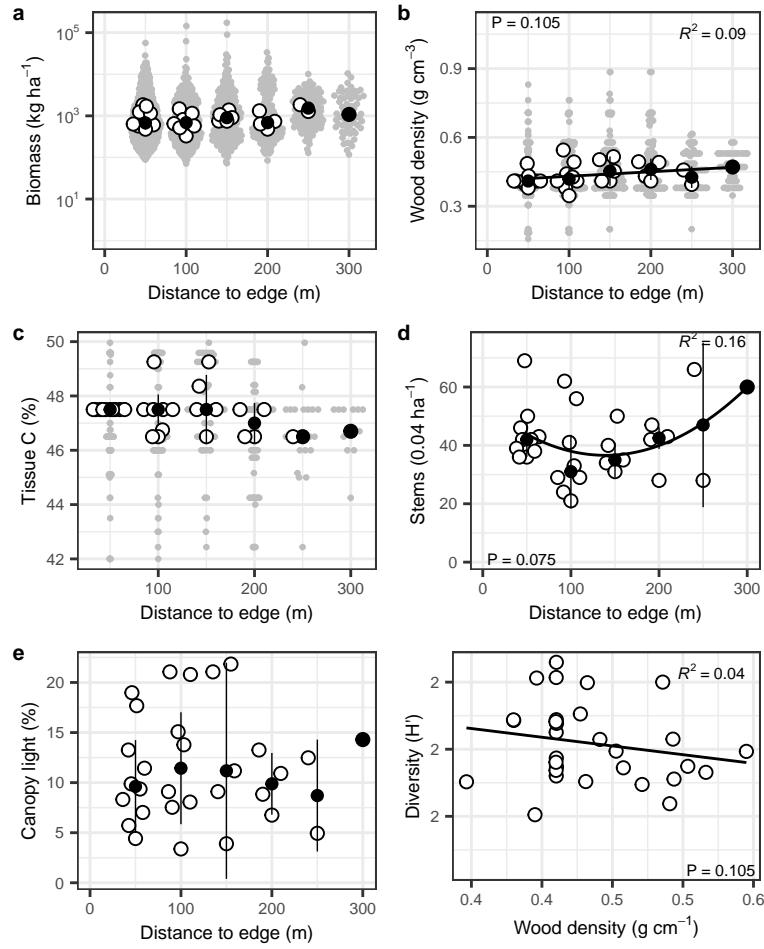


Figure 2: Plot stand properties, namely (a) biomass, (b) wood density, (c) tissue carbon, (d) stem density, (e) canopy light availability, all across distance to primary forest edge gradient, and (e) diversity against wood density. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

206 tended to decrease with distance to primary forest edge (Fig 3e), while *Ficus* decreased
 207 marginally significantly ($p=0.088$) and linearly by -62.6 ± 25.1 per m with $\sim 20\%$ variance
 208 among distance strata explained (Fig 3f).

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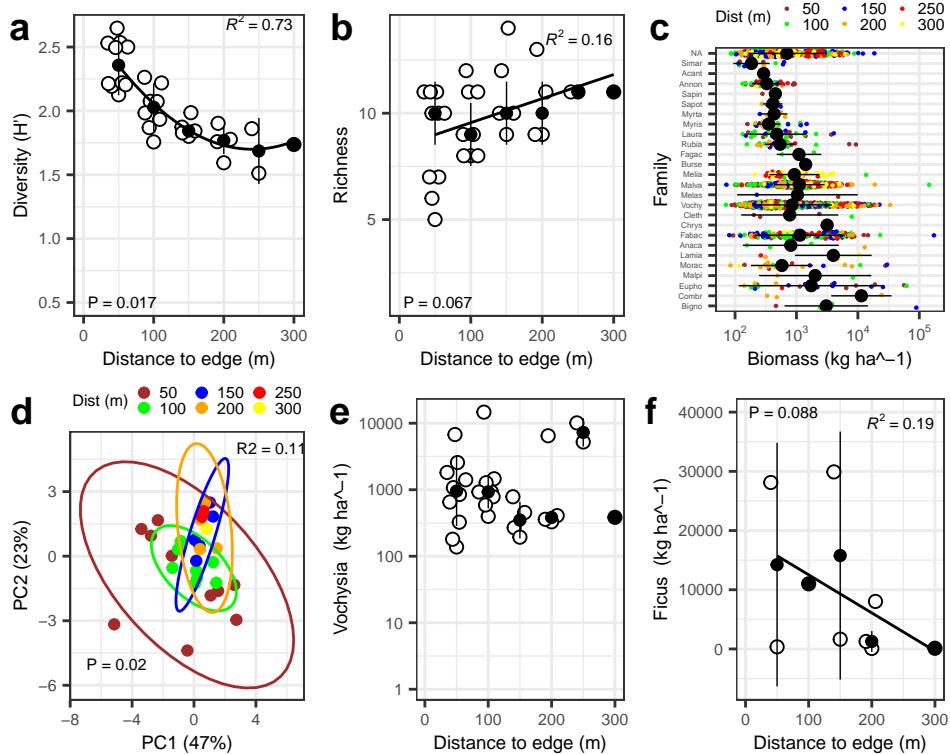


