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

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Abstract

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

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

Abstracto

Más de la mitad de bosques son tropicales y secundarios, indicando que la regeneración de bosques tropicales es integral al futuro de bosques, globalmente. Biomasa arboreal y *riqueza* taxonomica pueden recuperarse en algunas décadas, pero abundancias relativas pueden durar más de un siglo. Dado que la mayoría de bosques están entre un km de su orilla, *efectos de orilla* probablemente afectan la regeneración de composición de comnuidad, mediado por tolerancia a sombra y "traits"/characterísticas de *disperso*, y también historia de manejamiento. Este estudio *investiga* cómo regeneración de bosque secundario tropical húmedo es afectado por distancia a *orilla de habitat*, y *"hypothesizes"* que plantaciones de madera viejos facilitan regeneración porque favoran taxa tolerante a sombra o de *"succession"* tarde, y que orillas de bosque cercanos/*"adjacent" median* composición de comunidad. Una plantación de madera neotropical *al lado de* bosque primario fue *"censused"* por árboles siguiendo un transecto de 300 m midiendo un gradiente de distancia de orilla, y análisis combino taxa con characterísticas/*"traits"* usando literatura relevante.

Mientras distancia de bosque primario aumentó, densidad de madera y *"stems" "tended to"* aumentó *signifantemente*, con 10% variación explicado, mientras tanto biomasa y luz de dócel *"tended to"* quedarse igual. *Riquesa* de árboles también *"tended to"* aumentar *significantemente*, pero diversidad bajó profundamente y no-linearmente, y composición taxonomica varió notablemente. Finalmente, taxa de árboles asociado *etapas* de *"succession"* ambos temprano y tarde bajó *significativamente*, pero biomasa por modo de *disperso* no *"tended to"* cambiar. *Entre todo* este estudio apoya que composición es menos resiliente y más sujeto a *efectos de orilla* que biomasa y *riqueza*, sugiriendo que bosques globales probablemente serán *asemblajes* nuevos distintos en el futuro, con *"trade-offs"* entre producción de madera y biodiversidad *ocuriendo* basado en actividad de manejamiento local y regional.

1 Introduction

Forest and landscape restoration is a key international conservation and climate change adaptation strategy *(De Pinto et al., 2020)*, and while tropical forests specifically store most land biomass *(Pan et al., 2013)*, most are now secondary *(FAO, 2020)* and regenerating degraded functions *(Hubau et al., 2020)* amid increasing climate stressors *(Anderegg et al., 2022)* yet insufficient policy support *(Chazdon, 2018)* via skewed priorities *(Pyron and Mooers, 2022)*. Secondary forests can regenerate relatively quickly compared to old-growth forests in some ways, but in other ways remain distinct. Neotropical secondary forests can grow quickly enough to accumulate biomass >10x faster than old-growth forests *(Finegan, 1996; Poorter et al., 2016)*, and substantially offset carbon emissions, with estimates ranging from ~10% from Amazonian deforestation *(Smith et al., 2020)* to a decade of fossil fuel emissions from all of Latin American and the Caribbean *(Chazdon et al., 2016)*. They also recover taxonomic richness and biomass quite quickly, as well as tree height, averaging 80% of old-growth forest levels in just 20 years, especially in wetter regions *(Rozendaal et al., 2019)*. The recovery of species richness alone is beneficial in that it also tends to correlate with the recovery of some ecosystem services *(Guariguata and Ostertag, 2001; Stanturf et al., 2014)* like biomass and carbon storage *(Liu et al., 2018)*. However, secondary neotropical forests diverge widely in taxonomic composition *(Norden et al., 2015)*, potentially taking over a century to recover *(Poorter et al., 2021)* with added variability *(Atkinson et al., 2022)*. Despite being one of the slowest ecosystem properties to recover, restoring recovering community composition is often important for preserving rare taxa *(Carlo and Morales, 2016)*, which can be keystone to locally-adapted food webs, including birds *(Maas et al., 2016)*. As a result, understanding secondary forest regeneration remains important...

