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EFEITOS DAS VARIÁVEIS AMBIENTAIS NA ESTRUTURA FLORESTAL
AO LONGO DE UM GRADIENTE SUCESSIONAL EM PROPRIEDADES
RIBEIRINHAS DA AMAZONIA ORIENTAL, BRASIL

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Tropical (PPGBIO) da Universidade Federal do Amapá, como requisito parcial à obtenção do título de Mestre em Biodiversidade Tropical.

Orientador: Dr. Darren Norris

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Dedico a minha família, pai, mãe, irmãos e marido que me apoiam a cada passo dado na minha carreira profissional.

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RESUMO

Caron, Tassiana Maylla Fontoura. Efeitos das variáveis ambientais na estrutura florestal ao longo de um gradiente sucessional em propriedades ribeirinhas na Amazonia oriental, Brasil. Macapá, 2020. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

A restauração de florestas tropicais degradadas é uma prioridade para garantir que as metas de desenvolvimento sustentável sejam cumpridas. Estudos anteriores sugerem que as florestas amazônicas de rebrota podem levar décadas para se recuperar, mas fatores como a proximidade com florestas antigas podem acelerar trajetórias de sucessão de rebrota. Aqui, usamos dados de campo coletados em 15 propriedades de pequenos agricultores da Amazônia para examinar as relações entre estrutura florestal, diversidade de mamíferos, tipo de rebrota, idade de rebrota, topografia e hidrografia. A estrutura da floresta foi quantificada juntamente com a diversidade de mamíferos em 30 parcelas pareadas de controle de rebrota. O estágio de rebrota florestal foi classificado em três grupos: floresta secundária de regeneração tardia, floresta secundária de regeneração precoce e pastagem abandonada. A área basal nas parcelas de rebrota permaneceu menos da metade da registrada nas parcelas de controle, mesmo após 20 a 25 anos. Embora a área basal tenha aumentado em sequência desde a pastagem, em parcelas precoces e até tardias, houve um declínio significativo na área basal das parcelas de controle tardias associadas a um declínio na proporção de árvores grandes. Também houve suporte contrastante para diferentes hipóteses não mutuamente exclusivas, com proporção de árvores pequenas (DAP <20 cm) mais fortemente relacionada à topografia (altitude e inclinação), enquanto a proporção de árvores grandes (DAP > 60 cm) relacionada à classe de rebrota, diversidade de mamíferos e tempo. Essas descobertas apoiam os esforços crescentes para conservar ativamente árvores grandes, a fim de evitar a sucessão retrogressiva das florestas degradadas da Amazônia.

Palavras-chave: Floresta amazônica; área basal; biodiversidade; resiliência ecológica; restauração florestal; histórico de uso da terra; regeneração natural; florestas de rebrota; sucessão; floresta tropical úmida.

ABSTRACT

Caron, Tassiana Maylla Fontoura. Effects of environmental variables in the forest structure along a successional gradient in riverside properties in eastern Amazonia, Brazil. Macapá, 2020. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

The restoration of degraded tropical forests is a priority to ensure sustainable development goals are met. Previous studies suggest that Amazonian regrowth forests can take decades to recover, yet factors such as proximity to old-growth forest may accelerate trajectories of regrowth succession. Here we use field data collected across 15 lowland Amazon smallholder properties to examine the relationships between forest structure, mammal diversity, regrowth type, regrowth age, topography and hydrography. Forest structure was quantified together with mammal diversity in 30 paired regrowth-control plots. Forest regrowth stage was classified into three groups: late second-regrowth forest, early second-regrowth forest and abandoned pasture. Basal area in regrowth plots remained less than half that recorded in control plots even after 20-25 years. Although basal area did increase in sequence from pasture, early to late-regrowth plots, there was a significant decline in basal area of late-regrowth control plots associated with a decline in the proportion of large trees. There was also contrasting support for different non-mutually exclusive hypotheses, with proportion of small trees (DBH < 20 cm) most strongly supported by topography (altitude and slope) whereas the proportion of large trees (DBH > 60 cm) supported by regrowth class, mammal diversity and time. These findings support calls for increased efforts to actively conserve large trees to avoid retrogressive succession of degraded Amazon forests.

Keywords: Amazon forest; basal area; biodiversity; ecological resilience; forest restoration; land use history; natural regeneration; regrowth forests; succession; tropical wet forest.

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1. INTRODUÇÃO GERAL

Florestas tropicais saudáveis fornecem bens e serviços às populações humanas e perdas florestais na Amazônia comprometem os principais serviços ecossistêmicos que ela oferece como o armazenamento de carbono na biomassa e nos solos, a regulação do balanço hídrico e do fluxo dos rios, a modulação dos padrões climáticos regionais e a melhoria das doenças infecciosas (Folley et al. 2007). Os trópicos apresentam uma maior perda de floresta com uma razão maior de perda/ganho e uma tendência estatisticamente significativa na perda anual de florestas, com um aumento estimado de perda de 2101 km² / ano (Hansen et al. 2013) . A taxa consolidada gerada pelo Projeto de Monitoramento do Desmatamento na Amazônia Legal por Satélite (PRODES), do Instituto Nacional de Pesquisas Espaciais (INPE), apontou o resultado de 6.947 km² de corte raso no período de agosto de 2016 a julho de 2017 (INPE, 2018).

Estudos de longo prazo revelaram que a estrutura e a dinâmica de muitas florestas tropicais estão mudando, mas as causas e conseqüências dessas mudanças permanecem em debate, ao investigar as mudanças na composição, aumentamos não apenas nossa compreensão da ecologia das florestas tropicais e suas respostas a distúrbios em larga escala, mas também nossa capacidade de prever como a mudança global futura terá impacto em alguns dos serviços críticos fornecidos por esses importantes ecossistemas (Feeley et al. 2019). A perda florestal na Amazônia leva também a perda dos serviços ambientais que tem um valor maior que os usos pouco sustentáveis que substituem a floresta, o valor de cada hectare de floresta em pé pode ser até duas ordens de magnitudes maior que o ganho da venda de madeira e de carne de gado (Fearnside. 2006).

Mais da metade das florestas do mundo sofrem interferências antrópicas e entender como os ecossistemas se recuperam após essas perturbações é importante para a manutenção dos serviços ecossistêmicos (Lohbeck et al. 2015). Além de serviços ambientais, florestas tropicais como a Amazônia tem um valor de utilidade tradicional e a sua perda também compromete a sociobiodiversidade ao eliminar culturas indígenas e extrativistas (Fearnside 2006).

Vários são as causas do desmatamento na Amazônia, entre elas destacam-se a pecuária, abertura de estradas oficiais e não oficiais, exploração de madeira e atividades

agrícolas (Jusys 2016). Segundo Fearnside (2006) os atores que impulsionam o desmatamento variam em diferentes regiões e ao longo do tempo, em geral, grandes e médios fazendeiros respondem por boa parte do desmatamento, mas em alguns lugares, pequenos produtores podem atuar como forças importantes nos lugares onde estão concentrados.

Florestas ribeirinhas são particularmente ameaçadas e sofrem perdas devido principalmente à conversão da cobertura florestal em pastagens comprometendo a manutenção dos fluxos hídricos (Nunes et al. 2019). A taxa de crescimento de florestas secundárias é lenta, principalmente por que a maioria das áreas abandonadas são compostas de antigas pastagens de solos compactados com perdas de nutrientes (Fearnside. 2006). A recuperação de áreas degradadas é necessária para resgatar o valor da floresta em pé e a Amazônia oferece uma excelente oportunidade de recuperação devido ao seu potencial natural para a regeneração (Rocha et al. 2016).

A restauração dos ecossistemas florestais após perturbações como o uso do solo envolve principalmente estratégias de restauração passiva como a regeneração natural, no entanto, os resultados ecológicos desse tipo de restauração ainda é incerto (Brancalion et al. 2016). Diversos fatores influenciam na restauração e é necessário investigar melhor a influencia desses fatores (Rocha et al. 2016). A regeneração natural sem interferência humana é amplamente aplicada no bioma Amazônia por possuir baixo custo e maior probabilidade de sucesso devido ao seu potencial de recuperação (Brancalion et al. 2016).

Durante a recuperação, o ecossistema passa por diferentes fases de sucessão ecológica onde as taxas dos processos ecossistêmicos mudam durante cada fase e um fator forte para explicar estes processos é a biomassa acima do solo (Lohbeck et al. 2015). Um forte fator que explica os padrões espaciais de biomassa acima do solo compreende variáveis de suporte como estrutura e composição da floresta (Baraloto et al. 2011). Há uma forte relação entre a biomassa e variáveis utilizadas em equações alométricas como diâmetro, altura e peso específico de madeira (Chave et al. 2005), além de densidade de haste e área basal (Chave et al. 2004). Além disso, produção e biomassa nas florestas está relacionado com vários outros fatores, por exemplo densidade e riqueza de vertebrados (Sobral et al. 2017).

