

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

₃

₄

₅

₆

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

₉

₁₀

₁₁

₁₂ ***Corresponding author:** Nicholas Medina, nmedina@umich.edu

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*). } Back into
more sections

65 Secondary forests can regenerate relatively quickly compared to old-growth forests in some
~~Vague; either clarify or omit~~
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 "recovery of"

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 ~~also~~ 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
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

Edge = ΔAGB, ↓ tree height, JLM
Management - timber edge = ↑ pioneer spp

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,
compared to what? (Previously den)

¹¹² canopy light availability would increase, while stand biomass and diversity would decrease.
What is new about this work?

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*).

I don't have an answer for this, but I struggle w/ unen sampling in my work as well. That is, I'm not sur if the metrics calculated from $n=1$ plot can be comparable with $n=8$ and $n=11$

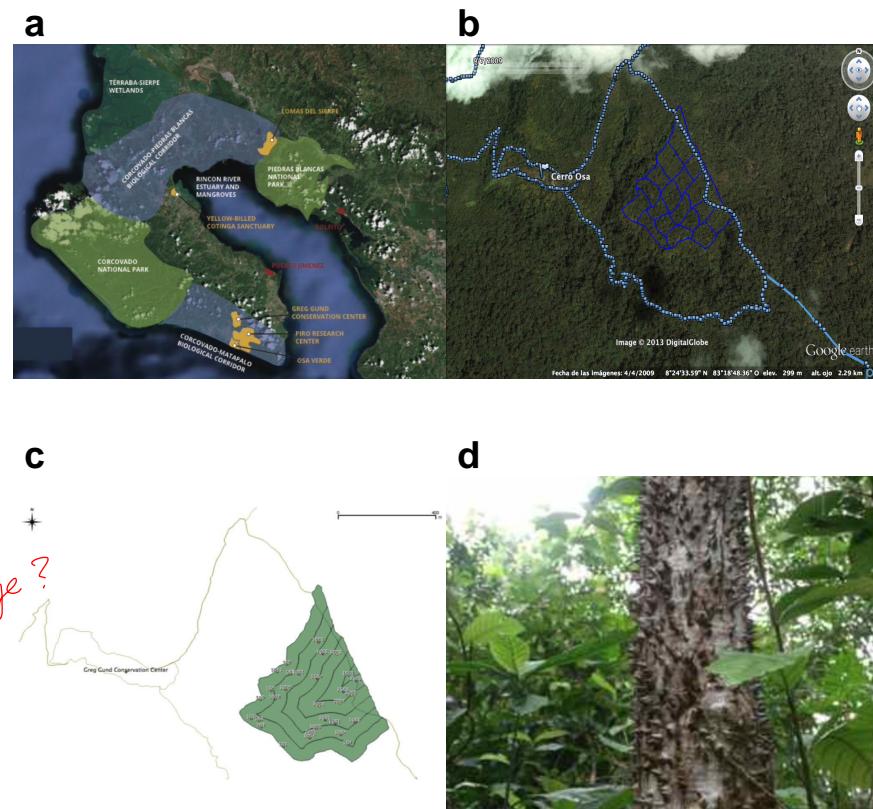


Figure 1: Map of (a) conservation areas and (b) study site (c) showing plot design among distance strata, and focal plantation timber taxon (c) *Bombacopsis quinata* on Osa Peninsula, Costa Rica. Map image data © 2009 Google, © 2022 Osa Conservation. Photo credit: Nicholas Medina.

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.

(wind, animal, water)
(early, late)

165 Traits including successional stage^A and main dispersal mode^B 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

$R^2=0.1$
 $\uparrow \text{interior} \uparrow \text{WD} \times \text{AGB} \times C_{\text{tissue}} \uparrow \text{stem density} \times \text{canopy cover}$

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).

195 ## |

$R^2=0.73$ $R^2=0.16$
 $\uparrow \text{interior} \downarrow \text{diversity} \uparrow \text{richness}$

196 3.2 Composition

Intro: What do other studies on
2nd forests find, along edge,
when there were non-timber
management? You reported more
pioneer spp, but did those edges
have less diversity?