Figure 3: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

210 **3.3 Traits**

211 Overall trait regeneration highlighted successional stage associations over primary dispersal
 212 mode along distance to primary forest (Fig 4). Taxa associated with both early and late
 213 successional stages decreased significantly ($p=0.042$) and curvi-linearly by $\sim -584.9 \pm 167.3$
 214 kg per m with distance to edge explaining $\sim 14\%$ variance among distance strata medians

215 (Fig 4a). Dispersal modes did not show consistent trends in biomass with increasing distance
 216 to edge (Fig 4b).

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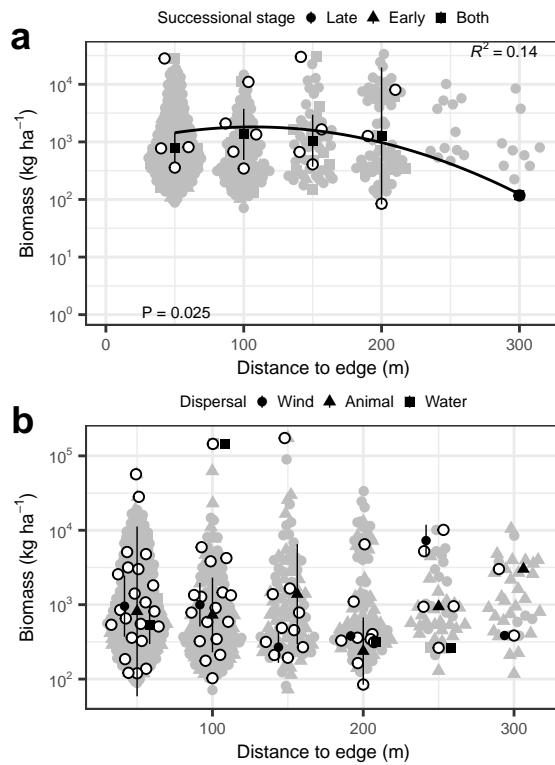


Figure 4: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

220 **4 Discussion**

221 This study found significant edge effects on secondary forest stand wood and stem density,
 222 tree diversity and community composition, and some functional traits, yet not on overall

aboveground biomass. It was initially hypothesized that community composition would vary with distance to edge, favoring more shade-tolerant taxa, due to light availability and dispersal potential, and the evidence presented here supported edge effects on community composition and biomass of taxa associated with both early- and late-successional stages, but without detectable roles for light availability or general dispersal mode. Accordingly, this suggests that edge effects do significantly change humid tropical forest community taxonomic and functional composition, but primarily due to factors other than light competition or dispersal limitation (*Krishnadas et al., 2020*), and also suggests that aboveground biomass and even low taxonomic richness are resilient after a decade of regeneration.