Secondary forest regeneration is often affected by edge effects, or changes near an ecosystem boundary, as well as land-use history, especially in heterogeneously-managed landscapes *(Melo et al., 2013; Perfecto et al., 2009)*. About 70% of all forests have been estimated

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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)*. Edge effects also have the potential to shape community composition, 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)*. The traits of existing taxa also depend on land-use history and previous management *(Omeja et al., 2012)*, which historically has favored tree taxa that tend to pioneering, or be faster-growing, have lower wood densities, and be less shade-tolerant *(Tabarelli et al., 2008)*. Legacy effects from management like intensive timber planting could in theory 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)*. Overall, while edge effects near degraded habitat edges are often negative, meta-population *(Levins, 1979)* and -community *(Leibold et al., 2004; Warren et al., 2015)* theories highlight dispersal as a key process for offsetting extinction debt and thus maintaining biodiversity. Near primary forest, dispersal may facilitate secondary forest regeneration, and help explain relatively high biodiversity compared to adjacent stands that can be found in agroforests *(Oliveira-Neto et al., 2017)*, forests affected by logging *(Clark and Covey, 2012; Edwards et al., 2014)*, and timber plantations *(Pryde et al., 2015)*.

This study reports tree regeneration patterns of an abandoned wet neotropical timber plantation, highlighting edge effects from an adjacent primary forest. We hypothesized that remaining timber trees would mediate forest regrowth by maintaining shade that would suppress less shade-tolerant pioneer tree taxa and allow for more tree diversity closer to the primary forest edge. Accordingly, we predicted that further from the primary forest edge, canopy light availability would increase, while stand biomass and diversity would decrease.

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2 Methods

2.1 Study site

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

and August.

2.2 Census design

Edge effects were studied by dividing the secondary forest area into six 50 m strata spanning 0 - 300 m away from the primary forest edge on the S and NW sides, going inward to the E (Fig **??**), using available GIS software (*ArcGIS 10 from 2010*, esri.com, and *QGIS 2 from 2013*, qgis.org). Each stratum was randomly filled with a number of 21 x 21 m square census plots oriented N that was proportional to its area–specifically with 11, eight, five, three, two, and one plot(s), respectively, as distance away from primary forest increased. The total area of the 30 census plots equaled ~1 ha or 5% of the total secondary forest stand area, which is comparable to similar studies *(Onyekwelu and Olabiwonnu, 2016)*.

2.3 Plot measurements

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

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

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

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

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

with diameter D in cm, height H in m, and wood density or specific gravity p in *g cm^{-3}*. DBHs and heights were measured in the field and wood densities were extracted from available literature. Where information was limited, values at the genus level were used and unrepresented taxa were assumed to be *0.58* following World Agroforestry Database guidelines (worldagroforestry.org).

Original values found and recorded were later updated to modern values using the pipeline developed in the *BIOMASS* 2.1.8 R software package by *Réjou-Méchain et al. (2017)*, which notably replaced unknown wood density values with plot-level averages instead during stem biomass calculations.

2.4 Statistical analyses

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

Non-linear regressions were run using the function *poly()* in the base R package *stats* 4.2.0,

which was only ultimately recorded for stem density and richness variables, based on significance and explained variance over linear models. All trees censused were included in each analysis including unidentified taxa that represented a single group in taxa-specific analyses. Community analysis and ordination was done as a PERMANOVA with the *adonis()* function from the *vegan* 2.6.2 R package *(Dixon, 2003)*. Data and code were organized with R packages *here (Müller, 2020)*, *bookdown (Xie, 2022)*, and *grateful (Rodríguez-Sánchez et al., 2022)*, and are available at nmedina17.github.com/osa.

3   Results

3.1   Biomass

Aboveground biomass did not tend to change with distance to primary forest edge (Fig 1a), despite significant trends with underlying related variables (Fig 1).