Características ambientais como por exemplo a disponibilidade de luz propiciam o crescimento de espécies e podem aumentar a área basal (Silva et al. 1995), a biomassa está

intimamente ligada a área basal e em florestas tropicais tanto fatores climáticos quanto edáficos são fortes preditores para o aumento ou diminuição dessa biomassa (Slik et al. 2010).

A Floresta Amazônica abriga uma rica variedade de espécies vegetais e animais sendo uma das biorregiões mais importantes do planeta (Foley et al. 2007). Possui diferentes ecossistemas que embora muito importantes, ainda são pouco amostrados e compreendidos, dentre eles, temos as florestas de terra firme que são os mais complexos, seguidos das florestas de várzea (Myster 2016). A Amazônia é uma região com muitas incertezas nas estimativas de biomassa pela difícil amostragem, assim, técnicas de sensoriamento remoto são muito utilizadas para fornecer estas estimativas, no entanto, imagens de satélite subestimam sistematicamente áreas de florestas ribeirinhas (Nunes et al. 2019). É indispensável a análise de dados coletados em campo para se obter uma compreensão mais exata da estrutura florestal.

Diante da necessidade de entender os padrões de estrutura florestal em florestas de terra firme na Amazônia, este estudo objetiva identificar como fatores bióticos e abióticos podem explicar as diferenças estruturais nas vegetações de áreas em regeneração natural em diferentes gradientes sucessionais e quais destes fatores se mostram mais determinantes neste processo.

2. HIPÓTESES

- Fatores abióticos relacionados a topografia, como altitude e inclinação do terreno, podem explicar padrões na sucessão ecológica por impulsionar e modular a distribuição de espécies, além de estarem relacionadas à disponibilidade de água no solo e mortalidade de árvores.
- Fatores relacionados a hidrografia do local, como índice topográfico de umidade (TWI) e proximidade de drenagem podem afetar a estrutura da floresta por estarem associados ao controle de umidade no solo.
- A classe de rebrota (floresta secundária de regeneração tardia, floresta secundária de regeneração precoce e pastagem abandonada) é fator determinante da estrutura florestal, pois a história do uso da terra tem uma forte influência nas taxas de recuperação da floresta.
- O tempo é uma das principais variáveis determinantes para a recuperação da estrutura florestal nas pequenas propriedades. Quanto maior o tempo de abandono da cultura de uso da terra, maior a área basal.
- Abundância relativa em espécies de mamíferos de médio e grande porte podem explicar variação na estrutura florestal ao longo de um gradiente sucessional em propriedades ribeirinhas. A diversidade de mamíferos está positivamente relacionada à biomassa das árvores e à concentração de carbono no solo.

3. OBJETIVOS

3. 1. GERAL

Identificar padrões que expliquem como a estrutura florestal se recupera naturalmente em propriedades ribeirinhas.

3. 2. ESPECÍFICOS

- Caracterizar a vegetação das propriedades para avaliar as comunidades vegetais do ponto vista estrutural.
- Estabelecer relação entre as variáveis ambientais bióticas e abiótica e área basal.
- Identificar as variáveis mais determinantes para a regeneração natural do ecossistema nas áreas estudadas.

4. REFERÊNCIAS

- Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E., Fine, P. V. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*. 17:2677–2688.
- Brancalion, P. H. S., D. Schweizer, U. Gaudare, J. R. Mangueira, F. Lamonato, and F. T. Farah. 2016. Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes : the case of Brazil. *Biotropica* 48:856–867.
- Chave J, Andalo C, Brown S et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99.
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R. 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 359, 409–420.
- Fearnside, P. M. 1991. Desmatamento na Amazônia brasileira: história , índices e conseqüências. *Acta Amazônica*. VOL. 36(3) 2006: 395 - 400
- Feeley, K. J., S. J. Davies, R. Perez, S. P. Hubbell, R. B. Foster, K. J. Feeley, S. J. Davies, R. Perez, S. P. Hubbell, and R. B. Foster. 2019. Directional changes in the species composition of a tropical forest Published by : Wiley on behalf of the Ecological Society of America Stable URL : <https://www.jstor.org/stable/41151211> REFERENCES Linked references are available on JSTOR for this article : Directional changes in the species composition of a tropical forest 92:871–882.
- Foley, J. A., G. P. Asner, M. H. Costa, M. T. Coe, R. Defries, H. K. Gibbs, E. A. Howard, S. Olson, J. Patz, N. Ramankutty, and P. Snyder. 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin In a nutshell. *Frontiers in Ecology and the Environment* 5:25-32.
- Hansen, M. C., P. V Potapov, R. Moore, M. Hancher, S. A. Turubanova, and A. Tyukavina. 2013. High-Resolution Global Maps of 134:850–854.

- Jusys, T. 2016. Fundamental causes and spatial heterogeneity of deforestation in Legal Amazon. *Applied Geography* 75:188–199.
- INPE. 2018. Projeto de Monitoramento do Desmatamento na Amazônia Legal por Satélite (PRODES) < <http://www.obt.inpe.br/OBT/assuntos/programas/amazonia/prodes>>. (Acesso em fevereiro de 2018).
- Lohbeck, M., L. Poorter, M. Martinez-ramos, and F. Bongers. 2015. tropical forest succession Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96: 1242-1252.
- Myster, R. W. 2016. The Physical Structure of Forests in the Amazon Basin : a Review. *The Botanical Review*:407–427.
- Nunes, S., J. Barlow, T. Gardner, M. Sales, D. Monteiro, and C. Souza. 2019. Land Use Policy Uncertainties in assessing the extent and legal compliance status of riparian forests in the eastern Brazilian Amazon. *Land Use Policy* 82:37–47.
- Rocha, G. P. E., D. L. M. Vieira, and M. F. Simon. 2016. Forest Ecology and Management Fast natural regeneration in abandoned pastures in southern Amazonia. *FOREST ECOLOGY AND MANAGEMENT* 370:93–101.
- Silva, J. N. M., J. O. P. De Carvalho, J. C. A. Lopes, B. F. De Almeida, and D. H. M. Costa. 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging *71*:267–274.
- Slik, J. W. F., S. Aiba, F. Q. Brearley, C. H. Cannon, O. Forshed, K. Kitayama, H. Nagamasu, R. Nilus, J. Payne, G. Paoli, A. D. Poulsen, N. Raes, and D. Sheil. 2010. Environmental correlates of tree biomass , basal area , wood specific gravity and stem density gradients in Borneo ’ s tropical forests:50–60.
- Sobral, M., Silvius, K. M., Overman, H. O., Oliveira, L. F. B., Raab, T. K., Fragoso, J. M. V. 2017. Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. *Nature Ecology & Evolution* 1:1670-1676.

Big trees drive forest structure patterns across a lowland Amazon regrowth gradient

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Big trees drive forest structure patterns across a lowland Amazon regrowth gradient

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Abstract

Degraded Amazonian forests can take decades to recover and the ecological results of natural regeneration are still uncertain. Here we use field data collected across 15 lowland Amazon smallholder properties to examine the relationships between forest structure, mammal diversity, regrowth type, regrowth age, topography and hydrography. Forest structure was quantified together with mammal diversity in 30 paired regrowth-control plots. Forest regrowth stage was classified into three groups: late second-regrowth, early second-regrowth and abandoned pasture. Basal area in regrowth plots remained less than half that recorded in control plots even after 20-25 years. Although basal area did increase in sequence from pasture, early to late-regrowth plots, there was a significant decline in basal area of late-regrowth control plots associated with a decline in the proportion of large trees. There was also contrasting support for different non-mutually exclusive hypotheses, with proportion of small trees (DBH <20cm) most strongly supported by topography (altitude and slope) whereas the proportion of large trees (DBH >60cm) supported by plot type and regrowth class. These findings support calls for increased efforts to actively conserve large trees to avoid retrogressive succession of degraded Amazon forests.

Introduction

Healthy tropical forests provide goods and services to human populations. Yet tropical forests show worrying rates of forest loss with an elevated loss / gain ratio and a statistically significant trend in annual forest loss of 2101 km²/year¹. One option to revert tropical forest loss is the restoration of degraded forests and deforested landscapes^{2,3}. Although the post-disturbance restoration of forest ecosystems often involves passive restoration strategies (i.e. natural regeneration), the ecological results of this type of restoration are still uncertain²⁻⁴.