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

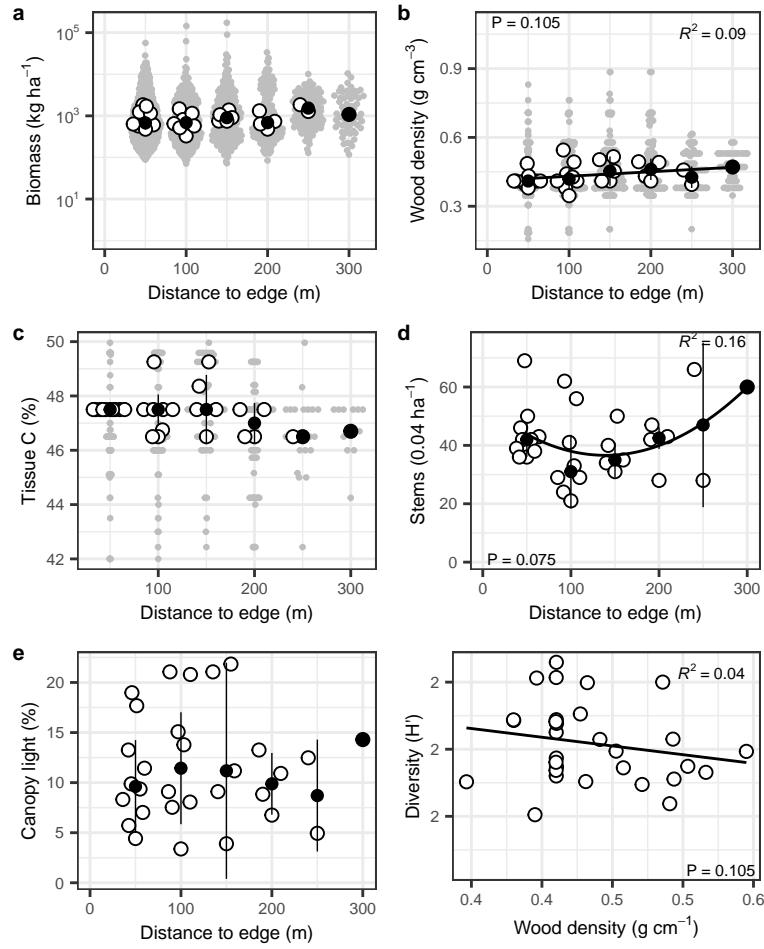


Figure 2: Plot stand properties, namely (a) biomass, (b) wood density, (c) tissue carbon, (d) stem density, (e) canopy light availability, all across distance to primary forest edge gradient, and (e) diversity against wood density. Grey dots show individual tree values, white dots with border show plot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

209 ## |

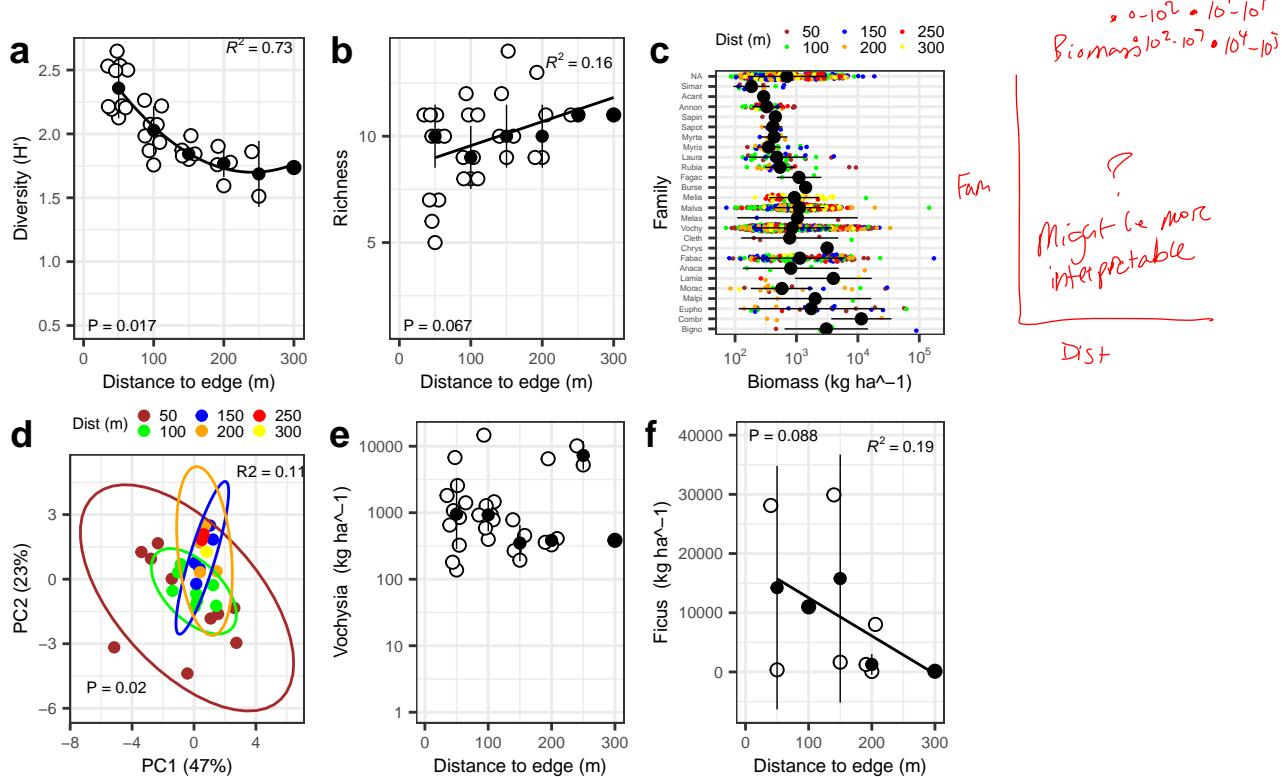


Figure 3: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or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

