

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

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¹¹ effect; aboveground biomass; shade

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₁₆ **Abstract**

₁₇ About half of all forests are tropical and secondary, making tropical forest regeneration
₁₈ integral to future forests. Tree stand biomass and taxonomic richness can recover in a few
₁₉ decades, but relative abundances may lag indefinitely. Since most forests are within a km of
₂₀ a habitat edge, edge effects likely affect community composition regeneration, mediated by
₂₁ shade tolerance and dispersal traits, along with management history. This study addressed
₂₂ how wet tropical secondary forest regeneration was affected by distance to habitat edge, and
₂₃ hypothesized that old timber plantations facilitate regeneration by favoring shade tolerant
₂₄ or late successional taxa, and adjacent forest edges mediate community composition. An
₂₅ abandoned neotropical timber plantation adjacent to primary forest was censused for trees
₂₆ along a 300 m edge distance gradient, and analysis matched taxa to traits using relevant
₂₇ literature.

₂₈ As distance from primary forest edge increased, stem and wood density tended to increase
₂₉ significantly, with ca 10% variation explained, while biomass and canopy light tended to stay
₃₀ the same. Stand tree richness also tended to increase significantly, but diversity decreased
₃₁ steeply and non-linearly, and taxonomic composition varied notably. Finally, tree taxa as-
₃₂ sociated with both early and late successional stages decreased significantly, but biomass by
₃₃ dispersal mode did not tend to change. Overall this study supports that stand composi-
₃₄ tion is less resilient and more subject to edge effects than biomass and richness, suggesting
₃₅ that global forests will likely be distinctly new assemblages in the future, with timber and
₃₆ biodiversity trade-offs occurring based on local and regional management activity.

³⁷ Abstracto

³⁸ Más de la mitad de bosques son tropicales y secundarios, indicando que la regeneración de
³⁹ bosques tropicales es integral al futuro de bosques, globalmente. Biomasa arboreal y riqueza
⁴⁰ taxonómica pueden recuperarse en algunas décadas, pero abundancias relativas pueden durar
⁴¹ más de un siglo. Dado que la mayoría de bosques quedan entre un km de su orilla, efec-
⁴² tos de borde probablemente afectan la regeneración de composición de comunidad, mediado
⁴³ por tolerancia a sombra y características de disperso, y también historia de manejo. Este
⁴⁴ estudio investigó cómo la regeneración de bosque secundario tropical húmedo fue afectado
⁴⁵ por distancia a borde de hábitat, e hipotetizó que plantaciones de madera viejas facilitan
⁴⁶ regeneración porque favorecen a taxa tolerantes a sombra o de sucesión tarde, y que oril-
⁴⁷ las de bosque adyacente median cambios a composición de comunidad. Una plantación de
⁴⁸ madera neotropical adyacente a bosque primario fue censada por árboles siguiendo un tran-
⁴⁹ secto de 300 m midiendo un gradiente de distancia de orilla, y análisis combinó taxa con
⁵⁰ características ecológicas usando literatura relevante.

⁵¹ Mientras distancia de bosque primario aumentó, densidad de madera y tallos tendieron a
⁵² aumentar significativamente, con 10% variación explicado, mientras tanto biomasa y luz de
⁵³ dócel tendió a quedarse igual. Riquesa taxonómica de árboles también tendió a aumentar
⁵⁴ significativamente, pero diversidad bajó profundamente y no-linealmente, y composición tax-
⁵⁵ onomica varió notablemente. Finalmente, biomasa de taxa de árboles asociados con etapas
⁵⁶ de sucesión ambos temprano y tarde bajaron significativamente, pero biomasa por modo de
⁵⁷ disperso no tendió a cambiar. Entre todo este estudio apoya que composición taxonómica es
⁵⁸ menos resiliente y más sujeto a efectos de borde negativos que biomasa y riqueza taxonómica,
⁵⁹ sugeriendo que bosques globales probablemente serán ensamblajes nuevamente distintos en el
⁶⁰ futuro, con compensaciones entre producción de madera y biodiversidad que ocurren basado
⁶¹ en manejo local y regional.

