

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

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¹⁹ **Abstract**

²⁰ About half of all forests are tropical and secondary, making tropical forest regeneration integral
²¹ to future forests. Tree stand biomass and taxonomic richness can recover in a few decades, but
²² relative abundances may lag indefinitely. Since most forests are within a km of a habitat edge,
²³ edge effects likely affect community composition regeneration. However, most studies assess
²⁴ how degraded edges affect intact forests, leaving it unclear whether higher-quality edges could
²⁵ facilitate regeneration of nearby degraded forests. Notably, higher quality edges near intact
²⁶ forests could promote processes like dispersal and wood biomass accumulation that effectively
²⁷ accelerate succession, leading to better performance of shade-tolerant taxa compared to
²⁸ pioneer taxa in the early stages of forested plantation regeneration. This study addressed how
²⁹ wet tropical forested plantation regeneration was affected by distance to adjacent intact forest
³⁰ edge. It was hypothesized that old timber plantations facilitate regeneration by increasing
³¹ available shade, favoring the presence and biomass of later-successional taxa, ultimately
³² changing community composition overall. A wet neotropical timber plantation reforested
³³ after 20 years and adjacent to primary forest was censused for trees along a 300 m edge
³⁴ distance gradient, and analysis matched identified taxa to broad dispersal mode and wood
³⁵ density traits using relevant literature.

³⁶ As distance from primary forest edge increased, stem and wood density tended to increase
³⁷ significantly, with ~10% variation explained, while biomass and canopy light surprisingly
³⁸ tended to stay the same. Stand tree richness also tended to increase significantly, but
³⁹ diversity decreased steeply and non-linearly, explained in part by wood density, and taxonomic
⁴⁰ composition varied notably. Finally, tree taxa associated with both early and late successional
⁴¹ stages decreased significantly, as well as genus *Ficus*, but biomass by dispersal mode did not
⁴² tend to change. Overall this study supports that stand composition is less resilient and more
⁴³ subject to edge effects than biomass and richness, suggesting that global forests will likely be
⁴⁴ distinctly new assemblages in the future, with timber and biodiversity trade-offs occurring

⁴⁵ based on local and regional management activity.

⁴⁶ **Introduction**

⁴⁷ Forest and landscape restoration is a key international conservation and climate change
⁴⁸ adaptation strategy (*De Pinto et al., 2020*). While tropical forests specifically store most land
⁴⁹ biomass (*Pan et al., 2013*), most are now secondary (*FAO, 2020*) and functionally degraded
⁵⁰ (*Hubau et al., 2020*). This likely amplifies amid increasing climate stressors (*Anderegg et al.,*
⁵¹ *2022*) and collective management issues, including insufficient policy support (*Chazdon, 2018*)
⁵² via skewed priorities (*Pyron and Mooers, 2022*). Overall, secondary forests can regenerate
⁵³ relatively quickly compared to old-growth forests, in some ways. Neotropical secondary forests
⁵⁴ can grow quickly enough to accumulate biomass >10x faster than old-growth forests (*Finegan,*
⁵⁵ *1996; Poorter et al., 2016*), and substantially offset carbon emissions, with estimates ranging
⁵⁶ from ~10% from Amazonian deforestation (*Smith et al., 2020*) to a decade of fossil fuel
⁵⁷ emissions from all of Latin American and the Caribbean (*Chazdon et al., 2016*). They also
⁵⁸ recover taxonomic richness and biomass quite quickly, as well as tree height, averaging 80%
⁵⁹ of old-growth forest levels in just 20 years, especially in wetter regions (*Rozendaal et al.,*
⁶⁰ *2019*). The recovery of species richness alone is beneficial in that it also tends to correlate
⁶¹ with the recovery of some ecosystem services (*Guariguata and Ostertag, 2001; Stanturf et al.,*
⁶² *2014*) like biomass and carbon storage (*Liu et al., 2018*). However, recovery of secondary
⁶³ neotropical forests diverge widely in taxonomic composition (*Norden et al., 2015*), potentially
⁶⁴ taking over a century to recover (*Poorter et al., 2021*) with added variability (*Atkinson et al.,*
⁶⁵ *2022*). Despite being one of the slowest ecosystem properties to recover, restoring recovering
⁶⁶ community composition is often important for preserving rare taxa (*Carlo and Morales,*
⁶⁷ *2016*), which can be keystone to locally-adapted food webs, including birds (*Maas et al.,*
⁶⁸ *2016*). Overall, understanding secondary forest regeneration is key for global biodiversity
⁶⁹ conservation at the global scale.

