

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

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HIGHLIGHTS

- Old plantations may facilitate wet tropical secondary forest regeneration
- Aboveground biomass and light were resilient to edge effects across 300 m, while wood and stem density tended to increase across 300 m habitat edge
- Diversity lowered non-linearly and community composition varied notably
- Taxa associated with early- and late-stage succession tended to lose biomass
- Future forests likely show some resilience in functions but not biodiversity

INTRODUCTION

Secondary forest regeneration

- 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 (Robin L. Chazdon 2018) via skewed priorities (Pyron and Moores 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 (R. L. 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 (Pozndal et al. 2019).
- The recovery of species richness alone is also likely to correlate with the recovery of some ecosystem services (Guangyuta and Ostertag 2001; Stanturf, Palk, and Dumrese 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 (Wass et al. 2019).
- Understanding secondary 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).

Edge effects

- 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 (Perfecto, Vandermeer, and Wright 2009; Melo et al. 2013).
- About 70% of all forests have been estimated to be within a km of their edge (Haddad et al. 2015), resulting in tropical forests having been estimated to lose ~22% aboveground carbon along heavily-managed edges >100m, in part due to shortening trees and lighter leaf mass (Ordway and Asner 2020).
- 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 (Thomson et al. 2011; Tamme et al. 2014).
- The traits of existing taxa also depend on land-use history and previous management (Ormeja 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, Lopes, and Peres 2008).
- Legacy effects from management like intensive timber planting could in theory delay or result in non-linear changes between successional stages (Abrish, Rammer, and Seid 2020; Gough et al. 2021), which would make future management more uncertain, unlike more sustainable thinning practices and agroforestry (Lefland, Huff, and Donahue 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, Nascimento, and Carvalho 2017), forests affected by logging (Clark and Covey 2012; Edwards et al. 2014), and timber plantations (Pydy et al. 2015).

Purpose/Question — This study reports tree regeneration patterns of an abandoned wet neotropical timber plantation, highlighting edge effects from an adjacent primary forest.

Hypothesis — 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.

Predictions — Accordingly, we predicted that further from the primary forest edge, canopy light availability would increase, while stand biomass and diversity would decrease.

METHODS

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 *Bombacopsis quinata* abandoned in ~1990 after the dry-adapted species from the Guanacaste region (Pérez Cordero and Kanninen 2002; Hulshof and Powers 2020) 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 1) 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.