217 ## |
 218 ## |
 219 ## |

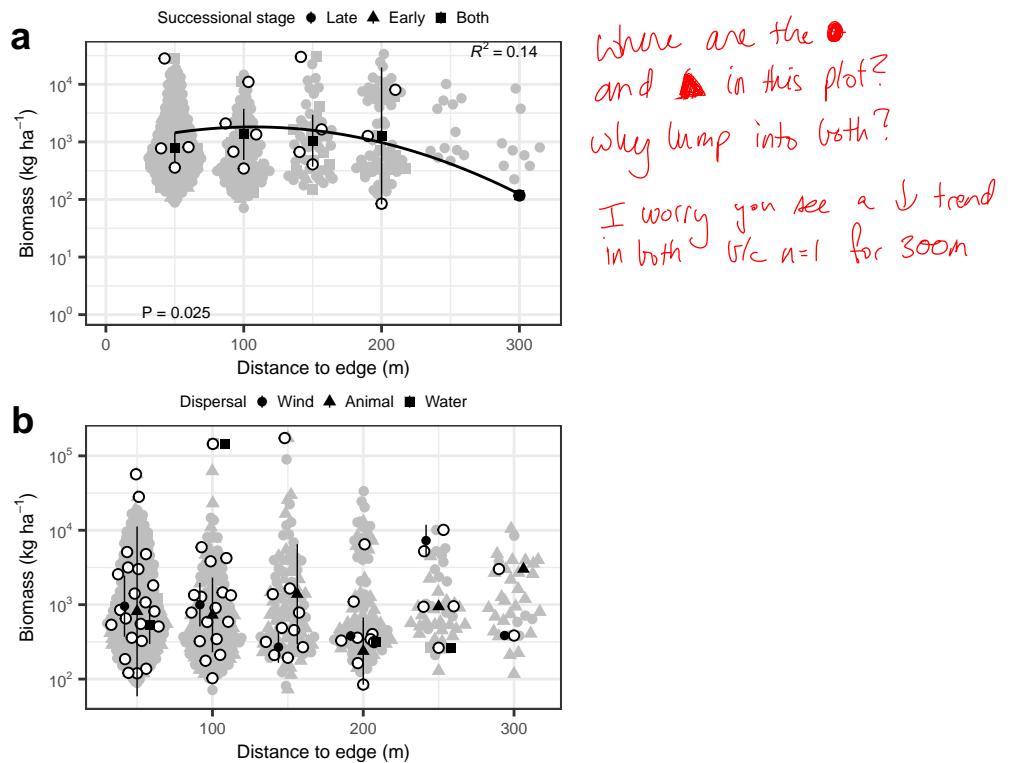


Figure 4: Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear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

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 assoociated 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.

²⁸⁸ **Funding**

²⁸⁹ This study was funded by Brandeis University Hiatt Career Center World of Work Fellowship.

²⁹⁰ **Declaration of interests**

²⁹¹ Authors declare no conflicts of interest.

²⁹² ->

²⁹³ **Data statement**

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

295 **References**

- 296 Albrich, K., Rammer, W., Seidl, R., 2020. Climate change causes critical transitions and
297 irreversible alterations of mountain forests. *Global Change Biology* 26, 4013–4027. <https://doi.org/10.1111/gcb.15118>
- 298
- 299 Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., Salas, G. de las, Valle, I. del, Lema,
300 A., Moreno, F., Orrego, S., Rodríguez, L., 2012. Tree above-ground biomass allometries
301 for carbon stocks estimation in the natural forests of Colombia. *Forest Ecology and
302 Management* 267, 297–308. <https://doi.org/10.1016/j.foreco.2011.12.013>
- 303 Anderegg, W.R.L., Chegwidden, O.S., Badgley, G., Trugman, A.T., Cullenward, D., Abat-
304 zoglou, J.T., Hicke, J.A., Freeman, J., Hamman, J.J., 2022. Future climate risks from
305 stress, insects and fire across US forests. *Ecology Letters* ele.14018. [https://doi.org/10.
306 1111/ele.14018](https://doi.org/10.1111/ele.14018)
- 307 Anderson, J.A., McClean, C.J., Sim, S., Pettorelli, N., Jelling, A., Tangah, J., Hill, J.K.,
308 2022. Weak edge effects on trees in Bornean rainforest remnants bordering oil palm.
309 *Biotropica* btp.13115. <https://doi.org/10.1111/btp.13115>
- 310 Atkinson, J., Brudvig, L.A., Mallen-Cooper, M., Nakagawa, S., Moles, A.T., Bonser, S.P.,
311 2022. Terrestrial ecosystem restoration increases biodiversity and reduces its variability,
312 but not to reference levels: A global meta-analysis. *Ecology Letters* ele.14025. <https://doi.org/10.1111/ele.14025>
- 313
- 314 Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T.,
315 Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A.,
316 Neill, D.A., Patiño, S., Pitman, N.C.A., M. Silva, J.N., Vásquez Martínez, R., 2004.
317 Variation in wood density determines spatial patterns in Amazonian forest biomass: Wood
318 specific gravity and Amazonian biomass estimates. *Global Change Biology* 10, 545–562.
319 <https://doi.org/10.1111/j.1365-2486.2004.00751.x>
- 320 Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., Sexton,
321 J.O., Song, D., Huth, A., 2017. High resolution analysis of tropical forest fragmentation

- 322 and its impact on the global carbon cycle. *Nature Communications* 8, 14855. <https://doi.org/10.1038/ncomms14855>
- 323
- 324 Carlo, T.A., Morales, J.M., 2016. Generalist birds promote tropical forest regeneration and
325 increase plant diversity via rare-biased seed dispersal. *Ecology* 97, 1819–1831. <https://doi.org/10.1890/15-2147.1>
- 326
- 327 Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H.,
328 Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H.,
329 Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks
330 and balance in tropical forests. *Oecologia* 145, 87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- 331
- 332 Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H. ter, Webb, C.O.,
333 2006. REGIONAL AND PHYLOGENETIC VARIATION OF WOOD DENSITY
334 ACROSS 2456 NEOTROPICAL TREE SPECIES. *Ecological Applications* 16, 2356–
335 2367. [https://doi.org/10.1890/1051-0761\(2006\)016%5B2356:RAPVOW%5D2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016%5B2356:RAPVOW%5D2.0.CO;2)
- 336
- 337 Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C.,
338 Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A.,
339 Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A.,
340 Nogueira, E.M., Ortiz-Malavassi, E., Pélassier, R., Ploton, P., Ryan, C.M., Saldarriaga,
341 J.G., Vieilledent, G., 2015. Improved allometric models to estimate the aboveground
342 biomass of tropical trees. *Global Change Biology* 20, 3177–3190. <https://doi.org/10.1111/gcb.12629>
- 343
- 344 Chazdon, R.L., 2018. Protecting intact forests requires holistic approaches. *Nature Ecology
and Evolution* 2, 915. <https://doi.org/10.1038/s41559-018-0546-y>
- 345
- 346 Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A.,
347 Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D.,
348 Almeida-Cortez, J.S., Cabral, G.A.L., Jong, B. de, Denslow, J.S., Dent, D.H., DeWalt,
S.J., Dupuy, J.M., Duran, S.M., Espirito-Santo, M.M., Fandino, M.C., Cesar, R.G., Hall,