⁷⁰ Modern secondary forest regeneration is often affected by edge effects, or changes near an
⁷¹ 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

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

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

₁₂₁ **Methods**

₁₂₂ **Study site**

₁₂₃ This study was done in a neotropical lowland rainforest on the Osa Peninsula at the Greg
₁₂₄ Gund Conservation Center (approx. 8.3778176, -83.2935426) near the Piro Biological Station
₁₂₅ run by Osa Conservation. (See *Taylor et al. (2015)* for a broader ecosystem description
₁₂₆ of the region.) The study site was a regrowing 20 ha timber plantation of *Bombacopsis*
₁₂₇ *quinata* abandoned in ~1990 after the vulnerably dry-adapted species from the Guanacaste
₁₂₈ region (*Hulshof and Powers, 2020*) grew poorly in very wet conditions. This focal secondary
₁₂₉ forest area was roughly triangular, surrounded by primary forest on the two S and NW sides
₁₃₀ (Fig 1) and a wide service road on the third NE border, with primary forest beyond it. This
₁₃₁ census was done in 2013 during the rainy season months between June and August.

₁₃₂ **Census design**

₁₃₃ Edge effects were studied by dividing the secondary forest area into six discrete 50 m strata
₁₃₄ spanning 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to
₁₃₅ the E (Fig 1), using available GIS software (*ArcGIS 10*, esri.com, and *QGIS 2*, qgis.org). Note
₁₃₆ that in line with hypotheses about facilitated regeneration, this study most often referred
₁₃₇ to the “edge” of the regenerating plantation forest as the part closest to the unmanaged
₁₃₈ intact forest, where trees may be dispersing from, rather than the open service road, which is
₁₃₉ usually the focus of other studies evaluating effects of forest fragmentation and degradation,
₁₄₀ rather than restoration. Each stratum was randomly filled with a number of 21 x 21 m square
₁₄₁ census plots oriented N that was proportional to its area—specifically with 11, eight, five, three,
₁₄₂ two, and one plot(s), respectively, as distance away from primary forest increased. Given
₁₄₃ the small size of the last 300 m distance stratum (Fig 1c), one census plot was sufficiently
₁₄₄ representative. All data were later centered at the stratum level, so resulting trends were not

