

¹ Habitat edges affect tree diversity more than biomass
² regeneration in a reforested wet neotropical timber
³ plantation

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¹⁸ **Abstract**

¹⁹ About half of all forests are tropical and secondary, making tropical forest regeneration integral
²⁰ to future forests. Tree stand biomass and taxonomic richness can recover in a few decades, but
²¹ relative abundances may lag indefinitely. Since most forests are within a km of a habitat edge,
²² edge effects likely affect community composition regeneration. However, most studies assess
²³ how degraded edges affect intact forests, leaving it unclear whether higher-quality edges could
²⁴ facilitate regeneration of nearby degraded forests. Notably, higher quality edges near intact
²⁵ forests could promote processes like dispersal and wood biomass accumulation that effectively
²⁶ accelerate succession, leading to better performance of shade-tolerant taxa compared to
²⁷ pioneer taxa in the early stages of forested plantation regeneration. This study addressed how
²⁸ wet tropical forested plantation regeneration was affected by distance to adjacent intact forest
²⁹ edge. It was hypothesized that old timber plantations facilitate regeneration by increasing
³⁰ available shade, favoring the presence and biomass of later-successional taxa, ultimately
³¹ changing community composition overall. A wet neotropical timber plantation reforested
³² after 20 years and adjacent to primary forest was censused for trees along a 300 m edge
³³ distance gradient, and analysis matched identified taxa to broad dispersal mode and wood
³⁴ density traits using relevant literature.

³⁵ As distance from primary forest edge increased, stem and wood density tended to increase
³⁶ significantly, with ~10% variation explained, while biomass and canopy light surprisingly
³⁷ tended to stay the same. Stand tree richness also tended to increase significantly, but
³⁸ diversity decreased steeply and non-linearly, explained in part by wood density, and taxonomic
³⁹ composition varied notably. Finally, tree taxa associated with both early and late successional
⁴⁰ stages decreased significantly, as well as genus *Ficus*, but biomass by dispersal mode did not
⁴¹ tend to change. Overall this study supports that stand composition is less resilient and more
⁴² subject to edge effects than biomass and richness, suggesting that global forests will likely be
⁴³ distinctly new assemblages in the future, with timber and biodiversity trade-offs occurring

⁴⁴ based on local and regional management activity.

⁴⁵ Resumen

⁴⁶ Más de la mitad de bosques son tropicales y secundarios, indicando que la regeneración
⁴⁷ de bosques tropicales es integral al futuro de bosques, globalmente. Biomasa y riqueza
⁴⁸ taxonómica pueden recuperarse en algunas décadas, pero abundancias relativas pueden
⁴⁹ durar más de un siglo. Dado que la mayoría de bosques quedan entre un km de su borde,
⁵⁰ efectos de borde probablemente afectan la regeneración de composición de comunidad. Sin
⁵¹ embargo, la mayoría de estudios evalúan cómo bordes ya degradados afectan a bosques
⁵² intactos, dejándolo poco claro si bordes de más alta calidad podrían facilitar la regeneración
⁵³ de bosques cercanos previamente degradados. Notablemente, bordes de alta calidad cerca
⁵⁴ de bosques intactos podrían promover procesos como disperso y acumulación de biomasa
⁵⁵ maderosa que efectivamente aceleran a la sucesión, permitiendo mejor rendimiento de taxa
⁵⁶ tolerantes a sombra comparado con taxa más adaptados a alta luz en las etapas tempranas
⁵⁷ de regeneración de plantaciones foresterados. Este estudio investigó cómo la regeneración de
⁵⁸ bosque secundario tropical húmedo fue afectado por distancia a borde de hábitat, e hipotetizó
⁵⁹ que plantaciones de madera viejas facilitan regeneración porque favorecen a taxa tolerantes a
⁶⁰ sombra o de sucesión tarde, y que orillas de bosque adyacente median cambios a composición
⁶¹ de comunidad. Una plantación de madera neotropical adyacente a bosque primario fue
⁶² censada por árboles siguiendo un transecto de 300 m midiendo un gradiente de distancia de
⁶³ orilla, y análisis combinó taxa con características ecológicas usando literatura relevante.

⁶⁴ Mientras distancia de bosque primario aumentó, densidad de madera y tallos tendieron a
⁶⁵ aumentar significativamente, con 10% variación explicado, mientras tanto biomasa y luz
⁶⁶ de dócil asombrosamente tendió a quedarse igual. Riquesa taxonómica de árboles también
⁶⁷ tendió a aumentar significativamente, pero diversidad bajó profundamente y no-linealmente,
⁶⁸ explicado en parte por densidad de madera, y composición taxonomica varió notablemente.
⁶⁹ Finalmente, biomasa de taxa de árboles asociados con etapas de sucesión ambos temprano
⁷⁰ y tarde bajaron significativamente, tanto como el género Ficus, pero biomasa por modo de

71 disperso no tendió a cambiar. Entre todo este estudio apoya que composición taxonómica es
72 menos resiliente y más sujeto a efectos de borde negativos que biomasa y riqueza taxonómica,
73 sugiendo que bosques globales probablemente serán ensamblajes nuevamente distintos en el
74 futuro, con compensaciones entre producción de madera y biodiversidad que ocurren basado
75 en manejo local y regional.