62 1 Introduction

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

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

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

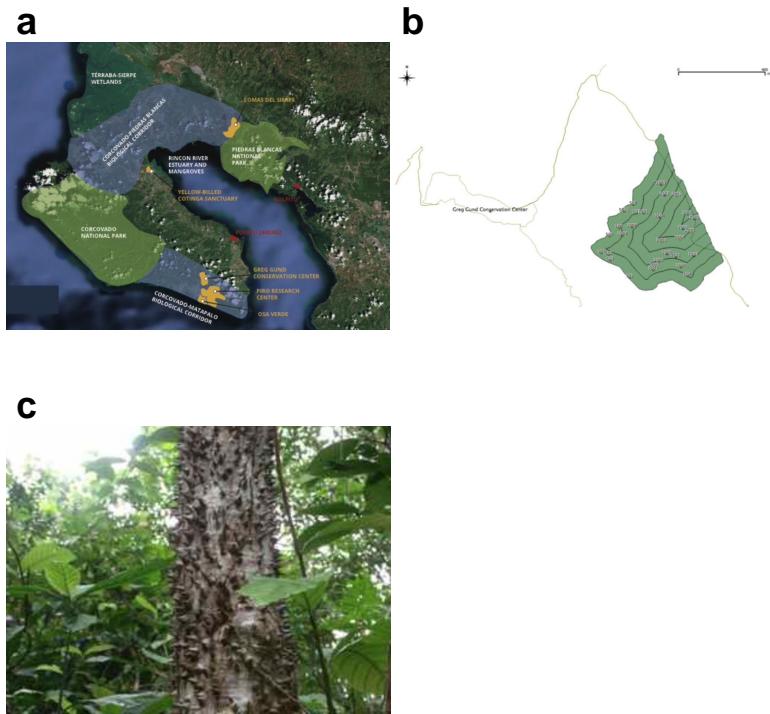
110 This study reports tree regeneration patterns of an abandoned wet neotropical timber plan-
111 tation, highlighting edge effects from an adjacent primary forest. We hypothesized that
112 remaining timber trees would mediate forest regrowth by maintaining shade that would sup-
113 press less shade-tolerant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

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

116 2 Methods

117 2.1 Study site

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



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¹²⁹ 2.2 Census design

¹³⁰ Edge effects were studied by dividing the secondary forest area into six 50 m strata spanning
¹³¹ 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to the
¹³² E (Fig ??), using available GIS software (*ArcGIS 10*, esri.com, and *QGIS 2*, qgis.org). Each
¹³³ stratum was randomly filled with a number of 21 x 21 m square census plots oriented N
¹³⁴ that was proportional to its area—specifically with 11, eight, five, three, two, and one plot(s),
¹³⁵ respectively, as distance away from primary forest increased. The total area of the 30 census
¹³⁶ plots equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to
¹³⁷ similar studies (*Onyekwelu and Olabiwonnu, 2016*).

¹³⁸ **2.3 Plot measurements**

¹³⁹ Light reaching the forest floor was measured at the center of each plot at chest height using
¹⁴⁰ a densiometer (*Forestry Suppliers, Inc.*), as an average of four readings taken facing each
¹⁴¹ cardinal direction.

¹⁴² The slope of the forest floor was measured using a rangefinder (*Bushnell, Forestry Suppliers,*
¹⁴³ *Inc*) to measure the distance the diagonal between two plot corners and triangulate the
¹⁴⁴ observation angle.

¹⁴⁵ The diameter of all stems >10 cm wide were recorded in each census plot, totaling over
¹⁴⁶ 1,000 trees. Following common forestry guidelines, in cases where a tree split into 2 or
¹⁴⁷ more stems below breast height, each stem was measured separately; in cases where a stem
¹⁴⁸ split only above breast height, it was measured as a single stem. Tree height was recorded
¹⁴⁹ by measuring distances to both the crown and the stem at chest height (~2.7 m) using a
¹⁵⁰ rangefinder (*Bushnell, Forestry Suppliers, Inc.*) and triangulating the missing side length.
¹⁵¹ Taxa were identified with localized knowledge and field guides matching common names to
¹⁵² Latin binomials, and trait information was gathered from the literature.