Continuing widespread forest losses across Amazonia compromises vital ecosystem services such as carbon storage, regulation of hydrological cycles and climate patterns⁵⁻⁷. Riverside forests are particularly threatened and suffer losses due to the conversion of forest cover to pastures, compromising the maintenance of water flows⁸. The recovery of degraded areas is necessary to recuperate the standing forest value and the Amazon offers an excellent recovery opportunity due to its natural potential for regeneration^{9,10}. Yet, the regrowth rate of degraded Amazon forests can be slow, as abandoned areas are typically on compacted poor quality soils^{11,12} and due to the high structural and biological diversity of the original forests¹³.

The diversity of Amazon forests means it is hard to separate the complex interactions driving recruitment and recovery patterns^{2,3,14,15}, yet previous studies show that different animal groups can generate important impacts. The recovery of faunal diversity and associated ecosystem services (e.g. seed dispersal) are essential for natural regeneration processes in degraded forests^{16,17}. For example, seeds can be preyed upon by both vertebrates and invertebrates^{18,19}, which may play key roles in limiting germination and subsequent recruitment. Indeed, exclosure experiments have demonstrated the impact of vertebrates on

seed and seedling survival, showing how this group contributes to the community structure of tropical forest trees²⁰⁻²².

Amazon mammals are important component of forest diversity^{20,23} including carbon²⁴ and biomass cycles²⁵. Mammals can also play an important role in the successional trajectory and recovery of degraded areas as dispersers and predators of both seeds and seedlings¹⁸. Mid- and large-bodied mammals (weight > 1 kg) can disperse a large numbers of seeds over long distances^{18,26}. For example, lowland tapirs can travel over 4 kilometers in a day²⁷ and disperse seeds of more than 70 tree species²⁸. The loss of mid- to large-bodied mammals may release some plant species from herbivory and increase their dominance, which subsequently decreases tropical forest biodiversity^{29,30}.

Given the need to understand the patterns of forest structure in Amazonian forests, here we aim to identify how biotic and abiotic factors (Table 1) can explain patterns in forest structure across a successional gradient.

Table 1. Explanatory variables.

Working Hypothesis/Model	Variables	Source	Description/Ecological relevance	Supporting references
	Plot type	In situ.	Categorical factor with two levels: control and regrowth. Included in all models.	
Topography	Altitude	SRTM-DEM	Altitude is a driver and modulator of species distribution patterns from microhabitat to biogeographic scales. Altitude not only affects soil, water availability, climate and a myriad of other abiotic and biotic variables	10,13,31,32
	Slope	SRTM-DEM	Slope affects soil, water availability and tree mortality rates.	
Hydrography	TWI	SRTM-DEM	Topographic wetness index accounts for the topographic control of water movement in sloped landscapes and the associated control on soil moisture.	33
	Drainage proximity	SRTM-DEM	Combination of water gravitational potential (Height above the nearest drainage (HAND)) and soil drainage (Horizontal distance from nearest drainage (HDND)).	34-36
Regrowth class	Regrowth class	In situ: interview	Land-use history has a strong influence on rates of forest recovery. Categorical factor with three levels of regrowth class derived from the land-use history: late second-regrowth forest, early second-regrowth and pasture.	
Time	Years since last use	In situ: interview		10,37-39
	Years since initial clearing	In situ: interview	Time is a major determinant of forest succession.	
Mammals	Species richness	In situ: camera-trap images		24,25,40,41
	Functional diversity	In situ: camera-trap images	Mammal diversity is positively related to tree biomass.	

Table 2. Summary of survey locations. Characteristics of 15 sites used to study forest structure. Values are means with ranges in parentheses.

Regrowth class	Sites/ Plots	Size (ha)	Distance		Forest cover (%)		Tree BA (m ² /ha)		Large tree BA (m ² /ha)	
			River (m)	Town (km)	1 km	5 km	Reg.	Cont.	Reg.	Cont.
Late	5/10	5.8 (2.0– 12.0)	288.15 (110– 554)	40.4 (35.0– 45.0)	91.5 (87.4– 95.4)	97.4 (96.4– 98.5)	17.6 (11.5– 25.3)	35.8 (21.7– 47.4)	1.5 (0.0– 7.7)	11.4 (0.0– 22.3)
Early	5/10	2.4 (1.0– 4.5)	348.5 (150– 554)	38.2 (30.0– 43.7)	90.7 (87.1– 96.0)	97.2 (96.4– 98.4)	11.1 (4.7– 19.2)	49.3 (34.6– 76.5)	0.0 (0.0– 0.0)	20.8 (0.0– 44.2)
Pasture	5/10	8.7 (6.8– 9.9)	266.8 (170– 461)	32.8 (26.8– 40.8)	88.8 (85.7– 91.1)	96.9 (95.5– 98.5)	5.8 (0.0– 15.9)	47.1 (32.6– 64.8)	0.0 (0.0– 0.0)	24.0 (12.0– 41.2)
Totals	15/30	5.6 (1.0– 12.0)	301.1 (110– 554)	37.1 (26.8– 45.0)	90.4 (85.7– 96.0)	97.2 (95.5– 98.5)	11.5 (0.0– 25.3)	44.1 (21.7– 76.4)	0.5 (0.0– 7.7)	18.8 (0.0– 44.2)

Results

Variation in stand structure variables

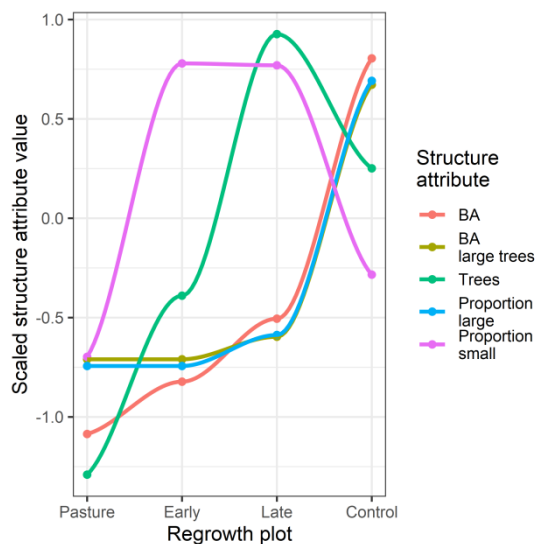


Figure 1: Forest structure changes across a lowland forest regrowth gradient. Showing mean values of five forest structure attributes recorded in 30 plots (15 control and 15 regrowth). Regrowth plot shows differences between control, late second-regrowth, early second-regrowth and pasture plots. Values are scaled (centered and scaled by the standard deviation) to enable simultaneous visual comparison of the different attributes. The lines are from LOESS smoothing as guides to aid visual interpretation.

There were clear differences in forest structure between control and regrowth plots (Figure 1). On average control plots had increased basal area and increased proportion of large trees (Figure 1). In contrast regrowth plots tended to have increased proportion of small trees (<20 cm DBH). The number and basal area of living trees tended to increase with altitude and this relationship was stronger in regrowth areas (Figure 2). The relationship with altitude was strongly affected by low lying (90 masl) pasture plots with no trees that generated significant leverage on the linear relationship (Figure 2).