⁷⁶ **Introduction**

⁷⁷ Forest and landscape restoration is a key international conservation and climate change
⁷⁸ adaptation strategy (*De Pinto et al., 2020*). While tropical forests specifically store most land
⁷⁹ biomass (*Pan et al., 2013*), most are now secondary (*FAO, 2020*) and functionally degraded
⁸⁰ (*Hubau et al., 2020*). This likely amplifies amid increasing climate stressors (*Anderegg et al.,*
⁸¹ *2022*) and collective management issues, including insufficient policy support (*Chazdon, 2018*)
⁸² via skewed priorities (*Pyron and Mooers, 2022*). Overall, secondary forests can regenerate
⁸³ relatively quickly compared to old-growth forests, in some ways. Neotropical secondary forests
⁸⁴ can grow quickly enough to accumulate biomass >10x faster than old-growth forests (*Finegan,*
⁸⁵ *1996; Poorter et al., 2016*), and substantially offset carbon emissions, with estimates ranging
⁸⁶ from ~10% from Amazonian deforestation (*Smith et al., 2020*) to a decade of fossil fuel
⁸⁷ emissions from all of Latin American and the Caribbean (*Chazdon et al., 2016*). They also
⁸⁸ recover taxonomic richness and biomass quite quickly, as well as tree height, averaging 80%
⁸⁹ of old-growth forest levels in just 20 years, especially in wetter regions (*Rozendaal et al.,*
⁹⁰ *2019*). The recovery of species richness alone is beneficial in that it also tends to correlate
⁹¹ with the recovery of some ecosystem services (*Guariguata and Ostertag, 2001; Stanturf et al.,*
⁹² *2014*) like biomass and carbon storage (*Liu et al., 2018*). However, recovery of secondary
⁹³ neotropical forests diverge widely in taxonomic composition (*Norden et al., 2015*), potentially
⁹⁴ taking over a century to recover (*Poorter et al., 2021*) with added variability (*Atkinson et al.,*
⁹⁵ *2022*). Despite being one of the slowest ecosystem properties to recover, restoring recovering
⁹⁶ community composition is often important for preserving rare taxa (*Carlo and Morales,*
⁹⁷ *2016*), which can be keystone to locally-adapted food webs, including birds (*Maas et al.,*
⁹⁸ *2016*). Overall, understanding secondary forest regeneration is key for global biodiversity
⁹⁹ conservation at the global scale.

¹⁰⁰ Modern secondary forest regeneration is often affected by edge effects, or changes near an
¹⁰¹ ecosystem boundary, especially in heterogeneously-managed landscapes (*Melo et al., 2013;*

Perfecto et al., 2009). About 70% of all forests have been estimated to be within a km of their edge (*Haddad et al., 2015*), resulting in tropical forests having been estimated to lose ~22% aboveground carbon along heavily-managed edges >100m, in part due to shortening trees and lighter leaf mass (*Ordway and Asner, 2020*). Effects of degraded edges have historically favored tree taxa that tend to be pioneering, or be faster-growing, have lower wood densities, and be less shade-tolerant (*Tabarelli et al., 2008*). Accordingly, secondary forest wood density may also tend to decrease near degraded habitat edges. Additionally, the dominance of pioneering taxa could lead to arrested succession (*Tymen et al., 2016*), which further delays the recruitment of shade-tolerant taxa, as well as associated increases in aboveground biomass, in part due to their higher survival with increasing shade, and tendency toward relatively higher wood densities. However, arrested succession could be prevented, and even typical succession accelerated, if intact forests that were adjacent to regenerating plantations functioned as contributing reservoirs of seeds from later-successional tree taxa. In this case, having a habitat edge near a relatively rich intact forest, rather than near a relatively degraded open area, would instead be an asset to regenerating plantation forest patches, rather than a detriment. Overall, edge effects ultimately have the potential to shape community composition, in part based on the local dispersal kernel patterns of existing taxa (*Wandrag et al., 2017*), which while complicated (*Muller-Landau and Hardesty, 2009*), can also correlate with simpler plant traits like height and seed mass (*Tamme et al., 2014; Thomson et al., 2011*).

Additionally, properties of the tropical forest carbon stores and tree community depend heavily on land-use history and previous management (*Omeja et al., 2012; Pyles et al., 2022*). Overall, legacy effects from management like intensive timber planting could potentially delay or result in non-linear changes between successional stages (*Albrich et al., 2020; Gough et al., 2021*), which would make future management more uncertain, unlike more sustainable thinning practices and agroforestry (*Lefland et al., 2018*). In some cases, the leftover timber stands could provide additional shade, which would not be available in a clear-cut harvested

¹²⁹ timber plantation, and this could help more shade-tolerant taxa establish and recruit better.
¹³⁰ Overall, edge effects near degraded habitat edges are often studied as negative, but conceptual
¹³¹ influences from meta-population (*Levins, 1979*) and meta-community (*Leibold et al., 2004*;
¹³² *Warren et al., 2015*) theories do highlight dispersal as a key process for offsetting extinction
¹³³ debt and thus maintaining biodiversity, thereby potentially making particular edge effects,
¹³⁴ specifically from adjacent intact forests, actually beneficial for regeneration plantation forest
¹³⁵ parcels. Taken together, these ideas suggest that edge effects specifically from adjacent intact
¹³⁶ primary forests, potentially via shade-tolerant dispersal and performance, may indeed facilitate
¹³⁷ plantation forest regeneration. Such a beneficial edge effect may ultimately help explain
¹³⁸ relatively high biodiversity, compared to adjacent stands, found in agroforests (*Oliveira-Neto*
¹³⁹ *et al., 2017*), forests affected by logging (*Clark and Covey, 2012; Edwards et al., 2014*), and
¹⁴⁰ timber plantations (*Pryde et al., 2015*).