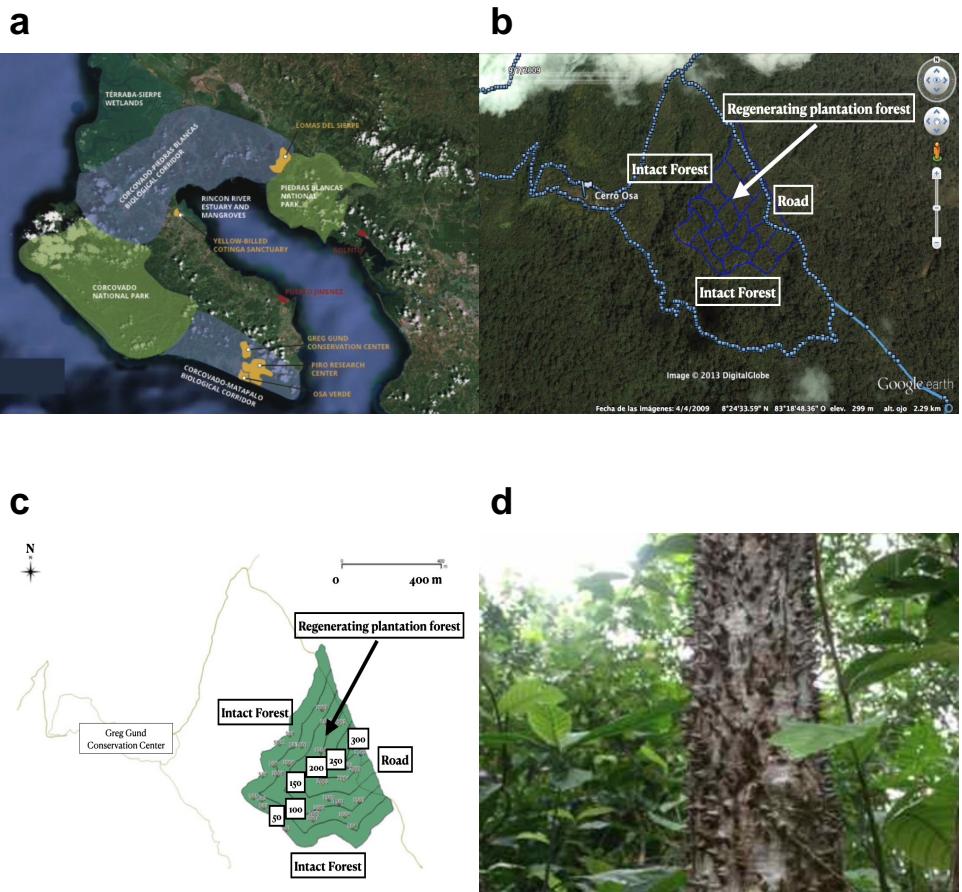


Figure 1: Map of (a) conservation areas and (b) study site (c) showing plot design with 50 m distance strata bins, and (d) focal plantation timber taxon *Bombacopsis quinata* on Osa Peninsula, Costa Rica. Map image data © 2022 Osa Conservation, © 2009 Google. Map GIS data and photo credit: Max Villalobos,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

¹⁴⁵ weighted by distance bands with more plots in them. The total area of the 30 census plots
¹⁴⁶ equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to similar
¹⁴⁷ studies (*Onyekwelu and Olabiwonnu, 2016*).

¹⁴⁸ Plot measurements

¹⁴⁹ Light reaching the forest floor was measured at the center of each plot at chest height using
¹⁵⁰ a densiometer (*Forestry Suppliers, Inc.*), as an average of four readings taken facing each
¹⁵¹ cardinal direction. The slope of the forest floor was measured using a rangefinder (*Bushnell,*
¹⁵² *Forestry Suppliers, Inc*) to measure the distance the diagonal between two plot corners and
¹⁵³ triangulate the observation angle.

¹⁵⁴ The diameter of all stems >10 cm wide were recorded in each census plot, totaling over 1,243
¹⁵⁵ trees. In cases where a tree split into 2 or more stems below breast height, each stem was
¹⁵⁶ measured separately; in cases where a stem split only above breast height, it was measured
¹⁵⁷ as a single stem. Tree height was recorded by measuring distances to both the crown and the
¹⁵⁸ stem at chest height (~2.7 m) using a rangefinder (*Bushnell, Forestry Suppliers, Inc.*) and
¹⁵⁹ triangulating the missing side length.

¹⁶⁰ Taxa were identified by local experts, and trait information was gathered from the literature.
¹⁶¹ Final traits used only included successional stage (early, late) and main dispersal mode (wind,
¹⁶² animal, water), which were ultimately matched to species using only the specific dataset made
¹⁶³ available by *Werden et al. (2020)*. Otherwise wood tissue carbon was matched to genera
¹⁶⁴ with the GLOWCAD database (*Doraisami et al., 2022*), given high taxonomic alignment of
¹⁶⁵ this trait above the species level (*Chave et al., 2006*).