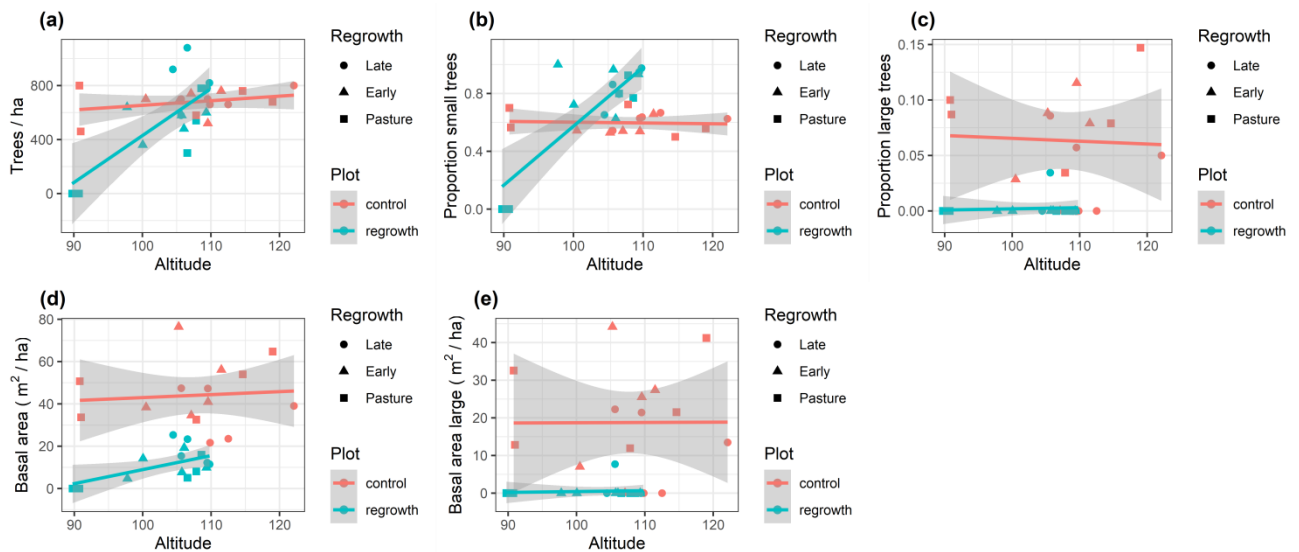


Figure 2: Forest structure along a lowland Amazon regrowth gradient. Showing trends in (a) number of trees (> 10 cm DBH) per ha, (b) proportion of small trees (10 – 20 cm DBH), (c) proportion of large (> 60 cm DBH) trees, (d) basal area and (e) basal area of large (>60 cm DBH) tree in 30 plots (15 control and 15 regrowth). Lines and shaded areas are mean values and 95% confidence intervals from linear models illustrating trends in basal area with increasing altitude (masl). Points with different shapes represent different regrowth classes.

Basal area ranged from 0 to 76.4 m²/ha across the 30 survey plots (Table 2), with control plots showing an average fourfold increase in basal area compared with regrowth plots

(mean basal area 44.1 and 11.5 m²/ha, control and regrowth respectively, Figure 2). The patterns in plot basal area also differed between regrowth classes (Figure 3, Supplementary Table S1). There was a significant interaction between plot type (control/regrowth) and regrowth stage, with basal area increasing across pasture, early and late regrowth plots but control plots showing the opposite trend, with basal area decreasing significantly in late-regrowth control plots (Figure 3).

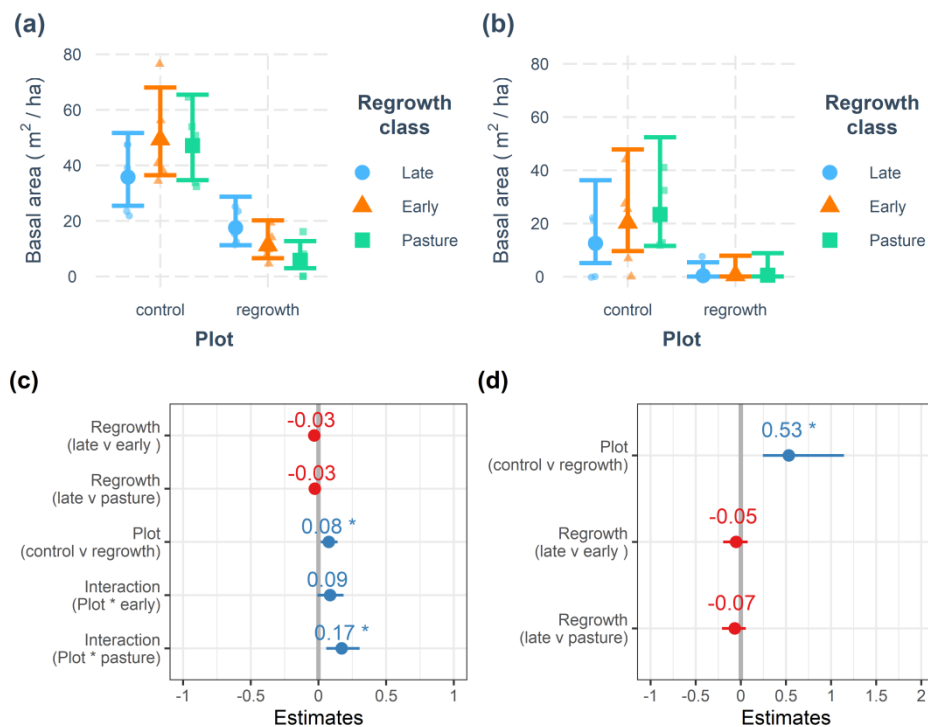


Figure 3: Basal area changes across a lowland forest regrowth gradient. The basal area of all (a and c) and large (b and d) living trees were recorded in 30 plots (15 control and 15 regrowth). Regrowth class shows differences between late second-regrowth, early second-regrowth and pasture plots contrasted with control forest plots. Top row shows Generalized Linear Model (GLM) predictions (mean and 95% confidence intervals) for basal area of (a) all and (b) large trees. Bottom row is the associated Forest-plot of the most parsimonious GLMs testing for interactions between regrowth class, plot type and years since last use in the basal area of (c) all and (d) large trees. Forest-plots show coefficient estimates and standard errors.

There was a highly significant positive linear relationship between overall basal area and large tree basal area ($F_{1,28} = 127.5$, $R^2 = 0.82$, $P < 0.0001$). The basal area of large trees

decreased significantly in regrowth compared with control plots (Figure 3). On average large trees accounted for 42% of the basal area in control plots compared with only 4% in regrowth plots (Table 2). Indeed a single large tree (>60 cm DBH) was recorded only once in a late-regrowth plot. This relationship was also reflected in the decline in basal area of late-regrowth control plots (Figure 3), which was associated with a decline on the proportion of large trees that accounted for a reduced 31% of the basal area in late-regrowth control plots (Table 2).

Relationships between forest structure, mammal diversity and environmental variables

Mammal diversity varied considerably across the survey plots (Figure 4). There appeared to be a tendency for basal area to increase with mammal diversity in Late-regrowth plots, yet basal area was only weakly associated with mammal diversity within the different regrowth classes (Figure 4). Indeed, the diversity of mammals was found to be only weakly informative for explaining the basal area of trees across the 30 sample plots (Table 3).

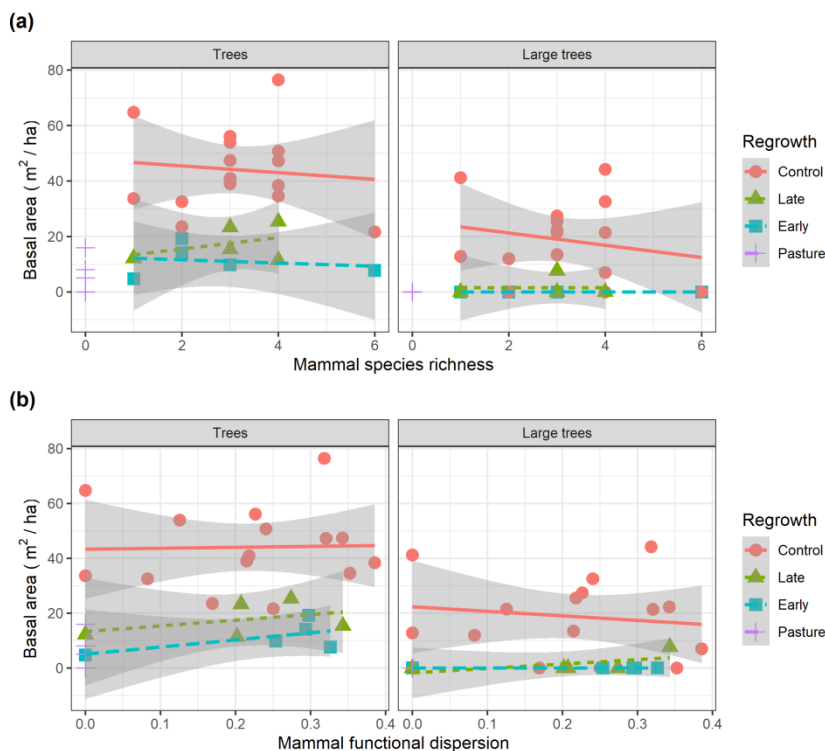


Figure 4. Mammal diversity and basal area across a lowland forest regrowth gradient. The basal area of (a) all and (b) large living trees were recorded together with the diversity (species richness and functional dispersion) of terrestrial mammals in 30 plots (15 control and 15 regrowth). Lines and shaded areas are mean values and 95% confidence intervals from linear models illustrating trends in basal area with increasing mammal diversity. Points with different shapes represent different regrowth plot types.