¹⁴¹ Influenced by restoration ecology for forest management, this study reports tree regeneration
¹⁴² patterns of an abandoned wet neotropical timber plantation, focused on highlighting edge
¹⁴³ effects from an adjacent primary forest on overall stand properties, tree community compo-
¹⁴⁴ sition, and limited functional trait recovery. We hypothesized that remaining timber trees
¹⁴⁵ would mediate forest regrowth by maintaining shade, which would suppress less shade-tolerant
¹⁴⁶ pioneer tree taxa, and in turn facilitate more shade-tolerant tree taxa, ultimately allowing for
¹⁴⁷ more tree diversity within the regenerating plantation forest in parts that were closer to the
¹⁴⁸ richer edge of the intact unmanaged forest. Accordingly, we predicted more specifically that
¹⁴⁹ further from the intact primary forest edge, canopy light availability would increase, while
¹⁵⁰ stand biomass and diversity would decrease.

₁₅₁ **Methods**

₁₅₂ **Study site**

₁₅₃ This study was done in a neotropical lowland rainforest on the Osa Peninsula at the Greg
₁₅₄ Gund Conservation Center (approx. 8.3778176, -83.2935426) near the Piro Biological Station
₁₅₅ run by Osa Conservation. (See *Taylor et al. (2015)* for a broader ecosystem description
₁₅₆ of the region.) The study site was a regrowing 20 ha timber plantation of *Bombacopsis*
₁₅₇ *quinata* abandoned in ~1990 after the vulnerably dry-adapted species from the Guanacaste
₁₅₈ region (*Hulshof and Powers, 2020*) grew poorly in very wet conditions. This focal secondary
₁₅₉ forest area was roughly triangular, surrounded by primary forest on the two S and NW sides
₁₆₀ (Fig 1) and a wide service road on the third NE border, with primary forest beyond it. This
₁₆₁ census was done in 2013 during the rainy season months between June and August.

₁₆₂ **Census design**

₁₆₃ Edge effects were studied by dividing the secondary forest area into six discrete 50 m strata
₁₆₄ spanning 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to
₁₆₅ the E (Fig 1), using available GIS software (*ArcGIS 10*, esri.com, and *QGIS 2*, qgis.org). Note
₁₆₆ that in line with hypotheses about facilitated regeneration, this study most often referred
₁₆₇ to the “edge” of the regenerating plantation forest as the part closest to the unmanaged
₁₆₈ intact forest, where trees may be dispersing from, rather than the open service road, which is
₁₆₉ usually the focus of other studies evaluating effects of forest fragmentation and degradation,
₁₇₀ rather than restoration. Each stratum was randomly filled with a number of 21 x 21 m square
₁₇₁ census plots oriented N that was proportional to its area—specifically with 11, eight, five, three,
₁₇₂ two, and one plot(s), respectively, as distance away from primary forest increased. Given
₁₇₃ the small size of the last 300 m distance stratum (Fig 1c), one census plot was sufficiently
₁₇₄ representative. All data were later centered at the stratum level, so resulting trends were not