Median plot wood density tended to increase marginally significantly (p=0.105) with edge distance by $1.9 \times 10^{-4} \pm 9.2 \times 10^{-5}$ per m explaining R2x100% of variance among median distance strata values (Fig 1b).

Plot stem density also tended to increase significantly (p=0.03) with edge distance but more strongly and non-linearly, by ~17.4 $\pm$ 3.4 per m (Fig 1c).

At this stage in forest regeneration, canopy light availability did not tend to change with distance from forest edge (Fig 1d).

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3.2   Composition

Overall diversity changed significantly with distance to primary forest edge (Fig 2).
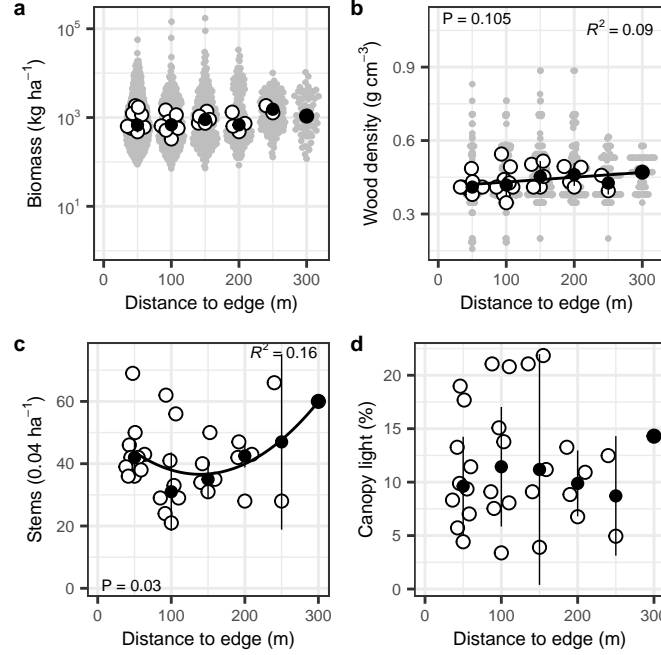
Figure 1: Plot stand properties, namely (a) biomass, (b) wood density, (c) stem density, and (d) canopy light availability. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians $\pm$ 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

Alpha diversity significantly (p=0.003) decreased non-linearly by ~0.5 $\pm$ 0 per m as distance to primary forest edge increased which explained R2x100% of variance among distance strata medians (Fig 2a) – while in contrast taxonomic richness increased slightly (p=0.067) and linearly by 0 $\pm$ 0 per m and had R2x100% variance explained among distance strata (Fig 2b).

Community composition and beta diversity also changed significantly (p=0.01) with 11.4% variance among distance strata explained by distance to primary forest edge, and the first two principal components explaining 47% and 23% totaling 70% of variance among calculated plot distances (Fig 2d).

Key abundant taxa Vochysia and Ficus showed different responses – Vochysia nearly tended to decrease with distance to primary forest edge (Fig 2e), while Ficus decreased marginally significantly (p=0.088) and linearly by -62.6 $\pm$ 25.1 per m with R2x100% variance among