Comparison of the models representing the alternative hypotheses showed that plot type (control v regrowth) and topography were the most important first ranked variables for the five forest structure attributes (Table 3). The most simple model including only plot type explained more than 50% of model deviance for all forest structure attributes except for the number of trees (DBH>10 cm). Plot type and regrowth class were both included in the 95% confidence set of models for the basal area of large trees (Table 3). In contrast Topography was the most important (first ranked) model for the number of trees, proportion of small trees and tree basal area (Table 3). Mammal diversity, Time and Hydrography models were not well supported and were not included in the 95% confidence set of models for any of the forest structure attributes (Table 3).

Table 3. Summary of the Generalized Linear Models created to explain forest structure in 30 plots (15 control and 15 regrowth). Models ordered by decreasing AIC (Akaike Information Criterion) values.

Forest structure	Model ^a	Dev. Exp	Loglik	BIC	AIC	Δ AIC	W_i AIC ^b
Trees							
	Topography	60.5	-100.6	231.9	219.3	0.0	0.91
	Regrowth class	49.8	-105.1	234.1	224.3	5.0	0.07
	Mammals	51.3	-104.7	240.0	227.3	8.1	0.02
	Hydrography	45.8	-106.3	243.1	230.5	11.3	0.00
	Time	42.9	-107.0	244.7	232.1	12.8	0.00
	Plot	6.5	-114.4	239.1	234.9	15.6	0.00
Proportion small trees							
	Topography	75.2	-64.3	155.7	144.5	0.0	0.96
	Hydrography	70.4	-67.5	162.2	151.0	6.5	0.04
	Mammals	66.4	-70.2	167.6	156.4	11.9	0.00
	Time	65.1	-71.0	169.3	158.1	13.6	0.00
	Plot	53.7	-78.7	164.3	161.5	17.0	0.00
	Regrowth class	55.4	-77.6	175.6	167.2	22.7	0.00
Proportion large trees							
	Plot	54.9	-30.5	67.8	65.0	0.0	0.88
	Regrowth class	60.6	-28.9	78.2	69.8	4.8	0.08
	Mammals	62.9	-28.3	83.7	72.5	2.8	0.02
	Time	62.8	-28.3	83.8	72.5	2.8	0.02
	Topography	54.7	-30.6	88.5	77.3	7.5	0.00
	Hydrography	52.8	-31.1	89.5	78.3	8.5	0.00
BA all trees							
	Topography	80.7	-100.9	232.3	220.4	0.0	0.89
	Regrowth class	72.9	-105.8	235.4	225.6	5.2	0.06
	Plot	62.9	-110.4	231.0	226.8	6.4	0.04
	Mammals	71.7	-106.4	243.4	230.8	10.4	0.01
	Time	69.3	-107.6	245.8	233.2	12.8	0.00
	Hydrography	66.0	-109.1	248.8	236.2	15.9	0.00
BA large trees							
	Plot	58.3	-61.5	133.1	128.9	0.0	0.87
	Regrowth class	67.1	-59.9	143.5	133.7	4.8	0.08
	Hydrography	70.9	-59.0	148.7	136.1	7.1	0.02
	Mammals	70.4	-59.2	148.9	136.3	7.4	0.02
	Time	65.7	-60.1	150.9	138.3	9.4	0.01
	Topography	60.8	-61.0	152.7	140.1	11.2	0.00

^a Models used to explain forest structure. All models contained plot type (control/regrowth) as categorical factor. Variables and associated estimates in the different models can be found as Supplementary Information Table S2 online.

^b Akaike weights (W_i) from largest to smallest.

Discussion

We integrate field and remotely sensed data to establish support for multiple non-mutually exclusive hypotheses explaining patterns in forest structure across a lowland Amazon regrowth gradient. We establish that different hypotheses are supported for different structure attributes. Here we discuss these findings in terms of prospects for the passive restoration of degraded Amazon forests.

The mean basal area value from our 15 control plots (44.1 m²/ha) was close to the mean from 42 Guyana Shield forest plots (43.4 m²/ha, range 10 – 65 m²/ha) in French Guiana ³¹. The results from Molto, et al. ³¹ were obtained from an extensive survey of 0.5 – 1 ha plots. Although our plot size was smaller compared to Molto, et al. ³¹, the similarity in mean values suggests that our plots do provide a representative sample of forest structure in the regrowth areas. The basal areas obtained from our regrowth plots followed a similar trajectory to those reported from abandoned pasture in Costa Rica ¹⁰, where the most recently abandoned pasture plots (<14 year) had mean basal area of 13.5 m²/ha, with basal area increasing to 26.1 m²/ha after 21 – 30 year ¹⁰. compared with 11.1 and 17.6 m²/ha respectively in our Early (1-5 year) and Late (20 – 25 year) regrowth plots. This also follows a similar pattern to values reported from 370 successional forest plots in the Brazilian Amazon, with basal area values typically < 10 m²/ha in early stages (< 5 year) and reaching 25 m²/ha after 15 years ⁴².

Although results from lowland forest sites in Costa Rica suggest rapid recovery of pasture areas ¹⁰ this could be related to the substantially lower basal area in the seven old

growth reference plots (26.1 m²/ha, range 19.3 – 32.2 m²/ha) compared with those in our study area. Our results are similar to those reported from the central Amazon, where 25 y of regrowth restored half of the mature-forest biomass³⁷. A recent analysis of 45 Neotropical secondary forest study sites found that secondary forests in the lowland tropics reach 90 percent of old growth biomass in a median time of 66 yr¹³. Our findings do suggest nuanced difference in successional trajectories. Basal area increased rapidly in early regrowth stages and this could be explained by the less intensive land use (i.e. lack of pasture) and the proximity to large areas of intact forest. In contrast basal area of late-regrowth areas was less than those reported from other areas^{10,42}. This could be related to soil productivity, as previous studies show that highly diverse Guyana Shield wet forests can take longer to establish¹³. With basal area of control plots dominated by large trees it seems likely that many decades will be necessary for forest structure (total basal area, proportion of large trees) to return to pre-disturbance values.

The success of active and passive restoration can depend on ecological conditions⁴³. We found topography was the most informative model for explaining patterns in number of trees, tree basal area and proportion of small trees (Table 3, Figure 2). Differences in altitude and slope have been shown to affect floristic structure of tropical forests from local to regional scales^{31,38,39,44-46}. Indeed, even relatively small variations in topography can generate changes in local-scale soil chemistry, hydrology and microclimate^{44,47}. The effects of topography do not operate in isolation from hydrology and the increased numbers of small trees and tree biomass with increasing altitude (Figure 3) agree with previous studies that show trees grow more slowly in more low lying (and often more waterlogged) terrain³⁸.

We found a weak association between mammal diversity and regrowth forest structure. Previous studies in a nearby protected area show that this group of mammals (mid- to large-

bodied Artiodactyla, Perissodactyla and Rodentia) are more strongly associated with factors such as access to water ⁴⁸ and altitude ^{48,49}. A recent study also showed that mammal abundances were more strongly associated with phenology (fruit fall) than basal area along 10 km in forests of the western Guyana Shied ⁵⁰. Additionally, regrowth class was found to be the primary driver of mammal species encountered independent of forest cover ⁵¹. For example the number of species detected in control and regrowth plots (all with forest cover >87%) varied between 1 and 6 (Figure 4). Mid- to large-bodied seed dispersers are a critical component of Amazon forests ^{20,25,52} and are also widespread and ubiquitous across myriad Amazonian forest types ⁵³⁻⁵⁵. The eight species are therefore not strictly dependent on the quality of forest habitat compared with other more specialist groups such as primates ⁵⁶. The lack of a strong relationship between diversity of these eight mammal seed dispersers and forest structure attributes (i.e. overall basal area and proportion of small trees) is therefore to be expected.

More than 20 years of research shows that myriad edge effects permeate up to 150 m into Amazon forests ^{57,58}. Therefore the natural regeneration and/or restoration of regrowth habitats in Amazon small-holder properties (typically < 100 ha) that are largely covered by such distances will depend strongly on the ecological responses of species to habitat edges ⁵⁹. Previous studies show that edge effects increase mortality of large trees, which in turn has major impacts on forest ecosystems ⁶⁰. Tabarelli, et al. ⁶¹ and Santos, et al. ⁶² raised the hypothesis that edge-effects can drive tree communities through a process of “retrogressive succession” and toward an early successional state that may persist indefinitely. This early successional state can be characterized by functional differences with larger slower-growing tree species with high wood density tending to decline whereas faster-growing tree and liana species with lower wood density increasing.

Our findings provide an early warning that even under a best case scenario there is potential for “retrogressive succession”. We found not only a lack of large trees in regrowth plots but also that large tree basal declined in older late-regrowth control plots. We suggest that this decline in large trees may be the primary driver of differences between regrowth and old growth forest and as such represent an unquantified component of resilience and time to recovery of Neotropical secondary forests. We also suggest that the continued presence of mid- and large bodied mammal seed dispersers in the study area are likely to be vital in order to avoid such “retrogressive succession”.