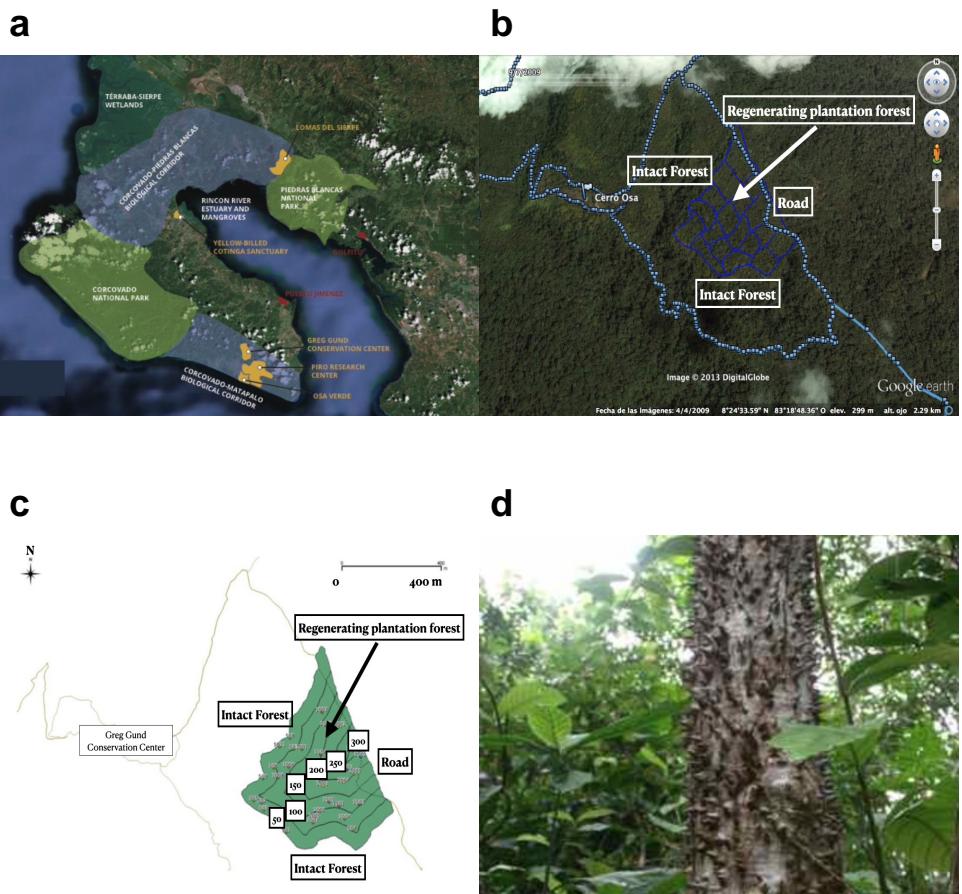


Figure 1: Map of (a) conservation areas and (b) study site (c) showing plot design with 50 m distance strata bins, and (d) focal plantation timber taxon *Bombacopsis quinata* on Osa Peninsula, Costa Rica. Map image data © 2022 Osa Conservation, © 2009 Google. Map GIS data and photo credit: Max Villalobos, Nicholas Medina.

¹⁷⁵ weighted by distance bands with more plots in them. The total area of the 30 census plots
¹⁷⁶ equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to similar
¹⁷⁷ studies (*Onyekwelu and Olabiwonnu, 2016*).

¹⁷⁸ Plot measurements

¹⁷⁹ Light reaching the forest floor was measured at the center of each plot at chest height using
¹⁸⁰ a densiometer (*Forestry Suppliers, Inc.*), as an average of four readings taken facing each
¹⁸¹ cardinal direction. The slope of the forest floor was measured using a rangefinder (*Bushnell,*
¹⁸² *Forestry Suppliers, Inc*) to measure the distance the diagonal between two plot corners and
¹⁸³ triangulate the observation angle.

¹⁸⁴ The diameter of all stems >10 cm wide were recorded in each census plot, totaling over 1,243
¹⁸⁵ trees. In cases where a tree split into 2 or more stems below breast height, each stem was
¹⁸⁶ measured separately; in cases where a stem split only above breast height, it was measured
¹⁸⁷ as a single stem. Tree height was recorded by measuring distances to both the crown and the
¹⁸⁸ stem at chest height (~2.7 m) using a rangefinder (*Bushnell, Forestry Suppliers, Inc.*) and
¹⁸⁹ triangulating the missing side length.

¹⁹⁰ Taxa were identified by local experts, and trait information was gathered from the literature.
¹⁹¹ Final traits used only included successional stage (early, late) and main dispersal mode (wind,
¹⁹² animal, water), which were ultimately matched to species using only the specific dataset made
¹⁹³ available by *Werden et al. (2020)*. Otherwise wood tissue carbon was matched to genera
¹⁹⁴ with the GLOWCAD database (*Doraisami et al., 2022*), given high taxonomic alignment of
¹⁹⁵ this trait above the species level (*Chave et al., 2006*).

¹⁹⁶ Aboveground biomass (AGB) was calculated at the individual stem level using the allometric
¹⁹⁷ equation by *Chave et al. (2015)* and later centered at the plot level. The equation specifically
¹⁹⁸ for wet tropical forests was used, which has performed slightly better compared to both
¹⁹⁹ pantropical and previous other models by (*Alvarez et al., 2012; Chave et al.; 2005; Ngomanda*

200 *et al., 2014*). The equation version with height was used since height was accessibly measurable
201 and has shown improved local accuracy (*Domke et al., 2012*). Wood density (or specific
202 gravity) values when available also improve biomass estimates even more than height (*Van
203 Breugel et al., 2011*). The equation used was:

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

204 with diameter D in cm, height H in m, and wood density or specific gravity p in $g\text{ cm}^{-3}$. DBHs
205 and heights were measured in the field and wood densities were extracted from available
206 literature. Values were updated using the pipeline developed in the *BIOMASS* 2.1.8 R
207 software package by *Réjou-Méchain et al. (2017)*, which notably replaced unknown wood
208 density values with plot-level averages instead during stem biomass calculations.

209 Statistical analyses

210 For all response variables, data were centered using medians at the plot level, followed by
211 the discrete distance stratum level where applicable, which was most cases and indicated on
212 figures. These medians were then subjected to linear regression with distance to intact forest
213 edge as the only independent variable, which was binned discretely according to census design.
214 All regressions were run through assumption checks of residual normality with Shapiro-Wilk
215 tests and equal variance with Levene tests, using base R version 4.2.1 (2022-06-23) and *rstatix*
216 0.7.0 package functions (*R Core Team, 2022*).

217 Non-linear regressions were run using the function *poly()* in the base R package *stats* 4.2.1,
218 which was only ultimately recorded for stem density and richness variables, based on sig-
219 nificance and explained variance over linear models. All trees censused were included in
220 each analysis, including unidentified taxa, which were only grouped together for taxonomic
221 analyses and whose exclusion did not affect observed patterns shown in results. Community
222 analysis and ordination was done as a PERMANOVA with the *adonis()* function from the

223 *vegan* 2.6.4 R package (*Dixon, 2003*). Data and code were organized with R packages *here*
224 (*Müller, 2020*), *bookdown* (*Xie, 2022*), and *grateful* (*Rodríguez-Sánchez et al., 2022*), and
225 internal pipeline *oir* (*Medina, 2022a*), and are stored at github.com/nmedina17/osa (*Medina,*
226 *2022b*).