¹⁶⁶ Aboveground biomass (AGB) was calculated at the individual stem level using the allometric
¹⁶⁷ equation by *Chave et al. (2015)* and later centered at the plot level. The equation specifically
¹⁶⁸ for wet tropical forests was used, which has performed slightly better compared to both
¹⁶⁹ pantropical and previous other models by (*Alvarez et al., 2012; Chave et al.; 2005; Ngomanda*

¹⁷⁰ *et al., 2014*). The equation version with height was used since height was accessibly measurable
¹⁷¹ and has shown improved local accuracy (*Domke et al., 2012*). Wood density (or specific
¹⁷² gravity) values when available also improve biomass estimates even more than height (*Van
173 Breugel et al., 2011*). The equation used was:

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

¹⁷⁴ with diameter D in cm, height H in m, and wood density or specific gravity p in $g\text{ cm}^{-3}$. DBHs
¹⁷⁵ and heights were measured in the field and wood densities were extracted from available
¹⁷⁶ literature. Values were updated using the pipeline developed in the *BIOMASS* 2.1.8 R
¹⁷⁷ software package by *Réjou-Méchain et al. (2017)*, which notably replaced unknown wood
¹⁷⁸ density values with plot-level averages instead during stem biomass calculations.

¹⁷⁹ Statistical analyses

¹⁸⁰ For all response variables, data were centered using medians at the plot level, followed by
¹⁸¹ the discrete distance stratum level where applicable, which was most cases and indicated on
¹⁸² figures. These medians were then subjected to linear regression with distance to intact forest
¹⁸³ edge as the only independent variable, which was binned discretely according to census design.
¹⁸⁴ All regressions were run through assumption checks of residual normality with Shapiro-Wilk
¹⁸⁵ tests and equal variance with Levene tests, using base R version 4.2.1 (2022-06-23) and *rstatix*
¹⁸⁶ 0.7.0 package functions (*R Core Team, 2022*).

¹⁸⁷ Non-linear regressions were run using the function *poly()* in the base R package *stats* 4.2.1,
¹⁸⁸ which was only ultimately recorded for stem density and richness variables, based on sig-
¹⁸⁹ nificance and explained variance over linear models. All trees censused were included in
¹⁹⁰ each analysis, including unidentified taxa, which were only grouped together for taxonomic
¹⁹¹ analyses and whose exclusion did not affect observed patterns shown in results. Community
¹⁹² analysis and ordination was done as a PERMANOVA with the *adonis()* function from the

¹⁹³ *vegan* 2.6.4 R package (*Dixon, 2003*). Data and code were organized with R packages *here*
¹⁹⁴ (*Müller, 2020*), *bookdown* (*Xie, 2022*), and *grateful* (*Rodríguez-Sánchez et al., 2022*), and
¹⁹⁵ internal pipeline *oir* (*Medina, 2022a*), and are stored at github.com/nmedina17/osa (*Medina,*
¹⁹⁶ *2022b*) and <https://doi.org/10.5281/zenodo.7406478> (*Medina, 2022c*).

¹⁹⁷ Results

¹⁹⁸ Biomass

¹⁹⁹ Aboveground biomass did not tend to change with distance to primary forest edge (Fig
²⁰⁰ 2a), despite significant trends with underlying related variables (Fig 2). Median plot wood
²⁰¹ density tended to increase marginally significantly ($p=0.105$) with edge distance by 0.00019
²⁰² per m explaining $\sim 10\%$ of variance among median distance strata values (Fig 2b), while
²⁰³ tissue carbon did not change significantly with distance to forest edge (Fig 2c). Plot stem
²⁰⁴ density also tended to increase significantly ($p=0.03$) with edge distance but more strongly
²⁰⁵ and non-linearly, by $\sim 17.39 \pm 3.4$ per m (Fig 2d). At this stage in forest regeneration, canopy
²⁰⁶ light availability did not tend to change with distance from forest edge (Fig 2e). Notably, tree
²⁰⁷ diversity decreased marginally significantly ($p=<0.0001$) by ~ 1 per g plot wood density, yet
²⁰⁸ only explaining $\sim 4\%$ of variance (Fig 2f). Additional variables tested, including maximum
²⁰⁹ height and diameter, tended to stay the same across the edge gradient (*data not shown*).