¹⁵³ Aboveground biomass (AGB) was estimated per stem using the allometric equation by *Chave*
¹⁵⁴ *et al.* (2015). The equation specifically for wet tropical forests was used, which has performed
¹⁵⁵ slightly better compared to both pantropical and previous other models by (*Alvarez et al.*,
¹⁵⁶ 2012; *Chave et al.*; 2005; *Ngomanda et al.*, 2014). The equation version with height was
¹⁵⁷ used since height was accessibly measurable and has shown improved local accuracy (*Domke*
¹⁵⁸ *et al.*, 2012; *Khan et al.*, 2020). Wood density (or specific gravity) values when available also
¹⁵⁹ improve biomass estimates even more than height (*Van Breugel et al.*, 2011). The equation
¹⁶⁰ used was:

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

¹⁶¹ with diameter D in cm, height H in m, and wood density or specific gravity p in $g\text{ cm}^{-3}$.

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

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

172 2.4 Statistical analyses

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

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

182 Community analysis and ordination was done as a PERMANOVA with the *adonis()* func-
183 tion from the *vegan* 2.6.2 R package (Dixon, 2003). Data and code were organized with R
184 packages *here* (Müller, 2020), *bookdown* (Xie, 2022), and *grateful* (Rodríguez-Sánchez et al.,
185 2022), and internal pipeline *oir* (Medina, 2022a) are stored at github.com/nmedina17/osa
186 (Medina, 2022b).

₁₈₇ **3 Results**

₁₈₈ **3.1 Biomass**

₁₈₉ Aboveground biomass did not tend to change with distance to primary forest edge (Fig 1a),
₁₉₀ despite significant trends with underlying related variables (Fig 1). Median plot wood density
₁₉₁ tended to increase marginally significantly ($p=0.598$) with edge distance by $8.2 \times 10^{-5} \pm$
₁₉₂ 1.4×10^{-4} per m explaining R₂x100% of variance among median distance strata values (Fig
₁₉₃ 1b). Plot stem density also tended to increase significantly ($p=0.82$) with edge distance but
₁₉₄ more strongly and non-linearly, by $\sim 65.9 \pm 78.9$ per m (Fig 1c). At this stage in forest
₁₉₅ regeneration, canopy light availability did not tend to change with distance from forest edge
₁₉₆ (Fig 1d).

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₁₉₈ **3.2 Composition**

₁₉₉ Overall diversity changed significantly with distance to primary forest edge (Fig 2). Diversity
₂₀₀ significantly ($p=0.414$) decreased non-linearly by $\sim 0.1 \pm 0.1$ per m as distance to primary
₂₀₁ forest edge increased, which explained R₂x100% of variance among distance strata medians
₂₀₂ (Fig 2a) – while in contrast taxonomic richness increased slightly ($p=0.067$) and linearly
₂₀₃ by 0 ± 0 per m and had R₂x100% variance explained among distance strata (Fig 2b).
₂₀₄ Community composition and beta diversity also changed significantly ($p=0.01$) with 25.6%
₂₀₅ variance among distance strata explained by distance to primary forest edge, and the first two
₂₀₆ principal components explaining 59% and 24% totaling 83% of variance among calculated
₂₀₇ plot distances (Fig 2d). Key abundant taxa *Vochysia* and *Ficus* showed different responses
₂₀₈ – *Vochysia* nearly tended to decrease with distance to primary forest edge (Fig 2e), while