227 Results

228 Biomass

229 Aboveground biomass did not tend to change with distance to primary forest edge (Fig
230 2a), despite significant trends with underlying related variables (Fig 2). Median plot wood
231 density tended to increase marginally significantly ($p=0.105$) with edge distance by 0.00019
232 per m explaining $\sim 10\%$ of variance among median distance strata values (Fig 2b), while
233 tissue carbon did not change significantly with distance to forest edge (Fig 2c). Plot stem
234 density also tended to increase significantly ($p=0.03$) with edge distance but more strongly
235 and non-linearly, by $\sim 17.39 \pm 3.4$ per m (Fig 2d). At this stage in forest regeneration, canopy
236 light availability did not tend to change with distance from forest edge (Fig 2e). Notably, tree
237 diversity decreased marginally significantly ($p=<0.0001$) by ~ 1 per g plot wood density, yet
238 only explaining $\sim 4\%$ of variance (Fig 2f). Additional variables tested, including maximum
239 height and diameter, tended to stay the same across the edge gradient (*data not shown*).

240 ## |

241 Composition

242 Overall diversity changed significantly with distance to primary forest edge (Fig 3). Diversity
243 significantly ($p=0.003$) decreased non-linearly by $\sim 0.5 \pm 0.029$ per m as distance to primary

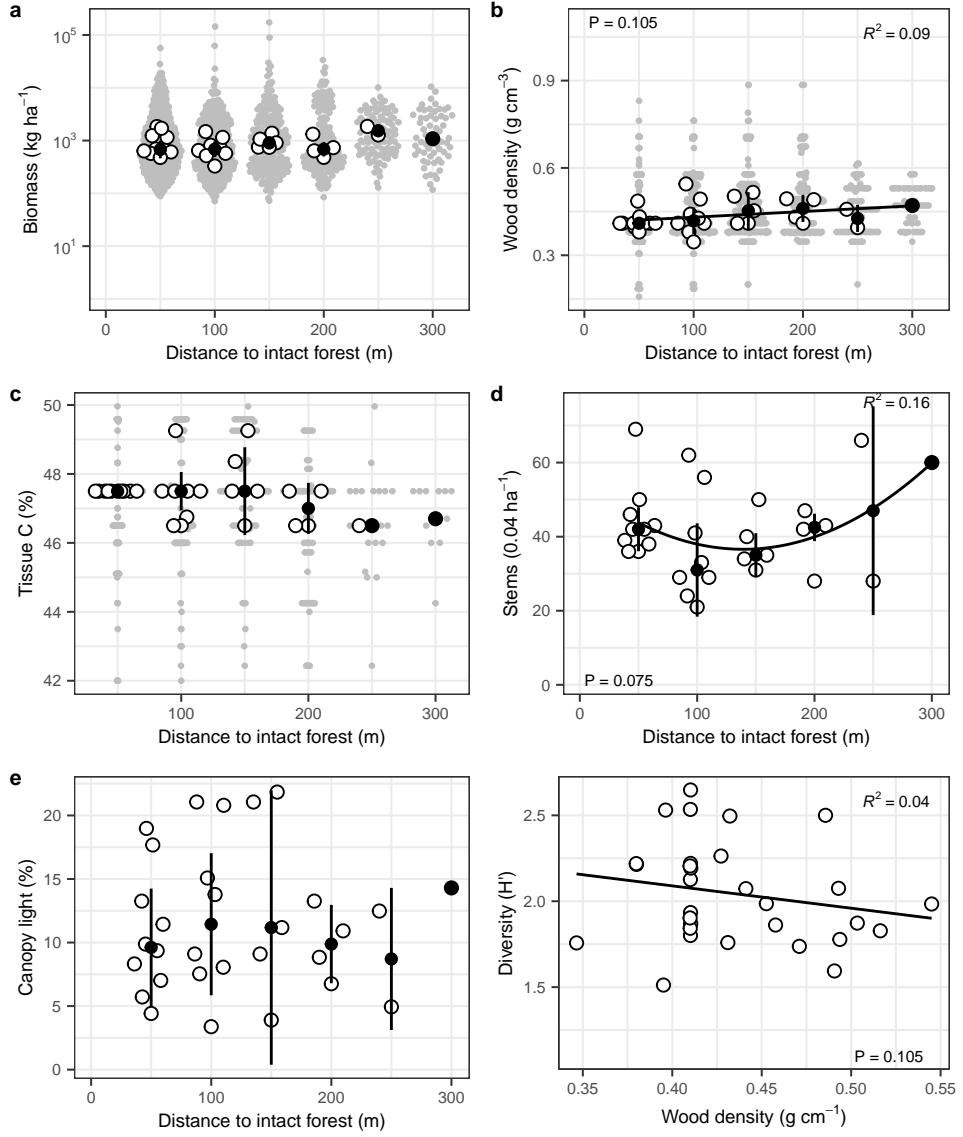


Figure 2: Plot stand properties, namely (a) biomass, (b) wood density, (c) tissue carbon, (d) stem density, (e) canopy light availability, all across distance to primary forest edge gradient, and (f) diversity against wood density. Grey dots show individual tree values, white dots with border show plot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