- 349 J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher,
350 S.G., Lohbeck, M., Martinez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora,
351 F., Munoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E.,
352 Pena-Claros, M., Perez-Garcia, E.A., Piotto, D., Powers, J.S., Rodriguez-Velazquez, J.,
353 Romero-Perez, I.E., Ruiz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B.,
354 Steininger, M.K., Swenson, N.G., Uriarte, M., Breugel, M. van, Wal, H. van der, Veloso,
355 M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016.
356 Carbon sequestration potential of second-growth forest regeneration in the Latin Amer-
357 ican tropics. *Science Advances*. <https://doi.org/10.1126/sciadv.1501639>
- 358 Chazdon, R.L., Fetcher, N., 1984. Photosynthetic Light Environments in a Lowland Tropical
359 Rain Forest in Costa Rica. *The Journal of Ecology* 72, 553. <https://doi.org/10.2307/2260066>
- 361 Clark, J.A., Covey, K.R., 2012. Tree species richness and the logging of natural forests: A
362 meta-analysis. *Forest Ecology and Management* 276, 146–153. <https://doi.org/10.1016/j.foreco.2012.04.001>
- 364 De Pinto, A., Cenacchi, N., Robertson, R., Kwon, H.-Y., Thomas, T., Koo, J., Begeladze,
365 S., Kumar, C., 2020. The Role of Crop Production in the Forest Landscape Restoration
366 Approach—Assessing the Potential Benefits of Meeting the Bonn Challenge. *Frontiers
367 in Sustainable Food Systems* 4, 61. <https://doi.org/10.3389/fsufs.2020.00061>
- 368 Dixon, P., 2003. VEGAN, a package of R functions for community ecology. *Journal of
369 Vegetation Science* 14, 927–930. <https://doi.org/10.1111/j.1654-1103.2003.tb02228.x>
- 370 Domke, G.M., Woodall, C.W., Smith, J.E., Westfall, J.A., McRoberts, R.E., 2012. Con-
371 sequences of alternative tree-level biomass estimation procedures on U.S. Forest carbon
372 stock estimates. *Forest Ecology and Management* 270, 108–116. <https://doi.org/10.1016/j.foreco.2012.01.022>
- 374 Doraisami, M., Kish, R., Paroshy, N.J., Domke, G.M., Thomas, S.C., Martin, A.R., 2022.
375 A global database of woody tissue carbon concentrations. *Scientific Data* 9, 284. <https://doi.org/10.1038/s41597-022-1083-2>

- 376 //doi.org/10.1038/s41597-022-01396-1
- 377 Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., Laurance, W.F., 2014. Maintaining
378 ecosystem function and services in logged tropical forests. Trends in Ecology and Evolution
379 29, 511–520. <https://doi.org/10.1016/j.tree.2014.07.003>
- 380 FAO, 2020. The State of the World's Forests 2020. FAO and UNEP. [https://doi.org/10.](https://doi.org/10.4060/ca8642en)
- 381 4060/ca8642en
- 382 Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: The first 100
383 years of succession. Trends in Ecology & Evolution.
- 384 Gonzalez J, E., Fisher, R.F., 1998. Variation in Selected Wood Properties of Vochysia
385 Guatimalensis from Four Sites in Costa Rica. Forest Science 7.
- 386 Gough, C.M., Bohrer, G., Hardiman, B.S., Nave, L.E., Vogel, C.S., Atkins, J.W., Bond-
387 Lamberty, B., Fahey, R.T., Fotis, A.T., Grigri, M.S., Haber, L.T., Ju, Y., Kleinke, C.L.,
388 Mathes, K.C., Nadelhoffer, K.J., Stuart-Haëntjens, E., Curtis, P.S., 2021. Disturbance-
389 accelerated succession increases the production of a temperate forest. Ecological Applications
390 31. <https://doi.org/10.1002/eap.2417>
- 391 Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: Changes in
392 structural and functional characteristics. Forest Ecology and Management 148, 185–206.
393 [https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1)
- 394 Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy,
395 T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers,
396 R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules,
397 C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015.
398 Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances
399 1, e1500052. <https://doi.org/10.1126/sciadv.1500052>
- 400 Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sánchez, A.,
401 Daniels, A.K., Ewango, C.E.N., Fauset, S., Mukinzi, J.M., Sheil, D., Sonké, B., Sullivan,
402 M.J.P., Sunderland, T.C.H., Taedoumg, H., Thomas, S.C., White, L.J.T., Abernethy,