Aboveground biomass storage is a key global ecosystem function and service, but edge effects 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 to explain most of biomass variation among tropical forest fragments, and wood density ~10% biomass variation (*Pyles et al., 2022*). This study adds that management via edge effects can also mediate ~10% of wood density variation without affecting local biomass, although median stem wood density can describe regional spatial biomass patterns (*Baker et al., 2004*). In this study, wood density and richness values may have been pulled down by early-successional clonal trees closest to the primary forest, which tend to have lower wood densities, lowering carbon (*Gonzalez J and Fisher, 1998; Pyles et al., 2022*), and increasing nearby stem density. Lower wood density can also reflect more dynamic forest stands (*Malhi et al., 2006*) with higher tree turnover, a consequence of forest fragmentation (*Nascimento and Laurance, 2004*) together with other global change drivers (*Laurance et al., 2014*), as well as may reflect possible differences in soil fertility (*Malhi et al., 2004*), all of which represent possible future research directions, beyond strictly neutral dynamics (*Terborgh et al., 1995*). Furthermore, light availability at the plot level did not affect biomass storage, but instead, individual light gaps may be more important for biomass dynamics (*Chazdon and Fetcher, 1984*).

250 Edge effects have been shown in other studies to lower both forest biomass and change com-
251 munity composition (*Anderson et al., 2022*), and this study adds that the decline in diversity
252 can be rapid and non-linear across edge gradients, along with supporting the likelihood of
253 lasting changes to community composition. This rapid loss of diversity across the edge gradi-
254 ent may be in part due to existing higher yet constant levels of shade limiting shade-intolerant
255 seedling recruitment and/or performance, together with insufficient time for slower-growing
256 shade-tolerant taxa to accumulate significant amounts of biomass. Another possible factor
257 may be overall short dispersal kernels, in part due to higher fungal pathogen pressure under
258 higher constant shade, also increasing tree mortality. Decomposing compositional changes
259 into key specific taxa, while the biomass of the most abundant taxon *Vochysia* was resilient
260 to edge effects in this study, that of the key taxon for frugivores like birds and bats *Ficus*
261 was significantly lowered across the secondary forest edge, pointing to potentially different
262 responses of biomass and food web associated ecosystem services. Community composition
263 also tended to show lower variance across the edge gradient, although this effect cannot be
264 confirmed here given the uneven sampling that accounted for variable forest area at different
265 distances from edge.

266 Characterizing community composition by functional traits is also increasingly studied (*Kear-
267 ney et al., 2021*), but less so regarding edge effects. A study in Madagascar found lower
268 phylogenetic diversity closer to degraded forest edge, but no change in aboveground biomass
269 (*Razafindratsima et al., 2018*). These results parallel in showing lower taxonomic diver-
270 sity, although biomass specifically of taxa associated with both early- and late-successional
271 stages also decreased with away from primary forest edge. This result by successional stage
272 can be explained by slightly lower habitat quality inferred near exposed habitat edges near
273 roads, and accordingly relatively higher habitat quality near closed primary forest edge.
274 While lower biomass of succession-agnostic taxa further from primary forest edge appears
275 consistent with dispersal kernels, the lack of pattern by broad dispersal mode limits this
276 explanation here, yet could be further tested by measuring taxon-specific dispersal kernels.

²⁷⁷ Overall, this study highlights how abandoned wet tropical timber plantation can regenerate in
²⁷⁸ alongside fragmented forests. Results support related syntheses that biomass and taxonomic
²⁷⁹ richness often regrows relatively quickly, while taxonomic composition recovers much more
²⁸⁰ slowly, if not diverging altogether (*Norden et al., 2015*). These findings can suggest that
²⁸¹ more efficient reforestation could more actively target biodiversity conservation over other
²⁸² resilient functions like carbon storage, and that restoration efforts could include focusing
²⁸³ activities like native species planting efforts on degraded habitat edges away from primary
²⁸⁴ forest edges, and investing less in areas closer to existing forest edges, where recruitment
²⁸⁵ may already maintain diversity levels. As forests continue to become fragmented (*Haddad*
²⁸⁶ *et al., 2015*), understanding how to work with natural regeneration patterns around edge
²⁸⁷ effects will likely become increasingly important.

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²⁹⁰ **Declaration of interests**

²⁹¹ Authors declare no conflicts of interest.

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²⁹³ **Data statement**

²⁹⁴ Code stored at github.com/nmedina17/osa (*Medina, 2022b*).

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