²⁴⁴ forest edge increased, which explained 73% of variance among distance strata medians (Fig
²⁴⁵ 3a) – while in contrast taxonomic richness increased slightly ($p=0.067$) and linearly by
²⁴⁶ 0.0063 ± 0.0025 per m and had 16% variance explained among distance strata (Fig 3b).
²⁴⁷ Community composition and beta diversity also changed significantly ($p=0.01$) with 11.38%
²⁴⁸ variance among distance strata explained by distance to primary forest edge, and the first two
²⁴⁹ principal components explaining 47% and 23% totaling 70% of variance among calculated
²⁵⁰ plot distances (Fig 3d). Key abundant taxa *Vochysia* and *Ficus* showed different responses –
²⁵¹ *Vochysia* nearly tended to decrease with distance to primary forest edge (Fig 3e), while *Ficus*
²⁵² decreased marginally significantly ($p=0.088$) and linearly by -62.62 ± 25.05 per m with ~20%
²⁵³ variance among distance strata explained (Fig 3f). Other taxa did not change significantly
²⁵⁴ with distance to intact forest (*data not shown*).

²⁵⁵ ## |

²⁵⁶ Traits

²⁵⁷ Overall trait regeneration highlighted successional stage associations over primary dispersal
²⁵⁸ mode along distance to primary forest (Fig 4). Taxa associated with both early and late
²⁵⁹ successional stages decreased significantly ($p=0.042$) and curvi-linearly by $\sim -584.87 \pm 167.31$
²⁶⁰ kg per m with distance to edge explaining ~14% variance among distance strata medians
²⁶¹ (Fig 4a). Dispersal modes did not show consistent trends in biomass with increasing distance
²⁶² to edge (Fig 4b).

²⁶³ ## |

²⁶⁴ ## |

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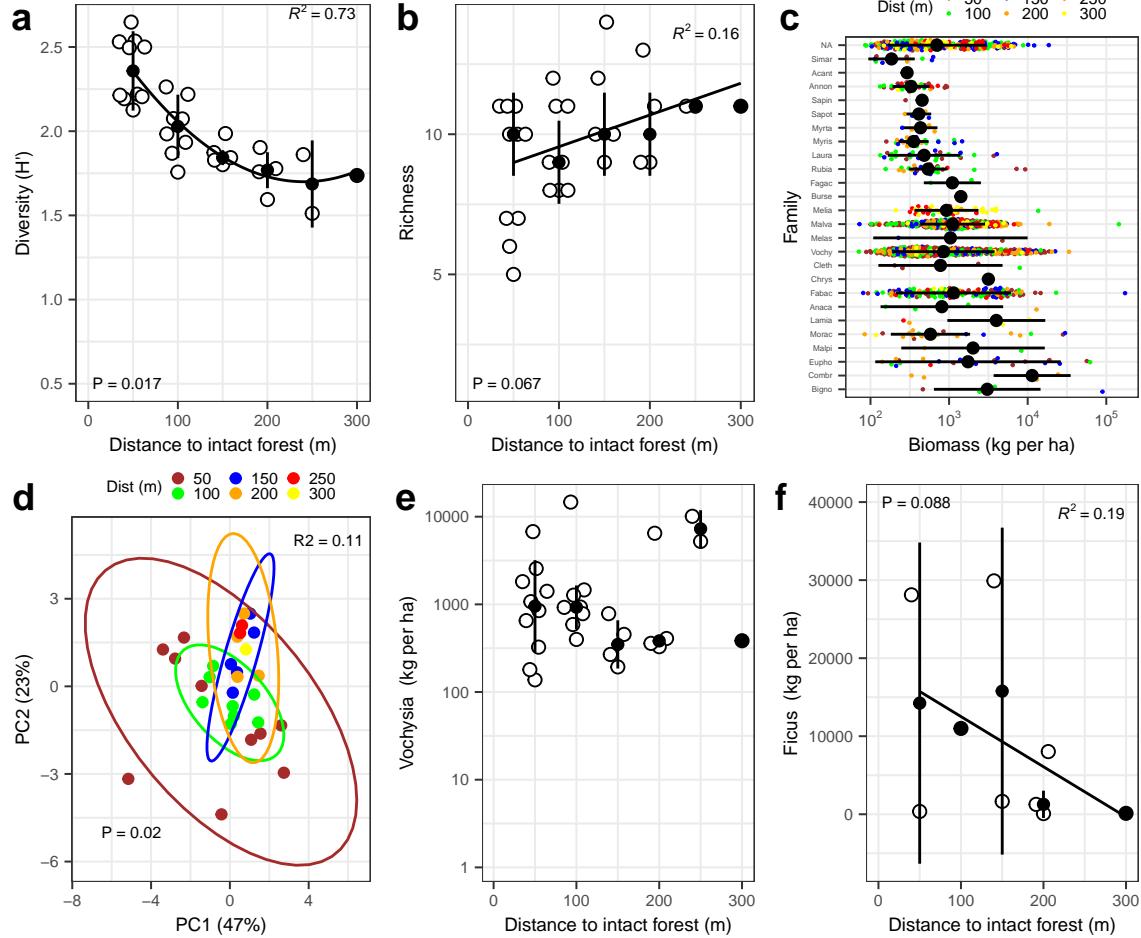