- 403 K.A., Adu-Bredou, S., Amani, C.A., Baker, T.R., Banin, L.F., Baya, F., Begne, S.K.,
404 Bennett, A.C., Benedet, F., Bitariho, R., Bocko, Y.E., Boeckx, P., Boundja, P., Brienen,
405 R.J.W., Brncic, T., Chezeaux, E., Chuyong, G.B., Clark, C.J., Collins, M., Comiskey,
406 J.A., Coomes, D.A., Dargie, G.C., de Haulleville, T., Kamdem, M.N.D., Doucet, J.-L.,
407 Esquivel-Muelbert, A., Feldpausch, T.R., Fofanah, A., Foli, E.G., Gilpin, M., Gloor,
408 E., Gonmadje, C., Gourlet-Fleury, S., Hall, J.S., Hamilton, A.C., Harris, D.J., Hart,
409 T.B., Hockemba, M.B.N., Hladik, A., Ifo, S.A., Jeffery, K.J., Jucker, T., Yakusu, E.K.,
410 Kearsley, E., Kenfack, D., Koch, A., Leal, M.E., Levesley, A., Lindsell, J.A., Lisingo, J.,
411 Lopez-Gonzalez, G., Lovett, J.C., Makana, J.-R., Malhi, Y., Marshall, A.R., Martin, J.,
412 Martin, E.H., Mbayu, F.M., Medjibe, V.P., Mihindou, V., Mitchard, E.T.A., Moore, S.,
413 Munishi, P.K.T., Bengone, N.N., Ojo, L., Ondo, F.E., Peh, K.S.-H., Pickavance, G.C.,
414 Poulsen, A.D., Poulsen, J.R., Qie, L., Reitsma, J., Rovero, F., Swaine, M.D., Talbot,
415 J., Taplin, J., Taylor, D.M., Thomas, D.W., Toirambe, B., Mukendi, J.T., Tuagben, D.,
416 Umunay, P.M., van der Heijden, G.M.F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll,
417 H., Woods, J.T., Zemagho, L., 2020. Asynchronous carbon sink saturation in African
418 and Amazonian tropical forests. *Nature* 579, 80–87. <https://doi.org/10.1038/s41586-020-2035-0>
- 420 Hulshof, C.M., Powers, J.S., 2020. Tropical forest composition and function across space and
421 time: Insights from diverse gradients in Área de Conservación Guanacaste. *Biotropica*
422 52, 1065–1075. <https://doi.org/10.1111/btp.12689>
- 423 Kearney, M.R., Jusup, M., McGeoch, M.A., Kooijman, S.A.L.M., Chown, S.L., 2021. Where
424 do functional traits come from? The role of theory and models. *Functional Ecology* 35,
425 1385–1396. <https://doi.org/10.1111/1365-2435.13829>
- 426 Khan, M.N.I., Islam, M.R., Rahman, A., Azad, M.S., Mollick, A.S., Kamruzzaman, M.,
427 Sadath, M.N., Feroz, S.M., Rakkibu, M.G., Knohl, A., 2020. Allometric relationships of
428 stand level carbon stocks to basal area, tree height and wood density of nine tree species
429 in Bangladesh. *Global Ecology and Conservation* 22. <https://doi.org/10.1016/j.gecco>.

430 2020.e01025

- 431 Krishnadas, M., Agarwal, K., Comita, L.S., 2020. Edge effects alter the role of fungi and
432 insects in mediating functional composition and diversity of seedling recruits in a frag-
433 mented tropical forest. *Annals of Botany* 126, 1181–1191. <https://doi.org/10.1093/aob/mcaa138>
- 434
- 435 Laurance, W.F., Andrade, A.S., Magrach, A., Camargo, J.L.C., Campbell, M., Fearnside,
436 P.M., Edwards, W., Valsko, J.J., Lovejoy, T.E., Laurance, S.G., 2014. Apparent envi-
437 ronmental synergism drives the dynamics of Amazonian forest fragments. *Ecology* 95,
438 3018–3026. <https://doi.org/10.1890/14-0330.1>
- 439 Lefland, A.B., Huff, E.S., Donahue, B., 2018. A Community Forestry Model Linking Re-
440 search, Management, Education, and Stakeholder Engagement: Case Study Results from
441 the Town of Weston, Massachusetts, USA. *Small-scale Forestry* 17, 191–210. <https://doi.org/10.1007/s11842-017-9382-1>
- 442
- 443 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F.,
444 Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The
445 metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- 446
- 447 Levins, R., 1979. Coexistence in a Variable Environment. *The American Naturalist* 114,
448 765–783. <https://doi.org/10.1086/283527>
- 449
- 450 Liu, X., Trogisch, S., He, J.-S., Niklaus, P.A., Bruelheide, H., Tang, Z., Erfmeier, A., Scherer-
451 Lorenzen, M., Pietsch, K.A., Yang, B., Kühn, P., Scholten, T., Huang, Y., Wang, C.,
452 Staab, M., Leppert, K.N., Wirth, C., Schmid, B., Ma, K., 2018. Tree species richness in-
453 creases ecosystem carbon storage in subtropical forests. *Proceedings of the Royal Society
B: Biological Sciences* 285, 20181240. <https://doi.org/10.1098/rspb.2018.1240>
- 454
- 455 Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.-C., Lindell,
456 C.A., Maine, J.J., Mestre, L., Michel, N.L., Morrison, E.B., Perfecto, I., Philpott, S.M.,
Şekercioğlu, Ç.H., Silva, R.M., Taylor, P.J., Tscharntke, T., Van Bael, S.A., Whelan,