²¹⁰ ## |

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²¹¹ Composition

²¹² Overall diversity changed significantly with distance to primary forest edge (Fig 3). Diversity
²¹³ significantly ($p=0.003$) decreased non-linearly by $\sim 0.5 \pm 0.029$ per m as distance to primary

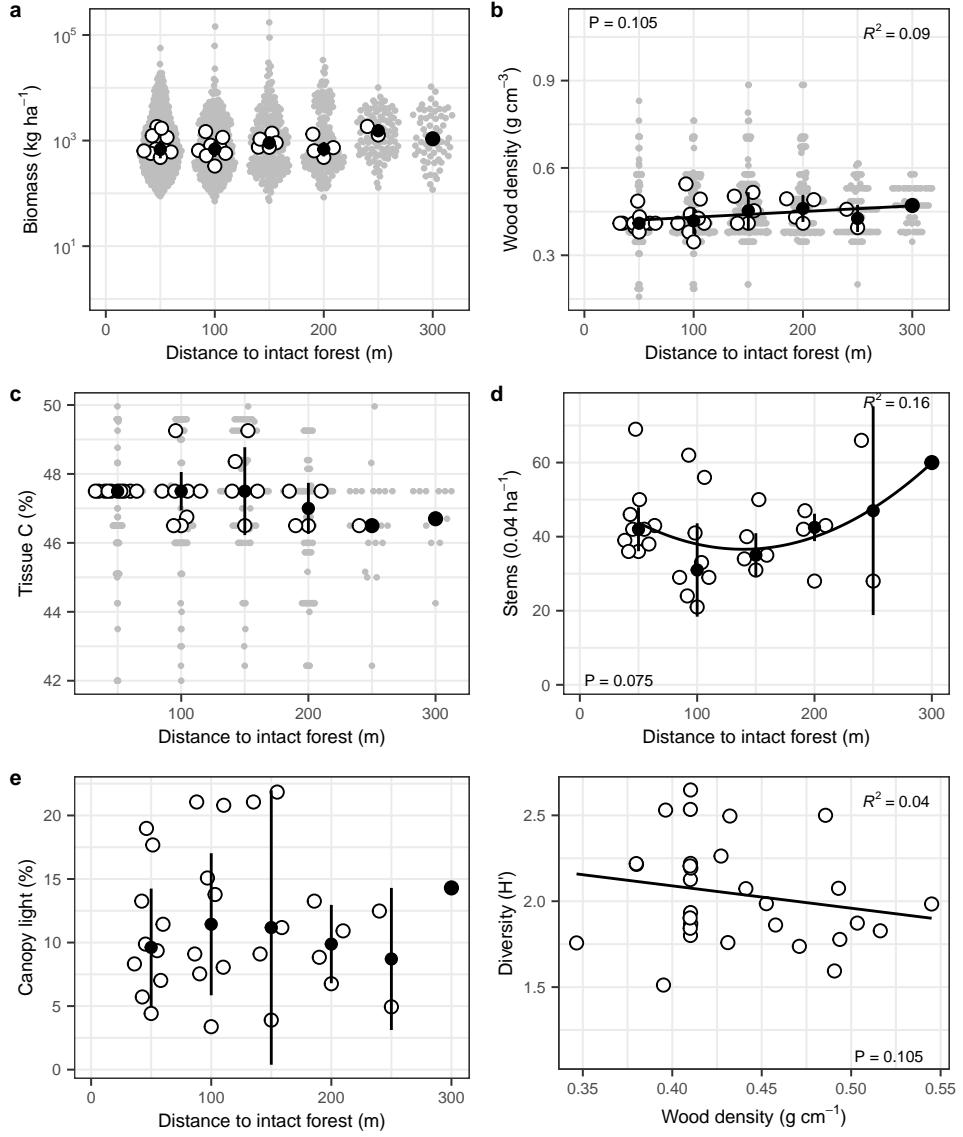


Figure 2: Plot stand properties, namely (a) biomass, (b) wood density, (c) tissue carbon, (d) stem density, (e) canopy light availability, all across distance to primary forest edge gradient, and (f) diversity against wood density. Grey dots show individual tree values, white dots with border show plot 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.

214 forest edge increased, which explained 73% of variance among distance strata medians (Fig
215 3a) – while in contrast taxonomic richness increased slightly ($p=0.067$) and linearly by
216 0.0063 ± 0.0025 per m and had 16% variance explained among distance strata (Fig 3b).