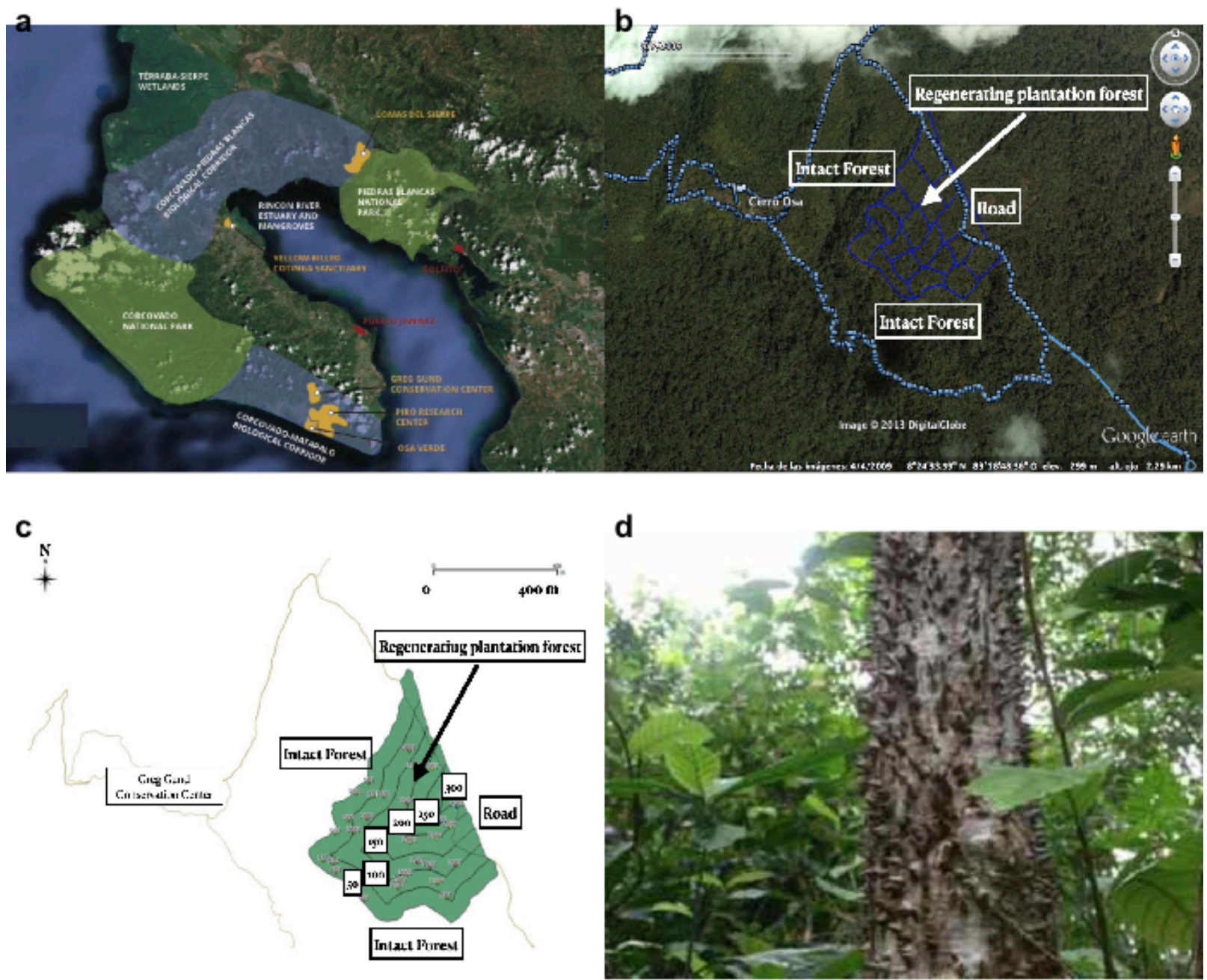


Fig 1 Map of (a) conservation areas and (b) study site (c) showing plot design with 50 m distance strata bins, and (d) focal plantation timber taxon *Bombacopsis quinata* on Osa Peninsula, Costa Rica. Map image data © 2022 Osa Conservation, © 2009 Google. Map GIS data and photo credit: Max Villalobos,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

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 1), using available GIS software (ArcGIS 10, esri.com, and QGIS 2, 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 Olabiwonu 2016).

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, totaling over 1,000 trees
- 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 Jérôme 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 J. Chave et al. (2005; Alvarez et al. 2012; 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:

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

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

Statistics

- For all response variables, data were analyzed using plot or distance strata 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, Jackson, and Hutchings 2022), and internal pipeline oir (Medina 2022a) are stored at github.com/nmedina17/osa (Medina 2022b).

ABSTRACT

Background/Question/Methods

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.

Results/Conclusions

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 negative 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.

RESUMEN

Contexto/Preguntas/Métodos

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 taxonómica pueden recuperarse en algunas décadas, pero abundancias relativas pueden durar más de un siglo.

Dado que la mayoría de bosques quedan entre un km de su orilla, efectos de borde probablemente afectan la regeneración de composición de comunidad, mediado por tolerancia a sombra y características de disperso, y también historia de manejo.

Este estudio investigó cómo la regeneración de bosque secundario tropical húmedo fue afectado por distancia a borde de hábitat, e hipotizó que plantaciones de madera viejas facilitan regeneración porque favorecen a taxa tolerantes a sombra o de sucesión tarde, y que orillas de bosque adyacente median cambios a composición de comunidad.

Una plantación de madera neotropical adyacente a bosque primario fue censada por árboles siguiendo un transecto de 300 m midiendo un gradiente de distancia de orilla, y análisis combinó taxa con características ecológicas usando literatura relevante.

Resultados/Conclusiones

Mientras distancia de bosque primario aumentó, densidad de madera y tallos tendieron a aumentar significativamente, con 10% variación explicado, mientras tanto biomasa y luz de dócel tendió a quedarse igual. Riqueza taxonómica de árboles también tendió a aumentar significativamente, pero diversidad bajo profundamente y no-linealmente, y composición taxonómica varió notablemente.