- 457 C.J., Williams-Guillén, K., 2016. Bird and bat predation services in tropical forests and
458 agroforestry landscapes. *Biological Reviews* 91, 1081–1101. <https://doi.org/10.1111/brv.12211>
- 460 Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czim-
461 czik, C.I., Fiore, A.D., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis,
462 S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patiño, S., Pitman,
463 N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Martínez, R.V., Ter-
464 borgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104
465 Neotropical forest plots: PRODUCTIVITY OF 104 NEOTROPICAL FOREST PLOTS.
466 Global Change Biology 10, 563–591. <https://doi.org/10.1111/j.1529-8817.2003.00778.x>
- 467 Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave,
468 J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F.,
469 Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A.,
470 Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martínez, R.V., Vinceti, B.,
471 2006. The regional variation of aboveground live biomass in old-growth Amazonian
472 forests: BIOMASS IN AMAZONIAN FORESTS. Global Change Biology 12, 1107–1138.
473 <https://doi.org/10.1111/j.1365-2486.2006.01120.x>
- 474 Medina, N., 2022a. Code for: Automating statistical decision trees for data exploration and
475 analysis revision workflow. <https://doi.org/10.5281/zenodo.6800299>
- 476 Medina, N., 2022b. Code for: Habitat edges affect tree diversity more than biomass regen-
477 eration in a wet neotropical secondary forest. <https://doi.org/10.5281/zenodo.6816612>
- 478 Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013.
479 On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolu-*
480 *tion* 28, 462–468. <https://doi.org/10.1016/j.tree.2013.01.001>
- 481 Mitchard, E.T.A., 2018. The tropical forest carbon cycle and climate change. *Nature* 559,
482 527–534. <https://doi.org/10.1038/s41586-018-0300-2>
- 483 Müller, K., 2020. Here: A simpler way to find your files.

- 484 Muller-Landau, H.C., Hardesty, B.D., 2009. Seed dispersal of woody plants in tropical
485 forests: Concepts, examples and future directions. *Biotic Interactions in the Tropics*
486 267–309. <https://doi.org/10.1017/cbo9780511541971.012>
- 487 Nascimento, H.E.M., Laurance, W.F., 2004. BIOMASS DYNAMICS IN AMAZONIAN
488 FOREST FRAGMENTS. *Ecological Applications* 14, 127–138. <https://doi.org/10.1890/01-6003>
- 489 Ngomanda, A., Obiang, N.L.E., Lebamba, J., Mavouroulou, Q.M., Gomat, H., Mankou,
490 G.S., Loumeto, J., Iponga, D.M., Ditsouga, F.K., Koumba, R.Z., Bobé, K.H.B., Okouyi,
491 C.M., Nyangadouma, R., Lépengué, N., Mbatchi, B., Picard, N., 2014. Site-specific
492 versus pantropical allometric equations: Which option to estimate the biomass of a moist
493 central African forest? *Forest Ecology and Management* 312, 1–9. <https://doi.org/10.1016/j.foreco.2013.10.029>
- 494 Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van
495 Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., Finegan,
496 B., Mesquita, R., Chazdon, R.L., 2015. Successional dynamics in Neotropical forests are
497 as uncertain as they are predictable. *Proceedings of the National Academy of Sciences*
498 112, 8013–8018. <https://doi.org/10.1073/pnas.1500403112>
- 499 Oliveira-Neto, N.E., Nascimento, D.R., Carvalho, F.A., 2017. Biodiversity inventory of trees
500 in a neotropical secondary forest after abandonment of shaded coffee plantation. *IForest*
501 10, 303–308. <https://doi.org/10.3832/ifor1901-009>
- 502 Omeja, P.A., Obua, J., Rwetsiba, A., Chapman, C.A., 2012. Biomass accumulation in
503 tropical lands with different disturbance histories: Contrasts within one landscape and
504 across regions. *Forest Ecology and Management* 269, 293–300. <https://doi.org/10.1016/j.foreco.2011.12.044>
- 505 Onyekwelu, J.C., Olabiwonnu, A.A., 2016. Can forest plantations harbour biodiversity simi-
506 lar to natural forest ecosystems over time? *International Journal of Biodiversity Science,*
507 *Ecosystem Services and Management* 12, 108–115. <https://doi.org/10.1080/21513732.2016.1160300>

- 511 2016.1162199
- 512 Ordway, E.M., Asner, G.P., 2020. Carbon declines along tropical forest edges correspond
513 to heterogeneous effects on canopy structure and function. Proceedings of the National
514 Academy of Sciences 117, 7863–7870. <https://doi.org/10.1073/pnas.1914420117>
- 515 Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The Structure, Distribution, and
516 Biomass of the World's Forests. Annual Review of Ecology, Evolution, and Systematics
517 44, 593–622. <https://doi.org/10.1146/annurev-ecolsys-110512-135914>
- 518 Pérez Cordero, L.D., Kanninen, M., 2002. Wood specific gravity and aboveground biomass
519 of *Bombacopsis quinata* plantations in Costa Rica. Forest Ecology and Management 165,
520 1–9. [https://doi.org/10.1016/S0378-1127\(01\)00627-2](https://doi.org/10.1016/S0378-1127(01)00627-2)
- 521 Perfecto, I., Vandermeer, J.H., Wright, A.L., 2009. Nature's matrix: Linking agriculture,
522 conservation and food sovereignty. Earthscan, London ; Sterling, VA.
- 523 Poorter, L., Bongers, F., Aide, T.M., Zambrano, A.M.A., Balvanera, P., Becknell, J.M.,
524 Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., Almeida-
525 Cortez, J.S.D., Cabral, G.A.L., Jong, B.H.J.D., Denslow, J.S., Dent, D.H., DeWalt, S.J.,
526 Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S.,
527 Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G.,
528 Licona, J.C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave,
529 J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona,
530 S., Oliveira, A.A.D., Orihuela-Belmonte, E., Pená-Claros, M., Pérez-García, E.A., Piotto,
531 D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruiz, J., Saldarriaga,
532 J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo,
533 M., Uriarte, M., Breugel, M.V., Wal, H.V.D., Veloso, M.D.M., Vester, H.F.M., Vicentini,
534 A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass
535 resilience of Neotropical secondary forests. Nature 530, 211–214. <https://doi.org/10.1038/nature16512>
- 536
- 537 Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F.,