217 Community composition and beta diversity also changed significantly ($p=0.01$) with 11.38%
218 variance among distance strata explained by distance to primary forest edge, and the first two
219 principal components explaining 47% and 23% totaling 70% of variance among calculated
220 plot distances (Fig 3d). Key abundant taxa *Vochysia* and *Ficus* showed different responses –
221 *Vochysia* nearly tended to decrease with distance to primary forest edge (Fig 3e), while *Ficus*
222 decreased marginally significantly ($p=0.088$) and linearly by -62.62 ± 25.05 per m with ~20%
223 variance among distance strata explained (Fig 3f). Other taxa did not change significantly
224 with distance to intact forest (*data not shown*).

225 ## |

226 Traits

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

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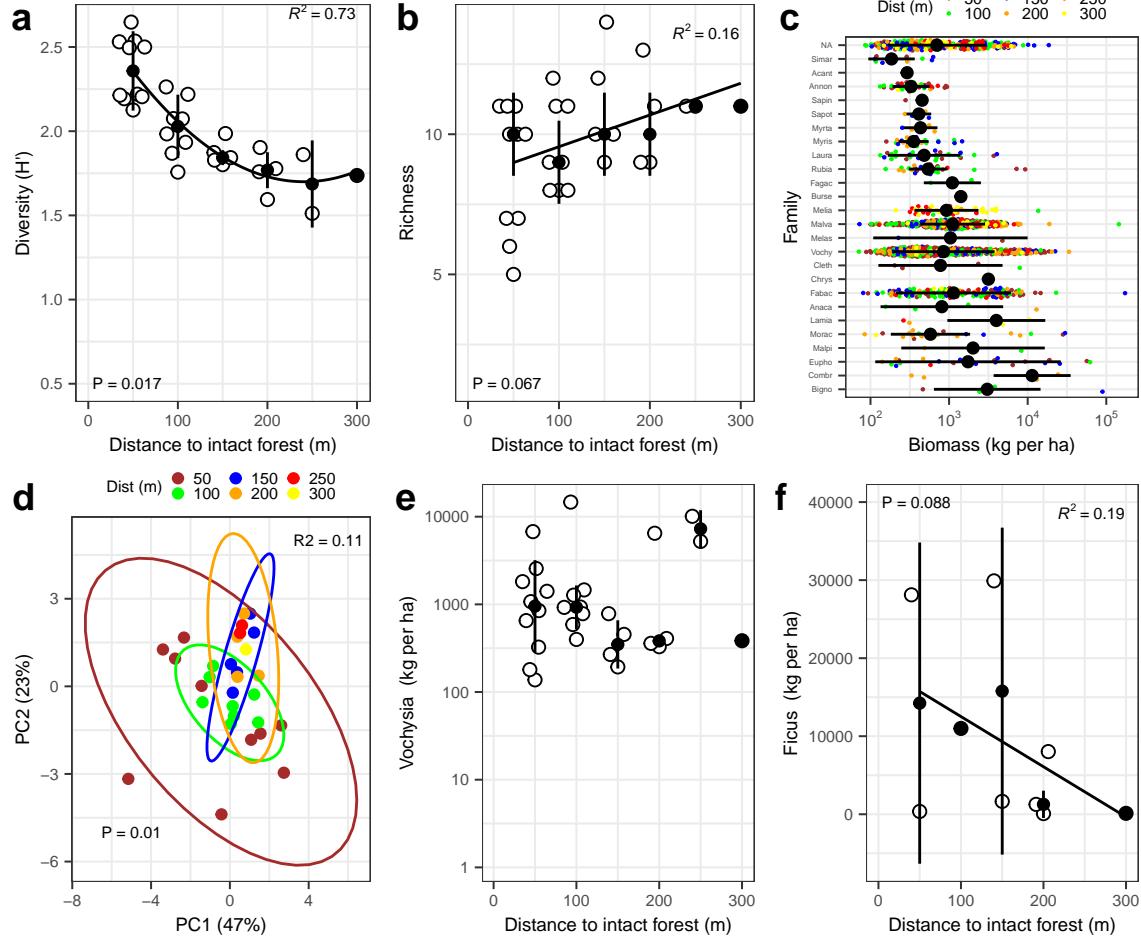