Finalmente, biomasa de taxa de árboles asociados con etapas de sucesión ambos temprano y tarde bajaron significativamente, pero biomasa por modo de disperso no tendió a cambiar.

Entre todo este estudio apoya que composición taxonómica es menos resiliente y más sujeto a efectos de borde negativos que biomasa y riqueza taxonómica, sugiriendo que bosques globales probablemente serán ensamblajes nuevamente distintos en el futuro, con compensaciones entre producción de madera y biodiversidad que ocurren basado en manejo local y regional.

RESULTS

Biomass

- Aboveground biomass **did not tend to change** with distance to primary forest edge (Fig 2a), despite significant trends with underlying related variables (Fig 2).
- Median plot **wood density tended to increase marginally** significantly ($p=0.598$) with edge distance by 0.00008 ± 0.0001 per m explaining ~10% of variance among median distance strata values (Fig 2b).
- Plot stem density also tended to increase significantly ($p=0.82$) with edge distance but more strongly and non-linearly, by $\sim 65.9 \pm 78.9$ per m (Fig 2c).
- At this stage in forest regeneration, **canopy light availability did not tend to change** with distance from forest edge (Fig 2d).

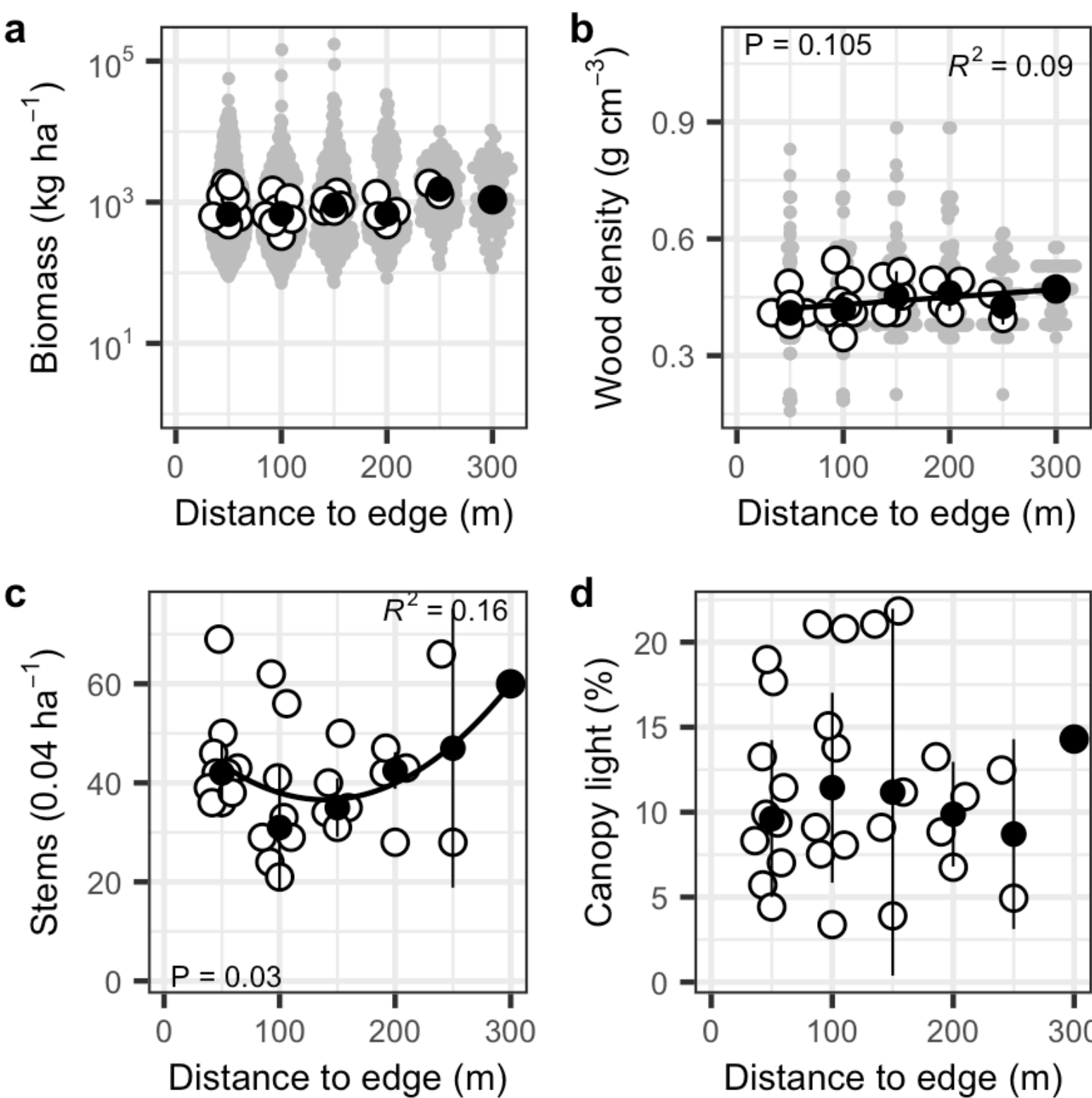


Fig 2 Plot stand properties, namely (a) biomass, (b) wood density, (c) stem density, and (d) canopy light availability. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear regression through strata medians.

Traits

- Overall functional regeneration highlighted successional stage associations over primary dispersal mode along distance to primary forest (Fig 4).
- Taxa associated with both early and late successional stages **decreased significantly ($p=0.042$) and curvi-linearly** by $\sim -584.9 \pm 167.3$ kg per m with distance to edge explaining 14% variance among distance strata medians (Fig 4a).
- Dispersal modes did not show consistent trends in biomass with increasing distance to edge (Fig 4b).