- 538 Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., Muñoz, R., Norden, N.,
539 Rüger, N., van Breugel, M., Almeyda Zambrano, A.M., Amani, B., Andrade, J.L.,
540 Brancalion, P.H.S., Broadbent, E.N., de Foresta, H., Dent, D.H., Derroire, G., DeWalt,
541 S.J., Dupuy, J.M., Durán, S.M., Fantini, A.C., Finegan, B., Hernández-Jaramillo,
542 A., Hernández-Stefanoni, J.L., Hietz, P., Junqueira, A.B., N'dja, J.K., Letcher, S.G.,
543 Lohbeck, M., López-Camacho, R., Martínez-Ramos, M., Melo, F.P.L., Mora, F., Müller,
544 S.C., N'Guessan, A.E., Oberleitner, F., Ortiz-Malavassi, E., Pérez-García, E.A., Pinho,
545 B.X., Piotto, D., Powers, J.S., Rodríguez-Buriticá, S., Rozendaal, D.M.A., Ruíz, J.,
546 Tabarelli, M., Teixeira, H.M., Valadares de Sá Barretto Sampaio, E., van der Wal, H.,
547 Villa, P.M., Fernandes, G.W., Santos, B.A., Aguilar-Cano, J., de Almeida-Cortez, J.S.,
548 Alvarez-Davila, E., Arreola-Villa, F., Balvanera, P., Becknell, J.M., Cabral, G.A.L.,
549 Castellanos-Castro, C., de Jong, B.H.J., Nieto, J.E., Espírito-Santo, M.M., Fandino,
550 M.C., García, H., García-Villalobos, D., Hall, J.S., Idárraga, A., Jiménez-Montoya, J.,
551 Kennard, D., Marín-Spiotta, E., Mesquita, R., Nunes, Y.R.F., Ochoa-Gaona, S., Peña-
552 Claros, M., Pérez-Cárdenas, N., Rodríguez-Velázquez, J., Villanueva, L.S., Schwartz,
553 N.B., Steininger, M.K., Veloso, M.D.M., Vester, H.F.M., Vieira, I.C.G., Williamson,
554 G.B., Zanini, K., Hérault, B., 2021. Multidimensional tropical forest recovery. *Science*
555 374, 1370–1376. <https://doi.org/10.1126/science.abb3629>
- 556 Pryde, E.C., Holland, G.J., Watson, S.J., Turton, S.M., Nimmo, D.G., 2015. Conservation
557 of tropical forest tree species in a native timber plantation landscape. *Forest Ecology
558 and Management* 339, 96–104. <https://doi.org/10.1016/j.foreco.2014.11.028>
- 559 Pyles, M.V., Magnago, L.F.S., Maia, V.A., Pinho, B.X., Pitta, G., de Gasper, A.L., Vibrans,
560 A.C., dos Santos, R.M., van den Berg, E., Lima, R.A.F., 2022. Human impacts as the
561 main driver of tropical forest carbon. *Science Advances* 8, eabl7968. <https://doi.org/10.1126/sciadv.abl7968>
- 562 Pyron, R.A., Mooers, A.Ø., 2022. The normative postulate problem: Hidden values in
563 ecology, evolution, and conservation. *Biological Conservation* 270, 109584. <https://doi.org/10.1016/j.biocon.2022.109584>

- 565 org/10.1016/j.biocon.2022.109584
- 566 R Core Team, 2022. R: A language and environment for statistical computing. R Foundation
567 for Statistical Computing, Vienna, Austria.
- 568 Razafindratsima, O.H., Brown, K.A., Carvalho, F., Johnson, S.E., Wright, P.C., Dunham,
569 A.E., 2018. Edge effects on components of diversity and above-ground biomass in a
570 tropical rainforest. *Journal of Applied Ecology* 55, 977–985. <https://doi.org/10.1111/1365-2664.12985>
- 572 Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. BIOMASS
573 : An R package for estimating above-ground biomass and its uncertainty in tropical
574 forests. *Methods in Ecology and Evolution* 8, 1163–1167. <https://doi.org/10.1111/2041-210X.12753>
- 576 Rodríguez-Sánchez, F., Jackson, C.P., Hutchins, S.D., 2022. Grateful: Facilitate citation of
577 r packages.
- 578 Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera,
579 P., Becknell, J.M., Bentos, T.V., Brancalion, P.H.S., Cabral, G.A.L., Calvo-Rodriguez,
580 S., Chave, J., César, R.G., Chazdon, R.L., Condit, R., Dallinga, J.S., Almeida-Cortez,
581 J.S.D., Jong, B.D., Oliveira, A.D., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M.,
582 Durán, S.M., Dutrieux, L.P., Espírito-Santo, M.M., Fandino, M.C., Fernandes, G.W.,
583 Finegan, B., García, H., Gonzalez, N., Moser, V.G., Hall, J.S., Hernández-Stefanoni,
584 J.L., Hubbell, S., Jakovac, C.C., Hernández, A.J., Junqueira, A.B., Kennard, D., Larpin,
585 D., Letcher, S.G., Licona, J.C., Lebrija-Trejos, E., Marín-Spiotta, E., Martínez-Ramos,
586 M., Massoca, P.E.S., Meave, J.A., Mesquita, R.C.G., Mora, F., Müller, S.C., Muñoz,
587 R., Neto, S.N.D.O., Norden, N., Nunes, Y.R.F., Ochoa-Gaona, S., Ortiz-Malavassi, E.,
588 Ostertag, R., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Aguilar-
589 Cano, J., Rodriguez-Buritica, S., Rodríguez-Velázquez, J., Romero-Romero, M.A., Ruíz,
590 J., Sanchez-Azofeifa, A., Almeida, A.S.D., Silver, W.L., Schwartz, N.B., Thomas, W.W.,
591 Toledo, M., Uriarte, M., Sampaio, E.V.D.S., Breugel, M.V., Wal, H.V.D., Martins, S.V.,