Methods

Ethics Statement

Fieldwork and data collection was conducted under research permit numbers SISBIO 40355–1, 47859-1 and 47859-2 to DN, issued by the Brazilian Ministério do Meio Ambiente (“MMA”). Data collection used non-invasive, remotely activated camera traps and did not involve direct contact or interaction with animals, thus no ethical approval was required. Interviews with local residents were approved by Brazilian Ministério do Meio Ambiente (SISBIO permits 45034-1, 45034-2, 45034-3) and the Ethics Committee in Research from the Federal University of Amapá (UNIFAP) (CAAE 42064815.5.0000.0003, Permit number 1.013.843).

Study area

Our study took place in 15 areas of regrowth on small holder properties in the center of the State of Amapá (Figure 5). The regional climate is classified by Koppen-Geiger as Am (Equatorial monsoon) ⁶³, with annual rainfall greater than 2500 mm ⁶⁴. The driest months are September to November (total monthly rainfall < 150 mm) and the wettest months from

February to April (total monthly rainfall > 300 mm)⁶⁴. The State of Amapá has the lowest deforestation rate in Brazil and > 70% of the Amapá receives some form of legal protection. There is no large scale agricultural developments or monocultures along the waterways and properties retain typically small (< 1000 ha) areas of opened land, which are cleared for small scale family agriculture, which focuses on acai, small scale production of fruits and vegetables for sustenance and limited commercial sale of regional produce (e.g. manioc flour) in local markets. There are some 54 properties upstream of the nearest town (Porto Grande)⁶⁵. There has never been any expansive clearcutting in the region and there are no monocultures (e.g. soy) or cattle production. All sites were at least 26 km from the nearest town by river, and all sites are surrounded by matrix of continuous closed canopy forest cover (Table 2). Pesticides and/or herbicides had never been used at any of the sites.

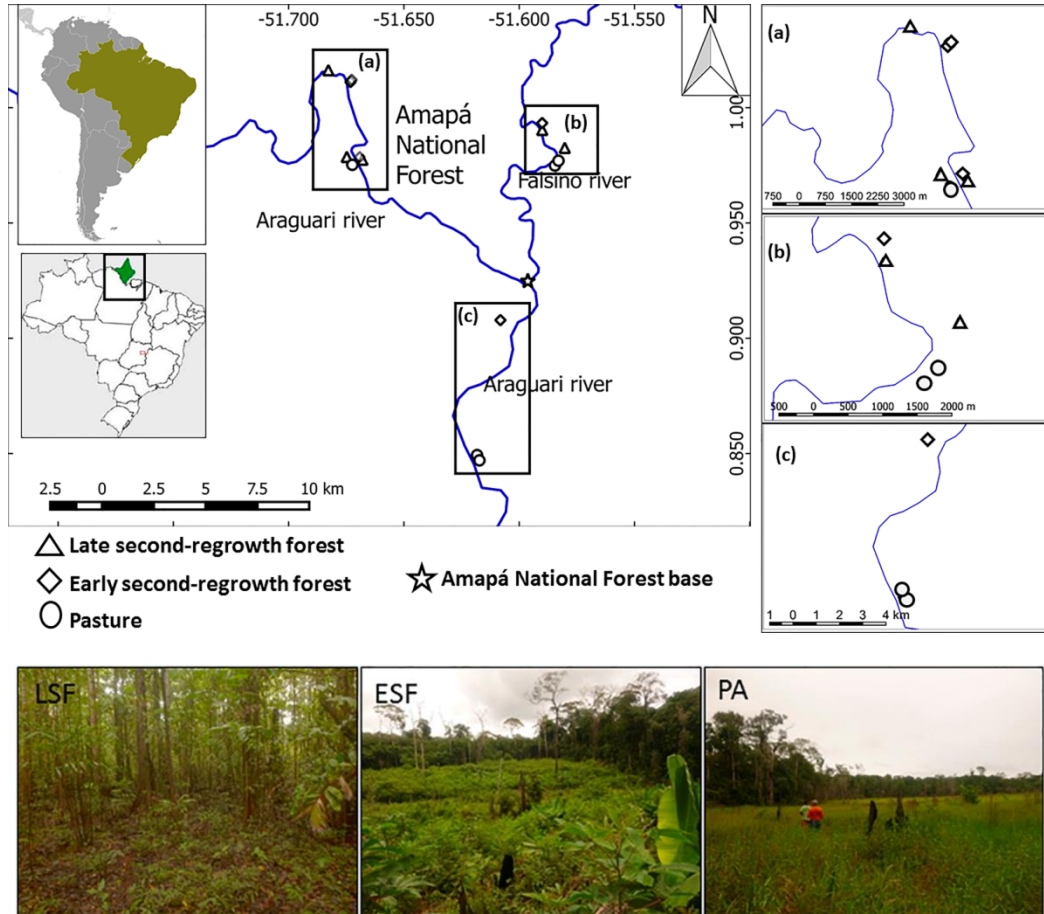


Fig. 5. Map of the study area in the eastern Amazon. Showing the location of 15 study sites, grouped into three regrowth stages in the small holder properties close to rivers (solid blue lines): late second-regrowth forest (LSF, triangles), early second-regrowth forest (ESF, squares) and pasture (PA, circles).

The 15 small-holder properties were selected based on differences in land-use histories and forest succession/regeneration stage. All sites were close (110 – 554m, Table 2) to 100 – 200 m wide rivers that are navigable by motorized boats, but due to riverbank formation the sites are never flooded. These 15 sites were grouped into three regrowth classes based on the land-use history: late second-regrowth forest (N = 5, most recent human disturbance between 20 and 25 years), early second-regrowth (N = 5, most recent human disturbance between 1 and 5 years), and pasture (N = 5, recently cleared and abandoned pasture areas dominated by grasses/herbs but that had never been used to raise livestock, with the most recent disturbance between 1 and 17 years). Each of the 15 regrowth sites was paired with a nearby (60 to 150 m) control site i.e. 20 – 30 m tall *terra-firme* forest site without a history of mechanized timber extraction. To reduce the possible confounding influence of edge effects that are known to strongly influence the distribution of trees in Neotropical forests, all regrowth and control sites were established at a standardized distance (approximately 30 m) from the nearest control-regrowth habitat edge.

Forest structure

Data were collected from May to August 2016. Forest structure data (i.e., number of trees and basal area) were obtained from plots measuring 50 x 10 m (500 m²), at each of the 30 points, totaling 1.5 hectare. This plot size was selected as it has been widely used to examine structural changes in tropical forests^{37,38,52,66} and several of the regrowth areas were too small (Table 2) to enable the establishment of larger spatially independent plots. We obtained five measures (responses) to characterize the forest structure in each plot. These were selected based on previous studies that show their appropriateness to distinguish

attributes of regrowth/successional stages related to biodiversity of Amazon forests ^{13,42,67,68}. The number of all trees ≥ 10 cm DBH (diameter at breast height at a standard 1.3 m above ground, or above tallest root buttress) was used to quantify the number of trees per area in each plot (m^2). This count included all trees which had at least half of their basal trunk inside the plot. The proportion of small (10 – 20 cm DBH) trees was calculated to represent the expected increase of younger trees in regrowth areas. The proportion of large (>60 cm DBH) trees was calculated as this is known as an important characteristic of mature/late succession areas ^{42,68}. We also calculated the basal area of all and large trees as this is known to be strongly correlated with tree biomass ⁶⁹. For example basal area and biomass were $> 99\%$ correlated in 23 plots from lowland Costa Rica ¹⁰.

Explanatory variables

We investigated predictions from multiple non-mutually exclusive hypotheses to explain patterns in basal area (Table 1). A total of 10 variables were used to form models to represent 5 working hypotheses (topography, hydrography, regrowth class, time and mammal diversity) that based on the findings from previous studies were likely to explain the observed patterns ^{10,13,24,36,37,70}. We chose to work with mainstream, widely available environmental variables. Four of these (the topographic and hydrographic model variables) were computed from remotely sensed digital terrain model (SRTM-DTM): altitude (masl), slope, TWI (Topographic wetness index), DND (Distance to Network Drainage) calculated from the interaction between HAND (Height above network drainage) and HDND (Horizontal distance to network drainage). The time model included years since the regrowth site was opened and years since last use, both of which were obtained from interviews with local landowners.

Mammal functional diversity was obtained from a camera-trap survey conducted at the same time (May to September 2016) and in the same plots as forest structure was sampled ⁵¹.