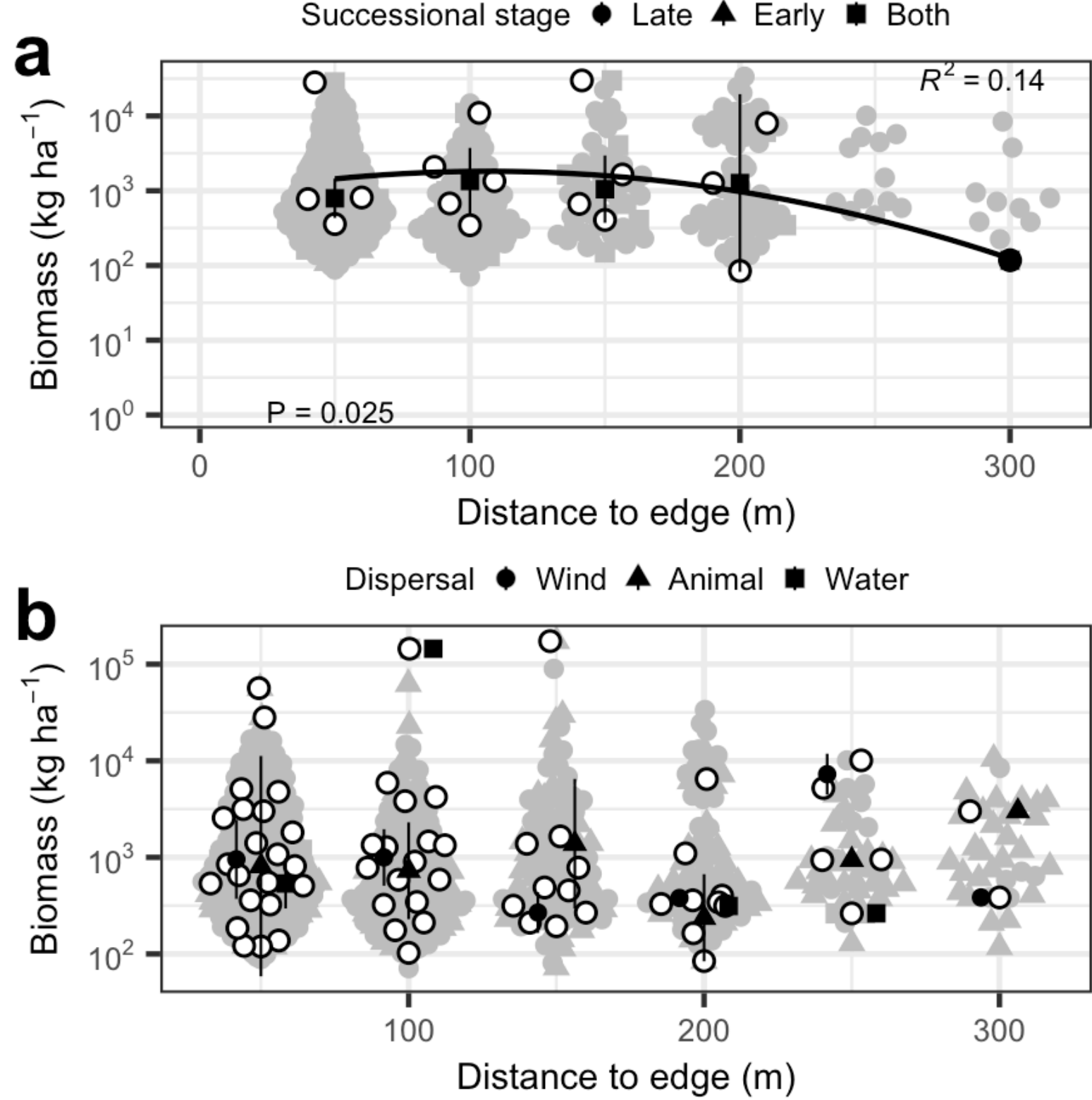


Fig 4 Functional regeneration based on taxa associations with (a) successional stages and (b) primary dispersal mode. Grey dots show individual tree values, white dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear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

Composition

- Overall diversity changed significantly with distance to primary forest edge (Fig 3).
- Diversity significantly ($p=0.017$) decreased non-linearly by $\sim 0.1 \pm 0.1$ per m as distance to primary forest edge increased, which explained 73% of variance among distance strata medians (Fig 3a) – while **in contrast taxonomic richness increased slightly** ($p=0.067$) and linearly by 2 ± 1 per 200 m and had 16% variance explained among distance strata (Fig 3b).
- Community composition and beta diversity also changed significantly ($p=0.01$) with 25.6% variance among distance strata explained by distance to primary forest edge, and the first two principal components explaining 59% and 24% totaling 83% of variance among calculated plot distances (Fig 3d).
- Key abundant taxa *Vochysia* and *Ficus* showed different responses – *Vochysia* nearly tended to decrease with distance to primary forest edge (Fig 3e), while *Ficus* decreased marginally significantly ($p=0.088$) and linearly by -62.6 ± 25.1 per m with ~20% variance among distance strata explained (Fig 3f).