- 592 Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Villa, P., Williamson, G.B.,
593 Zanini, K.J., Zimmerman, J., Poorter, L., 2019. Biodiversity recovery of Neotropical
594 secondary forests. *Science Advances* 5. <https://doi.org/10.1126/sciadv.aau3114>
- 595 Smith, C.C., Espírito-Santo, F.D.B., Healey, J.R., Young, P.J., Lennox, G.D., Ferreira,
596 J., Barlow, J., 2020. Secondary forests offset less than 10% of deforestation-mediated
597 carbon emissions in the Brazilian Amazon. *Global Change Biology* 26, 7006–7020. <https://doi.org/10.1111/gcb.15352>
- 599 Stanturf, J.A., Palik, B.J., Dumroese, R.K., 2014. Contemporary forest restoration: A
600 review emphasizing function. *Forest Ecology and Management* 331, 292–323. <https://doi.org/10.1016/j.foreco.2014.07.029>
- 602 Tabarelli, M., Lopes, A.V., Peres, C.A., 2008. Edge-effects drive tropical forest fragments
603 towards an early-successional system. *Biotropica* 40, 657–661. <https://doi.org/10.1111/j.1744-7429.2008.00454.x>
- 605 Tamme, R., Götzenberger, L., Zobel, M., Bullock, J.M., Hooftman, D.A.P., Kaasik, A.,
606 Pärtel, M., 2014. Predicting species' maximum dispersal distances from simple plant
607 traits. *Ecology* 95, 505–513. <https://doi.org/10.1890/13-1000.1>
- 608 Taylor, P., Asner, G., Dahlin, K., Anderson, C., Knapp, D., Martin, R., Mascaro, J.,
609 Chazdon, R., Cole, R., Wanek, W., Hofhansl, F., Malavassi, E., Vilchez-Alvarado, B.,
610 Townsend, A., 2015. Landscape-Scale Controls on Aboveground Forest Carbon Stocks
611 on the Osa Peninsula, Costa Rica. *PLOS ONE* 10, e0126748. <https://doi.org/10.1371/journal.pone.0126748>
- 613 Terborgh, J., Foster, R.B., Percy, N.V., 1995. Tropical Tree Communities: A Test of the
614 Nonequilibrium Hypothesis. *Ecology* 77, 561–567. <https://doi.org/10.2307/2265630>
- 615 Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is
616 more strongly correlated with plant height than with seed mass. *Journal of Ecology* 99,
617 1299–1307. <https://doi.org/10.1111/j.1365-2745.2011.01867.x>
- 618 Van Breugel, M., Ransijn, J., Craven, D., Bongers, F., Hall, J.S., 2011. Estimating carbon

- 619 stock in secondary forests: Decisions and uncertainties associated with allometric biomass
620 models. *Forest Ecology and Management* 262, 1648–1657. <https://doi.org/10.1016/j.foreco.2011.07.018>
- 621
- 622 Wandrag, E.M., Dunham, A.E., Duncan, R.P., Rogers, H.S., 2017. Seed dispersal increases
623 local species richness and reduces spatial turnover of tropical tree seedlings. *Proceedings*
624 of the National Academy of Sciences of the United States of America 114, 10689–10694.
625 <https://doi.org/10.1073/pnas.1709584114>
- 626 Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D.,
627 Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-
628 Palacios, J.M., Hengl, T., Norder, S.J., Rijsdijk, K.F., Sanmartín, I., Strasberg, D.,
629 Triantis, K.A., Valente, L.M., Whittaker, R.J., Gillespie, R.G., Emerson, B.C., Thébaud,
630 C., 2015. Islands as model systems in ecology and evolution: Prospects fifty years after
631 MacArthur-Wilson. *Ecology Letters* 18, 200–217. <https://doi.org/10.1111/ele.12398>
- 632 Werden, L.K., Holl, K.D., Rosales, J.A., Sylvester, J.M., Zahawi, R.A., 2020. Effects of
633 dispersal- and niche-based factors on tree recruitment in tropical wet forest restoration.
634 *Ecological Applications* 30. <https://doi.org/10.1002/eap.2139>
- 635 Xie, Y., 2022. Bookdown: Authoring books and technical documents with r markdown.