Figure 3: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show plot-level data binned into discrete distance strata medians ± 1 absolute deviation,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

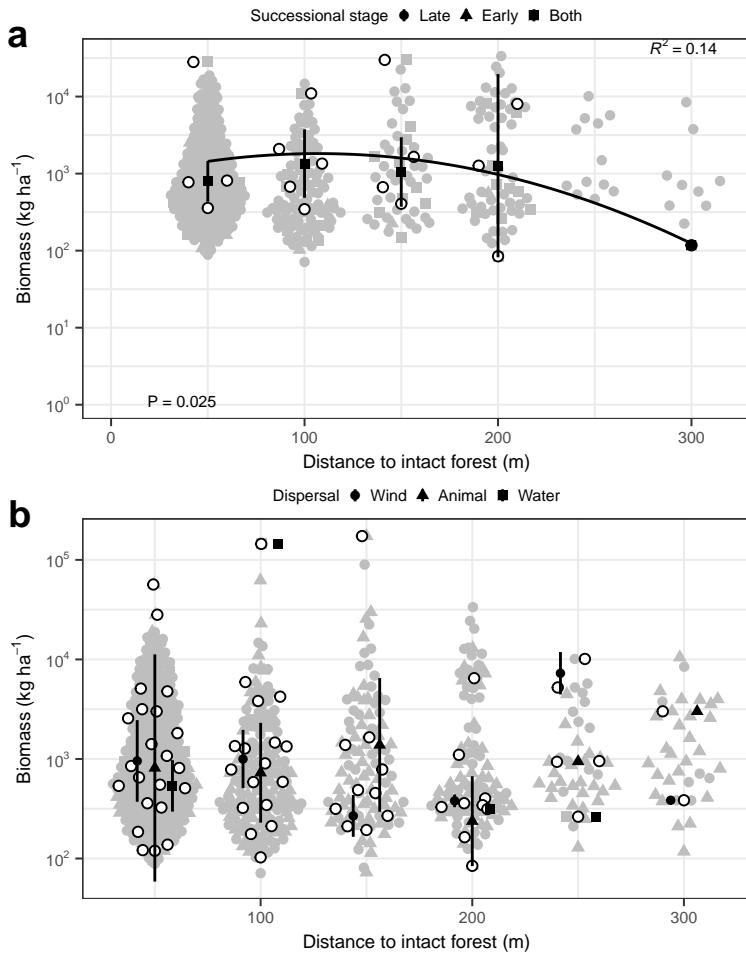


Figure 4: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show plot-level data binned into discrete distance strata medians ± 1 absolute deviation,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

²⁶⁶ **Discussion**

²⁶⁷ This study found significant edge effects on secondary forest stand wood and stem density,
²⁶⁸ tree diversity and community composition, and some functional traits, yet not on overall
²⁶⁹ aboveground biomass. It was initially hypothesized that community composition would vary
²⁷⁰ with distance to high-quality intact primary forest edge, favoring more shade-tolerant taxa,
²⁷¹ due to light availability and dispersal potential. The evidence presented here supported edge
²⁷² effects on community composition and biomass of taxa that were associated with both early-
²⁷³ and late-successional stages, but without detectable roles for light availability or general
²⁷⁴ dispersal mode. Accordingly, this suggests that edge effects do significantly change humid
²⁷⁵ tropical forest community taxonomic and functional composition, but primarily due to factors
²⁷⁶ other than light competition or dispersal limitation (*Krishnadas et al., 2020*), and also
²⁷⁷ suggests that aboveground biomass and even low taxonomic richness are resilient after a
²⁷⁸ decade of regeneration.

²⁷⁹ Aboveground biomass storage is a key global ecosystem function and service, but edge effects
²⁸⁰ tend to release about one-third of carbon lost from tropical deforestation (*Brinck et al., 2017*),
²⁸¹ with more expected in the future (*Mitchard, 2018*). Management has been found to explain
²⁸² most of biomass variation among tropical forest fragments, and wood density ~10% biomass
²⁸³ variation (*Pyles et al., 2022*). Additionally, this study contributes that management via
²⁸⁴ edge effects can also mediate ~10% of wood density variation without affecting local biomass,
²⁸⁵ although median stem wood density can describe regional spatial biomass patterns (*Baker et*
²⁸⁶ *al., 2004*). In this study, wood density and richness values may have been pulled down by
²⁸⁷ early-successional clonal trees closest to the primary forest, which tend to have lower wood
²⁸⁸ densities, lowering carbon (*Gonzalez J and Fisher, 1998; Pyles et al., 2022*), and increasing
²⁸⁹ nearby stem density. Lower wood density can also reflect more dynamic forest stands (*Malhi*
²⁹⁰ *et al., 2006*) with higher tree turnover, a consequence of forest fragmentation (*Nascimento*
²⁹¹ *and Laurance, 2004*) together with other global change drivers (*Laurance et al., 2014*), and

292 may also reflect possible differences in soil fertility (*Malhi et al., 2004*), all of which represent
293 possible future research directions, beyond strictly neutral dynamics (*Terborgh et al., 1995*).
294 Furthermore, light availability at the plot level did not affect biomass storage, but instead,
295 individual light gaps may be more important for biomass dynamics (*Chazdon and Fetcher,*
296 *1984*).