Camera traps equipped with infrared triggers (Bushnell Trophy Cam, 8MP, Overland Park, KS, USA) were installed in each of the 30 plots following standardized protocols^{48,49,71}. This camera trap survey [full details provide in⁵¹] including a sampling effort of 827 camera-trap days (450 and 377 camera-trap days, control and regrowth sites respectively) was used to estimate functional diversity of eight terrestrial mammal seed dispersers (*Cuniculus paca*, *Dasyprocta leporina*, *Myoprocta acouchy*, *Mazama americana*, *M. nemorivaga*, *Pecari tajacu*, *Tayassu pecari* and *Tapirus terrestris*).

Data analysis

Tree Basal Area in each plot was obtained as the sum of the basal area value for each individual tree derived from the DBH of each tree following the formula BA (basal area in m²)= 0.00007854 X DBH² (constant obtained by solving the following equation to obtain BA in m² from the DBH measured in cm⁶⁷):

$$BA = \frac{\pi \times (DBH/2)^2}{10000}$$

We calculated basal area of all and large (>60cm DBH) living trees^{67,68,70}. We also calculated the proportion of small stems (10 – 20 cm DBH trees) as this has been shown to be an important measure of stand structure in forest regrowth areas^{31,67}.

To represent diversity of terrestrial mammal seed dispersers we calculated a richness and functional diversity (FD) value for each of the 30 plots⁵¹. Richness was calculated as the observed number of species (hereafter “species richness”) at each plot. Although there are many diversity metrics, we chose species richness as it is widely used and clearly interpretable^{72,73} and with relatively few (eight) species and 30 plots there were strong correlations between species richness values and alternative diversity metrics such as Shannon

and Simpson diversity (Spearman rho > 0.89). We used Functional Dispersion (FDis)⁷⁴ as an index of functional diversity as it is not strongly influenced by outliers, accounts for relative abundances, is unaffected by species richness and can be calculated from any distance/dissimilarity measure^{74,75}. Functional Dispersion was estimated with the dbFD function⁷⁵ using default settings.

To examine patterns in forest structure attributes we used Generalized Linear Models. We used an information theoretic model averaging framework⁷⁶ to examine the support for five models representing the five non-mutually exclusive hypotheses – topography, hydrography, regrowth class, time and mammal diversity (see Table 1 for variable description and ecological relevance). We evaluated models based on their information content, as measured by AIC – Akaike Information Criterion. The relative importance of the models was measured by the models Akaike weights (Burnham & Anderson 2002 pp. 75-77, 167-172), which is a scaled measure of the likelihood ratio that ranges between 0 (least important) and 1 (most important). None of the unexplained variation (model residuals) was related to the geographic distance among plots so we did not need to control for spatial dependence. All analysis were conducted using the R language and environment for statistical computing⁷⁷, with base functions and functions available in the following packages: vegan⁷⁸, ggplot2⁷⁹, MuMIn⁸⁰, and tweedie⁸¹.

Data Availability Statement

The raw forest structure and environmental data used in the analysis of this study have been deposited in the OSF - Center for Open Science at DOI: 10.17605/OSF.IO/MC27U.

References

- 1 Hansen, M. C. *et al.* High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* **342**, 850-853, doi:[https://10.1126/science.1244693](https://doi.org/10.1126/science.1244693) (2013).
- 2 Chazdon, R. L. & Guariguata, M. R. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica* **48**, 716–730, doi:<https://doi.org/10.1111/btp.12381> (2016).
- 3 Holl, K. D. Restoring tropical forests from the bottom up. *Science* **355**, 455-456, doi:[https://10.1126/science.aam5432](https://doi.org/10.1126/science.aam5432) (2017).
- 4 Brancalion, P. H. S. *et al.* Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes: the case of Brazil. *Biotropica* **48**, 856-867, doi:[https://10.1111/btp.12383](https://doi.org/10.1111/btp.12383) (2016).
- 5 Foley, J. A. *et al.* Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment* **5**, 25-32, doi:[https://10.1890/1540-9295\(2007\)5\[25:ARFDAL\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[25:ARFDAL]2.0.CO;2) (2007).
- 6 Montibeller, B., Kmoch, A., Virro, H., Mander, Ü. & Uuemaa, E. Increasing fragmentation of forest cover in Brazil's Legal Amazon from 2001 to 2017. *Scientific Reports* **10**, 5803, doi:[https://10.1038/s41598-020-62591-x](https://doi.org/10.1038/s41598-020-62591-x) (2020).
- 7 Csillik, O., Kumar, P., Mascaro, J., O'Shea, T. & Asner, G. P. Monitoring tropical forest carbon stocks and emissions using Planet satellite data. *Scientific Reports* **9**, 17831, doi:[https://10.1038/s41598-019-54386-6](https://doi.org/10.1038/s41598-019-54386-6) (2019).
- 8 Nunes, S. *et al.* Uncertainties in assessing the extent and legal compliance status of riparian forests in the eastern Brazilian Amazon. *Land Use Policy* **82**, 37-47, doi:<https://doi.org/10.1016/j.landusepol.2018.11.051> (2019).
- 9 Rocha, G. P. E., Vieira, D. L. M. & Simon, M. F. Fast natural regeneration in abandoned pastures in southern Amazonia. *Forest Ecology and Management* **370**, 93-101, doi:<https://doi.org/10.1016/j.foreco.2016.03.057> (2016).
- 10 Letcher, S. G. & Chazdon, R. L. Rapid Recovery of Biomass, Species Richness, and Species Composition in a Forest Chronosequence in Northeastern Costa Rica. *Biotropica* **41**, 608-617, doi:[https://10.1111/j.1744-7429.2009.00517.x](https://doi.org/10.1111/j.1744-7429.2009.00517.x) (2009).
- 11 Fearnside, P. M. Deforestation in Brazilian Amazonia: History, Rates, and Consequences. *Conservation Biology* **19**, 680-688, doi:[https://10.1111/j.1523-1739.2005.00697.x](https://doi.org/10.1111/j.1523-1739.2005.00697.x) (2005).
- 12 Laurance, W. F. *et al.* Rain forest fragmentation and the proliferation of successional trees. *Ecology* **87**, 469-482, doi:[https://10.1890/05-0064](https://doi.org/10.1890/05-0064) (2006).
- 13 Poorter, L. *et al.* Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211-214, doi:[https://10.1038/nature16512](https://doi.org/10.1038/nature16512) (2016).
- 14 Camargo, J. L. C., Ferraz, I. D. K. & Imakawa, A. M. Rehabilitation of degraded areas of central Amazonia using direct sowing of forest tree seeds. *Restoration Ecology* **10**, 636-644, doi:[https://10.1046/j.1526-100X.2002.01044.x](https://doi.org/10.1046/j.1526-100X.2002.01044.x) (2002).
- 15 Guariguata, M. R. & Ostertag, R. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest ecology and management* **148**, 185-206, doi:[https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1) (2001).
- 16 Bowen, M. E., McAlpine, C. A., House, A. P. & Smith, G. C. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biological Conservation* **140**, 273-296, doi:<http://dx.doi.org/10.1016/j.biocon.2007.08.012> (2007).
- 17 Chazdon, R. L. & Uriarte, M. Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. *Biotropica* **48**, 709-715, doi:<http://dx.doi.org/10.1111/btp.12409> (2016).
- 18 Stoner, K. E., Riba-Hernández, P., Vulinec, K. & Lambert, J. E. The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their