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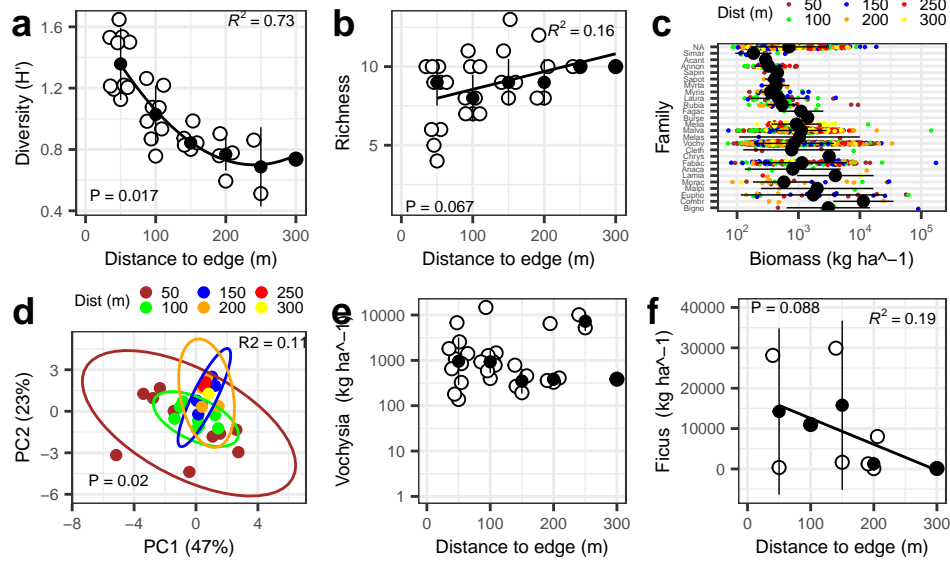
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Figure 2: Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e,f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians $\pm$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

3.3 Functions

Overall functional regeneration highlighted successional stage associations over primary dispersal mode along distance to primary forest (Fig 3).

Taxa associated with both early and late successional stages decreased marginally significantly (p=0.042) and curvi-linearly by $\sim$ -584.9 $\pm$ 167.3 per m with distance to edge explaining R2x100% variance among distance strata medians (Fig 3a).

Dispersal modes did not show consistent trends in biomass with increasing distance to edge (Fig 3b).

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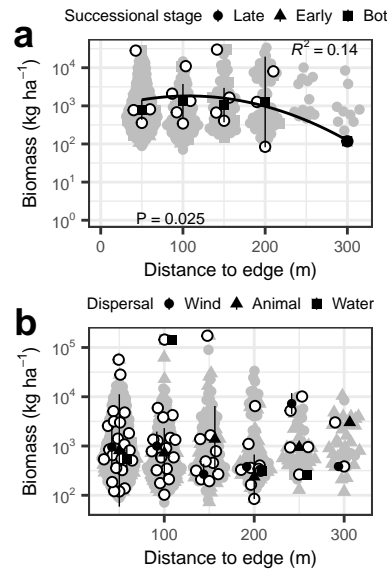219 ## | |

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 $\pm$ 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

4   Discussion

outline

222   1. assess hypotheses

223   2. infer causes of patterns - plantation structure, old legacy trees, or species traits?

224   3. compare inferences to other studies

225   4. recommend future conservation approaches, ecological studies

draft

This study found significant edge effects on tree diversity and community composition, but not aboveground biomass... functional diversity? These results were shown in Figs 1, 2, and 3...

attic

Under more sustainable forestry that maintains multiple functions, forest stand regeneration is likely more predictable, generally mirroring (i.e. near 1:1 replacement) the targeted tree cutting that is done using information collected about the ecological profiles and ages (when possible) of trees (Duah-Gyamfi et al 2014, Edwards et al 2014).

In contrast, under intensive silviculture that prioritizes the growth of select tree crop species, forest stands can show high wood production (Ferez et al 2015) while also usually showing negative trade-offs with other services, like that with biodiversity given reliance on mono-culture planting designs.

In some cases where management decisions are made primarily based on regional economic but not local ecological information, due to limited access to funded scientific reporting (Cook et al 2012), forest stands can perform very poorly all-around.

After this more extreme type of management, it remains uncertain how natural regeneration in secondary forests will proceed, how local ecosystem services will be restored, and how restoration could be managed locally (Laurance et al 2012), e.g. based on surrounding forest proximity.

The persistence of early-successional tree communities has been found to lower the standing biomass, likely due to lower wood density *(césar21?)*, and could therefore require a switch in focal timber species *(Karsten et al., 2014)*.

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Declaration of interests

Authors declare no conflicts of interest.

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Author contributions

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

Data statement

Data and code stored at github.com/nmedina17/osa.

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