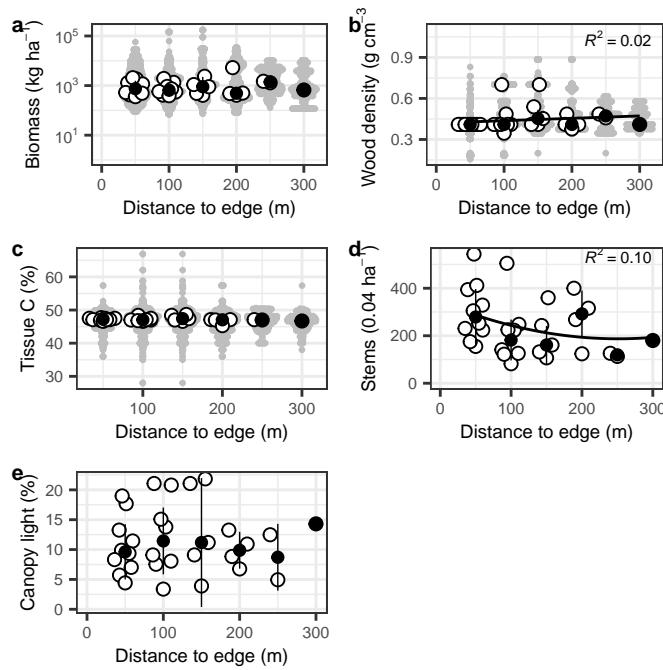


Figure 1: Plot stand properties, namely (a) biomass, (b) wood density, (c) stem density, and (d) canopy light availability. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear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

²⁰⁹ *Ficus* decreased marginally significantly ($p=0.088$) and linearly by -62.6 ± 25.1 per m with
²¹⁰ $R^2 \times 100\%$ variance among distance strata explained (Fig 2f).

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²¹² 3.3 Traits

²¹³ Overall trait regeneration highlighted successional stage associations over primary dispersal
²¹⁴ mode along distance to primary forest (Fig 3). Taxa associated with both early and late
²¹⁵ successional stages decreased significantly ($p=0.042$) and curvi-linearly by $\sim -584.9 \pm 167.3$
²¹⁶ kg per m with distance to edge explaining $R^2 \times 100\%$ variance among distance strata medians
²¹⁷ (Fig 3a). Dispersal modes did not show consistent trends in biomass with increasing distance
²¹⁸ to edge (Fig 3b).

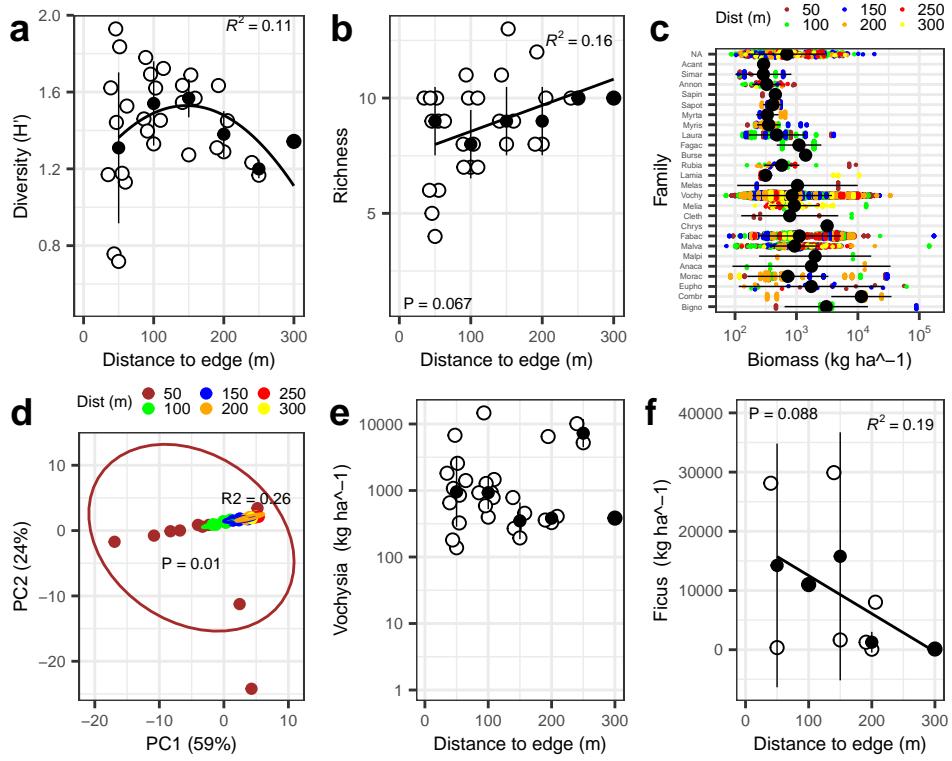


Figure 2: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or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