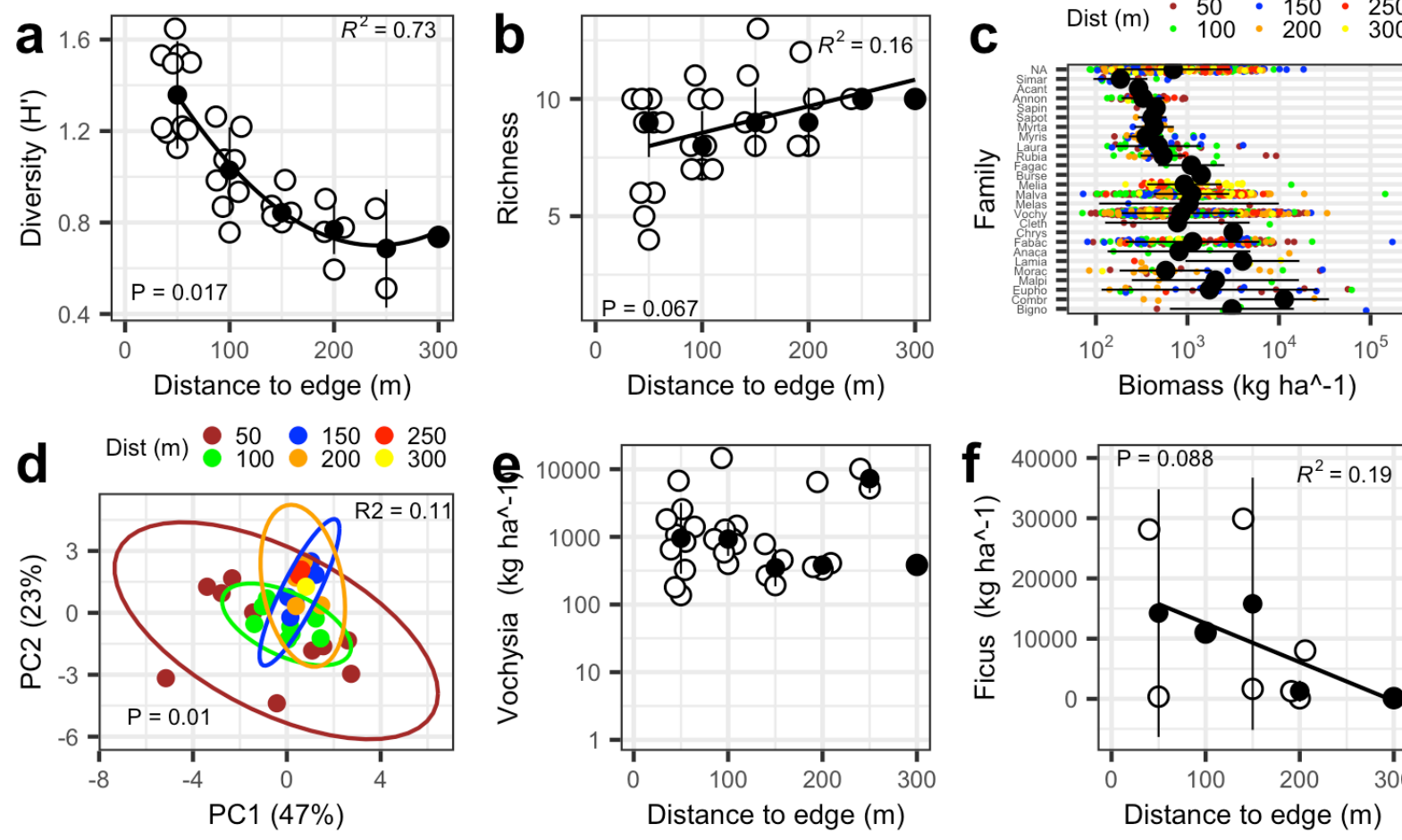


Fig 3 Taxonomic composition measures including (a) diversity, (b) richness, (c) overall biomass, (d) beta diversity, and (e, f) biomass of key taxa. White and colored dots with border show plot medians, black dots show distance strata medians ± 1 absolute deviation, and black lines show linear or non-linear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

DISCUSSION

- This study found significant edge effects on secondary forest stand wood and stem density, 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 this evidence supported edge effects on community composition and biomass of taxa associated with both early- and late-successional stages, but without detectable roles for light availability or general dispersal mode.
- Accordingly this suggests that edge effects do significantly change humid tropical forest community composition, but primarily due to factors other than light competition or dispersal limitation, as well as that aboveground biomass and even low taxonomic richness is resilient after a decade of regeneration.

Biomass

- 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).
- Overall, 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, Foster, and Percy 1995).
- Furthermore, light availability at the plot level may not affect biomass storage, but instead individual light gaps may be more important for biomass dynamics (Chazdon and Fetcher 1984).

Diversity