297 Edge effects have been shown in other studies not only to lower forest biomass, but also to
298 change community composition (*Anderson et al., 2022*), and in addition this study contributes
299 that the decline in diversity can be rapid and non-linear across edge gradients, along with
300 supporting the likelihood of changes to community composition lasting decades. This rapid
301 loss of diversity across the edge gradient may be in part due to existing higher yet constant
302 levels of shade limiting shade-intolerant seedling recruitment and/or performance, together
303 with insufficient time for slower-growing shade-tolerant taxa to accumulate significant amounts
304 of biomass. Another possible factor may be Janzen-Connell processes (*Terborgh, 2020; Wills,*
305 *2006*), including conspecific negative density-dependence of seedling survival on basal area
306 (*Comita and Hubbell, 2009*), as well as overall short dispersal kernels, whose effects can be
307 mediated by shade (*Comita et al., 2014*) and in part by higher fungal pathogen pressure near
308 conspecifics (*Jia et al., 2020*). While both diversity and community composition changed
309 significantly with distance to intact forest in this study, the biomass of most individual
310 taxa, surprisingly, tended to stay the same along the edge gradient. This lack of significant
311 individual taxon biomass responses along this edge gradient could be due to stochastic
312 population factors affecting their biomass growth, perhaps widening variability. Regardless
313 of the underlying process, these absent patterns do also help explain the lack of pattern
314 observed with plot biomass overall across the edge gradient. This explanation points to
315 future studies of taxon-specific responses to edge effects, to help explain overall forest biomass
316 dynamics near habitat edge. More specifically here, the biomass of the most abundant
317 taxon *Vochysia* was resilient to edge effects in this study, however, that of the taxon *Ficus*,
318 key for frugivores like birds and bats (*Cottee-Jones et al., 2015; Rafidison et al., 2020*),

319 was significantly lowered across the secondary forest edge, pointing to potentially different
320 responses of biomass and local food web associated ecosystem services. Results suggest that
321 this pattern is specific to this locally widespread *Ficus* genus, since the overall biomass of
322 other animal-dispersed taxa as a whole tended to stay the same across the edge gradient
323 studied here. Interestingly, community composition also appeared to show lower variance
324 across the edge gradient, although testing this observation in a forested area with evenly
325 distributed area among distance strata bands would provide additional support.

326 Characterizing community composition by functional traits is also increasingly studied
327 (*Kearney et al., 2021*), but less so regarding edge effects. A study in Madagascar found
328 lower phylogenetic diversity closer to degraded forest edge, but no change in aboveground
329 biomass (*Razafindratsima et al., 2018*). This study presents similar results in showing lower
330 taxonomic diversity, although biomass specifically of taxa associated with both early- and
331 late-successional stages also decreased with away from primary forest edge. This resulting
332 decrease by successional stage could be explained by slightly lower habitat quality inferred
333 near exposed habitat edges near roads, and accordingly relatively higher habitat quality near
334 closed primary forest edge (*Ries et al., 2004*). While lower biomass of succession-agnostic taxa
335 further from primary forest edge appears consistent with the expected forms of group-level
336 dispersal kernels as an explanation, the lack of significant pattern along forest edge when
337 binned by broad dispersal mode that was found here may limit the potential of seed dispersal
338 to explain biomass trends. Instead, seedling survival may have been more important than
339 dispersal in accumulating basal area and biomass (*Comita and Hubbell, 2009*). For taxa
340 primarily dispersed by animals instead of wind, this could be explained by potentially broader
341 local limitations in animal dispersal activity or abundance. Additionally, the potential for
342 nearby dispersal to facilitate reforestation could be tested in future studies by measuring
343 taxon-specific dispersal kernels.

344 Overall, this study highlights how abandoned wet tropical timber plantation can regenerate
345 in alongside fragmented forests. Results support related syntheses that tropical forest

³⁴⁶ biomass and taxonomic richness often regrows relatively quickly (*Davies et al., 2021*), while
³⁴⁷ taxonomic composition recovers much more slowly, if not diverging altogether (*Norden et*
³⁴⁸ *al., 2015*). These findings can suggest that more efficient reforestation could more actively
³⁴⁹ target biodiversity conservation over other resilient functions like carbon storage, and that
³⁵⁰ restoration efforts could include focusing activities like native species planting efforts on
³⁵¹ degraded habitat edges away from primary forest edges, and investing less in areas closer to
³⁵² existing forest edges, where recruitment may already maintain diversity levels. As forests
³⁵³ continue to become fragmented (*Haddad et al., 2015*), understanding how to work with
³⁵⁴ natural regeneration patterns around edge effects will likely become increasingly important.

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³⁶⁶ **Author contributions**

³⁶⁷ NM, MV and AJ contributed to study conceptualization, design, administration, and super-
³⁶⁸ vision; NM and AJ contributed to funding acquisition; NM, AM, and EC, contributed to key
³⁶⁹ data collection; NM and MV contributed to data analysis; NM wrote initial draft and later
³⁷⁰ revisions.

³⁷¹ Study team includes and recognizes diverse and historically-excluded contributions to research;
³⁷² with bilingual communication efforts completed and pending.

³⁷³ **Data statement**

³⁷⁴ Code stored at github.com/nmedina17/osa (*Medina, 2022b*).

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