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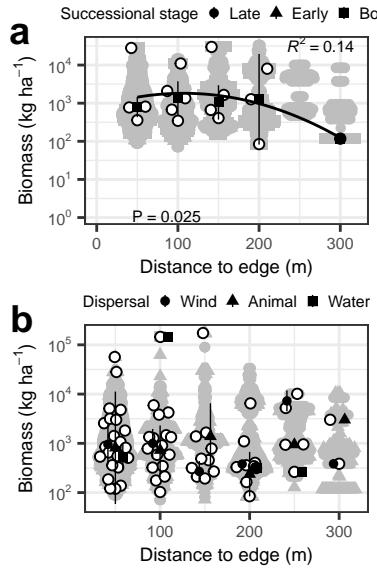


Figure 3: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear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

222 4 Discussion

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

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*).

Edge effects have been shown in other studies to lower both forest biomass and change community composition (*Anderson et al., 2022*), and this study adds that the decline in diversity can be rapid and non-linear across edge gradients, along with supporting the likelihood of lasting changes to community composition. 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

258 shade-tolerant taxa to accumulate significant amounts of biomass. Another possible factor
259 may be overall short dispersal kernels, in part due to higher fungal pathogen pressure under
260 higher constant shade, also increasing tree mortality. Decomposing compositional changes
261 into key specific taxa, while the biomass of the most abundant taxon *Vochysia* was resilient
262 to edge effects in this study, that of the key taxon for frugivores like birds and bats *Ficus*
263 was significantly lowered across the secondary forest edge, pointing to potentially different
264 responses of biomass and food web associated ecosystem services. Community composition
265 also tended to show lower variance across the edge gradient, although this effect cannot be
266 confirmed here given the uneven sampling that accounted for variable forest area at different
267 distances from edge.

268 Characterizing community composition by functional traits is also increasingly studied (*Kear-*
269 *ney et al., 2021*), but less so regarding edge effects. A study in Madagascar found lower
270 phylogenetic diversity closer to degraded forest edge, but no change in aboveground biomass
271 (*Razafindratsima et al., 2018*). These results parallel in showing lower taxonomic diver-
272 sity, although biomass specifically of taxa associated with both early- and late-successional
273 stages also decreased with away from primary forest edge. This result by successional stage
274 can be explained by slightly lower habitat quality inferred near exposed habitat edges near
275 roads, and accordingly relatively higher habitat quality near closed primary forest edge.

276 While lower biomass of succession-agnostic taxa further from primary forest edge appears
277 consistent with dispersal kernels, the lack of pattern by broad dispersal mode limits this
278 explanation here, yet could be further tested by measuring taxon-specific dispersal kernels.

279 Overall, this study highlights how abandoned wet tropical timber plantation can regenerate in
280 alongside fragmented forests. Results support related syntheses that biomass and taxonomic
281 richness often regrows relatively quickly, while taxonomic composition recovers much more
282 slowly, if not diverging altogether (*Norden et al., 2015*). These findings can suggest that
283 more efficient reforestation could more actively target biodiversity conservation over other
284 resilient functions like carbon storage, and that restoration efforts could include focusing

²⁸⁵ activities like native species planting efforts on degraded habitat edges away from primary
²⁸⁶ forest edges, and investing less in areas closer to existing forest edges, where recruitment
²⁸⁷ may already maintain diversity levels. As forests continue to become fragmented (*Haddad*
²⁸⁸ *et al.*, 2015), understanding how to work with natural regeneration patterns around edge
²⁸⁹ effects will likely become increasingly important.

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²⁹² **Declaration of interests**

²⁹³ Authors declare no conflicts of interest.

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³⁰¹ **Author contributions**

³⁰² MV and AJ contributed to study conceptualization, administration, and supervision; NM
³⁰³ and AJ contributed to funding acquisition; NM contributed to data collection; NM and MV
³⁰⁴ contributed to data analysis; NM wrote initial draft and later revisions.

³⁰⁵ **Data statement**

³⁰⁶ Code stored at github.com/nmedina17/osa (*Medina, 2022b*).

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