Figure 3: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show plot-level data binned into discrete distance strata medians ± 1 absolute deviation,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

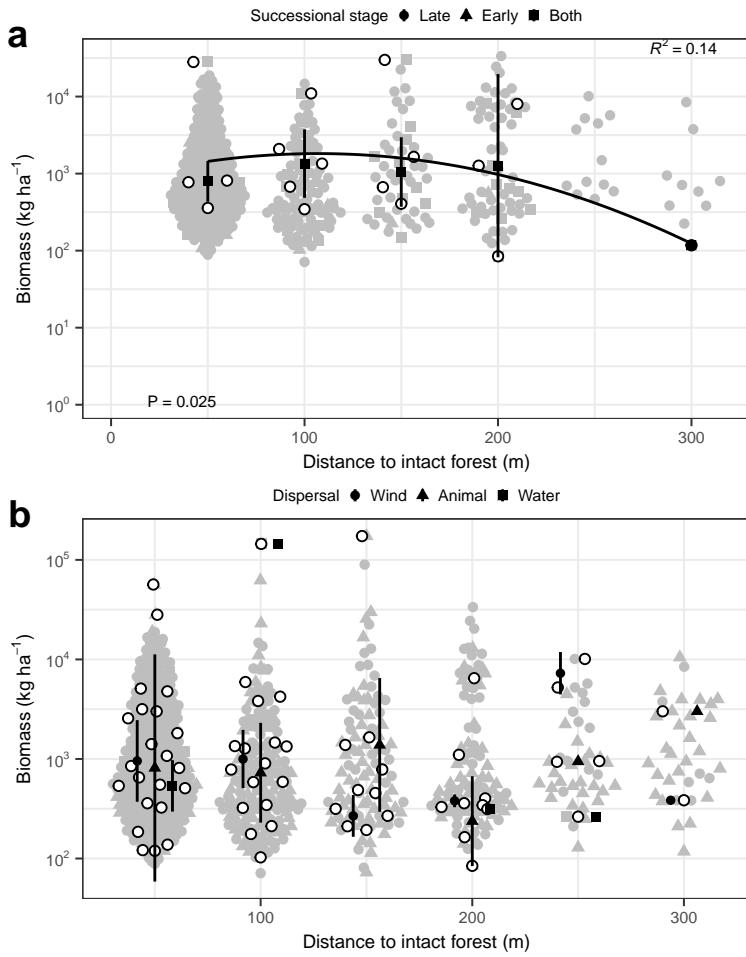


Figure 4: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show plot-level data binned into discrete distance strata medians ± 1 absolute deviation,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