- Edge effects have been shown to lower both forest biomass and also diversity, and this study adds that the decline can be rapid and non-linear across edge gradients, along with supporting the likelihood of lasting changes to community composition.
- The rapid diversity loss across the edge gradient may be in part due to finer variations in dispersal patterns among animal taxa, rather than overall dispersal mode more broadly.
- Similarly, stochastic factors like priority effects after dispersal may also affect offspring establishment and re-growth.

CONCLUSIONS

For wet secondary forest regeneration —

- Biomass and taxonomic richness appear resilient
- Community composition likely lags in recovery
- Focusing conservation efforts like native plantings along degraded habitat edges may improve outcomes

FUNDING

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

ACKNOWLEDGEMENTS

- Professor Dan Perlman for initial networking;
- concurrent Osa Conservation managers Max Villalobos and Andrea Johnson for project guidance and supervision;
- Lehigh University Professor Don Morris and interns Emma Capetz and Erin Lau along with field station staff Agustín Mendoza for direct field assistance;
- concurrent Osa Conservation general manager Manuel Ramirez, along with Piro Biological Station staff Juan Carlos Cruz Díaz, Annia Barrantes, Larry Villalobos, Hansel Vargas, and visitors for field support;
- James Fifer, Chau Ho, and Michelle Spicer for discussion of early drafts;
- and Luisa Valdez for translation assistance.

DATA STATEMENT

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

REFERENCES

See in-text and .bib file in code repository.