²³⁶ **Discussion**

²³⁷ This study found significant edge effects on secondary forest stand wood and stem density,
²³⁸ tree diversity and community composition, and some functional traits, yet not on overall
²³⁹ aboveground biomass. It was initially hypothesized that community composition would vary
²⁴⁰ with distance to high-quality intact primary forest edge, favoring more shade-tolerant taxa,
²⁴¹ due to light availability and dispersal potential. The evidence presented here supported edge
²⁴² effects on community composition and biomass of taxa that were associated with both early-
²⁴³ and late-successional stages, but without detectable roles for light availability or general
²⁴⁴ dispersal mode. Accordingly, this suggests that edge effects do significantly change humid
²⁴⁵ tropical forest community taxonomic and functional composition, but primarily due to factors
²⁴⁶ other than light competition or dispersal limitation (*Krishnadas et al., 2020*), and also
²⁴⁷ suggests that aboveground biomass and even low taxonomic richness are resilient after a
²⁴⁸ decade of regeneration.

²⁴⁹ Aboveground biomass storage is a key global ecosystem function and service, but edge effects
²⁵⁰ tend to release about one-third of carbon lost from tropical deforestation (*Brinck et al., 2017*),
²⁵¹ with more expected in the future (*Mitchard, 2018*). Management has been found to explain
²⁵² most of biomass variation among tropical forest fragments, and wood density ~10% biomass
²⁵³ variation (*Pyles et al., 2022*). Additionally, this study contributes that management via
²⁵⁴ edge effects can also mediate ~10% of wood density variation without affecting local biomass,
²⁵⁵ although median stem wood density can describe regional spatial biomass patterns (*Baker et*
²⁵⁶ *al., 2004*). In this study, wood density and richness values may have been pulled down by
²⁵⁷ early-successional clonal trees closest to the primary forest, which tend to have lower wood
²⁵⁸ densities, lowering carbon (*Gonzalez J and Fisher, 1998; Pyles et al., 2022*), and increasing
²⁵⁹ nearby stem density. Lower wood density can also reflect more dynamic forest stands (*Malhi*
²⁶⁰ *et al., 2006*) with higher tree turnover, a consequence of forest fragmentation (*Nascimento*
²⁶¹ *and Laurance, 2004*) together with other global change drivers (*Laurance et al., 2014*), and

may also 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*).

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

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

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

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

³¹⁶ biomass and taxonomic richness often regrows relatively quickly (*Davies et al., 2021*), while
³¹⁷ taxonomic composition recovers much more slowly, if not diverging altogether (*Norden et*
³¹⁸ *al., 2015*). These findings can suggest that more efficient reforestation could more actively
³¹⁹ target biodiversity conservation over other resilient functions like carbon storage, and that
³²⁰ restoration efforts could include focusing activities like native species planting efforts on
³²¹ degraded habitat edges away from primary forest edges, and investing less in areas closer to
³²² existing forest edges, where recruitment may already maintain diversity levels. As forests
³²³ continue to become fragmented (*Haddad et al., 2015*), understanding how to work with
³²⁴ natural regeneration patterns around edge effects will likely become increasingly important.

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³³⁴ translation assistance.

³³⁵ Authors declare no conflicts of interest.

³³⁶ **Author contributions**

³³⁷ NM, MV and AJ contributed to study conceptualization, design, administration, and super-
³³⁸ vision; NM and AJ contributed to funding acquisition; NM, AM, and EC, contributed to key
³³⁹ data collection; NM and MV contributed to data analysis; NM wrote initial draft and later
³⁴⁰ revisions.

³⁴¹ Study team includes and recognizes diverse and historically-excluded contributions to research;
³⁴² with bilingual communication efforts completed and pending.

³⁴³ **Data statement**

³⁴⁴ Code stored at github.com/nmedina17/osa (*Medina, 2022b*) with data stored at <https://doi.org/10.5281/zenodo.7406478> (*Medina, 2022c*).

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