- elimination. *Biotropica* **39**, 316-327, doi:<http://dx.doi.org/10.1111/j.1744-7429.2007.00292.x> (2007).
- 19 Griffiths, H. M., Bardgett, R. D., Louzada, J. & Barlow, J. The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proceedings of the Royal Society B* **283**, 20161634, doi:<http://dx.doi.org/10.1098/rspb.2016.1634> (2016).
- 20 Asquith, N. M. & Mejía-Chang, M. Mammals, edge effects, and the loss of tropical forest diversity. *Ecology* **86**, 379-390, doi:<http://dx.doi.org/10.1890/03-0575> (2005).
- 21 Beck, H., Snodgrass, J. W. & Thebpanya, P. Long-term exclosure of large terrestrial vertebrates: Implications of defaunation for seedling demographics in the Amazon rainforest. *Biological Conservation* **163**, 115-121, doi:<http://dx.doi.org/10.1016/j.biocon.2013.03.012> (2013).
- 22 Paine, C. E., Beck, H. & Terborgh, J. How mammalian predation contributes to tropical tree community structure. *Ecology* **97**, 3326-3336, doi:<https://doi.org/10.1002/ecy.1586> (2016).
- 23 Bascompte, J. & Jordano, P. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **38**, 567-593, doi:<http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095818> (2007).
- 24 Sobral, M. *et al.* Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. *Nature Ecology & Evolution* **1**, 1670-1676, doi:<https://10.1038/s41559-017-0334-0> (2017).
- 25 Peres, C. A., Emilio, T., Schiatti, J., Desmouliere, S. J. & Levi, T. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 892-897, doi:<https://10.1073/pnas.1516525113> (2016).
- 26 Wunderle, J. M. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99**, 223-235, doi:[http://dx.doi.org/10.1016/S0378-1127\(97\)00208-9](http://dx.doi.org/10.1016/S0378-1127(97)00208-9) (1997).
- 27 Fragoso, J. M. V. Tapir-Generated Seed Shadows: Scale-Dependent Patchiness in the Amazon Rain Forest. *Journal of Ecology* **85**, 519-529, doi:<http://dx.doi.org/10.2307/2960574> (1997).
- 28 Hibert, F. *et al.* Unveiling the diet of elusive rainforest herbivores in next generation sequencing era? The tapir as a case study. *PLoS One* **8**, e60799, doi:<http://dx.doi.org/10.1371/journal.pone.0060799> (2013).
- 29 Terborgh, J. *et al.* Tree recruitment in an empty forest. *Ecology* **89**, 1757-1768, doi:<http://dx.doi.org/10.1890/07-0479.1> (2008).
- 30 Wright, S. J. *et al.* The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* **39**, 289-291, doi:<http://dx.doi.org/10.1111/j.1744-7429.2007.00293.x> (2007).
- 31 Molto, Q. *et al.* Predicting tree heights for biomass estimates in tropical forests; a test from French Guiana. *Biogeosciences* **11**, 3121-3130, doi:<https://10.5194/bg-11-3121-2014> (2014).
- 32 Körner, C. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* **22**, 569-574, doi:<https://doi.org/10.1016/j.tree.2007.09.006> (2007).
- 33 Beven, K. & Kirkby, M. J. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Journal* **24**, 43-69, doi:<https://doi.org/10.1080/02626667909491834> (1979).
- 34 Campling, P., Gobin, A. & Feyen, J. Logistic Modeling to Spatially Predict the Probability of Soil Drainage Classes. *Soil Science Society of America Journal* **66**, 1390-1401, doi:<https://10.2136/sssaj2002.1390> (2002).
- 35 Nobre, A. D. *et al.* Height Above the Nearest Drainage – a hydrologically relevant new terrain model. *Journal of Hydrology* **404**, 13-29, doi:<http://dx.doi.org/10.1016/j.jhydrol.2011.03.051> (2011).

- 36 Schietti, J. *et al.* Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecology & Diversity* **7**, 241-253, doi:<https://10.1080/17550874.2013.783642> (2014).
- 37 Gehring, C., Denich, M. & Vlek, P. L. G. Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. *Journal of Tropical Ecology* **21**, 519-527, doi:<https://10.1017/S0266467405002543> (2005).
- 38 Feldpausch, T. R., Riha, S. J., Fernandes, E. C. M. & Wandelli, E. V. Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. *Earth Interactions* **9**, 1-22, doi:<https://10.1175/EI140.1> (2005).
- 39 Crouzeilles, R. *et al.* A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications* **7**, 11666, doi:<https://10.1038/ncomms11666> (2016).
- 40 Luskin, M. S., Ickes, K., Yao, T. L. & Davies, S. J. Wildlife differentially affect tree and liana regeneration in a tropical forest: An 18-year study of experimental terrestrial defaunation versus artificially abundant herbivores. *Journal of Applied Ecology* **56**, 1379-1388, doi:<https://10.1111/1365-2664.13378> (2019).
- 41 Chazdon, R. L. *et al.* The Potential for Species Conservation in Tropical Secondary Forests. *Conservation Biology* **23**, 1406-1417, doi:<https://10.1111/j.1523-1739.2009.01338.x> (2009).
- 42 Lu, D., Mausel, P., Brondízio, E. & Moran, E. Classification of successional forest stages in the Brazilian Amazon basin. *Forest Ecology and Management* **181**, 301-312, doi:[https://doi.org/10.1016/S0378-1127\(03\)00003-3](https://doi.org/10.1016/S0378-1127(03)00003-3) (2003).
- 43 Crouzeilles, R. *et al.* Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances* **3**, e1701345, doi:<https://10.1126/sciadv.1701345> (2017).
- 44 de Castilho, C. V. *et al.* Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *Forest Ecology and Management* **234**, 85-96, doi:<https://doi.org/10.1016/j.foreco.2006.06.024> (2006).
- 45 Jucker, T. *et al.* Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* **21**, 989-1000, doi:<https://10.1111/ele.12964> (2018).
- 46 Fortunel, C. *et al.* Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. *Ecology* **99**, 2272-2283, doi:<https://10.1002/ecy.2441> (2018).
- 47 Tiessen, H., Chacon, P. & Cuevas, E. Phosphorus and nitrogen status in soils and vegetation along a toposequence of dystrophic rainforests on the upper Rio Negro. *Oecologia* **99**, 145-150, doi:<https://10.1007/BF00317095> (1994).
- 48 Paredes, O. S. L., Norris, D., Oliveira, T. G. d. & Michalski, F. Water availability not fruitfall modulates the dry season distribution of frugivorous terrestrial vertebrates in a lowland Amazon forest. *PLOS ONE* **12**, e0174049, doi:<http://dx.doi.org/10.1371/journal.pone.0174049> (2017).
- 49 Michalski, L. J., Norris, D., de Oliveira, T. G. & Michalski, F. Ecological relationships of meso-scale distribution in 25 neotropical vertebrate species. *PLoS One* **10**, e0126114, doi:<http://dx.doi.org/10.1371/journal.pone.0126114> (2015).
- 50 Mendes Pontes, A. R. Tree reproductive phenology determines the abundance of medium-sized and large mammalian assemblages in the Guyana shield of the Brazilian Amazonia. *Animal Biodiversity and Conservation* **43.1**, 9-26, doi:<https://doi.org/10.32800/abc.2020.43.0009> (2020).
- 51 Arévalo-Sandi, A., Bobrowiec, P. E. D., Rodriguez Chuma, V. J. U. & Norris, D. Diversity of terrestrial mammal seed dispersers along a lowland Amazon forest regrowth gradient. *PLOS ONE* **13**, e0193752, doi:<https://10.1371/journal.pone.0193752> (2018).

- 52 Pessoa, M. S. *et al.* Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage. *Perspectives in Plant Ecology, Evolution and Systematics* **28**, 78-86, doi:<https://doi.org/10.1016/j.ppees.2017.09.001> (2017).
- 53 Arita, H. T., Robinson, J. G. & H REDFORD, K. Rarity in Neotropical forest mammals and its ecological correlates. *Conservation Biology* **4**, 181-192, doi:<http://dx.doi.org/10.1111/j.1523-1739.1990.tb00107.x> (1990).
- 54 Peres, C. A. & Palacios, E. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica* **39**, 304-315, doi:<http://dx.doi.org/10.1111/j.1744-7429.2007.00272.x> (2007).
- 55 Emmons, L. H. & Feer, F. *Neotropical rainforest mammals: A field guide.*, (The University of Chicago Press, 1997).
- 56 Michalski, F., Michalski, L. J. & Barnett, A. A. Environmental determinants and use of space by six Neotropical primates in the northern Brazilian Amazon. *Studies on Neotropical Fauna and Environment* **52**, 187-197, doi:<https://10.1080/01650521.2017.1335276> (2017).
- 57 Laurance, W. F. *et al.* Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. *Conservation Biology* **16**, 605-618, doi:<http://dx.doi.org/10.1046/j.1523-1739.2002.01025.x> (2002).
- 58 Norris, D., Peres, C. A., Michalski, F. & Hinchliffe, K. Terrestrial mammal responses to edges in Amazonian forest patches: a study based on track stations. *Mammalia* **72**, 15-23, doi:<https://10.1515/mamm.2008.002> (2008).
- 59 Martínez-Ramos, M. *et al.* Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica* **48**, 745-757, doi:<http://dx.doi.org/10.1111/btp.12382> (2016).
- 60 Laurance, W. F., Delamônica, P., Laurance, S. G., Vasconcelos, H. L. & Lovejoy, T. E. Rainforest fragmentation kills big trees. *Nature* **404**, 836-836, doi:<https://10.1038/35009032> (2000).
- 61 Tabarelli, M., Lopes, A. V. & Peres, C. A. Edge-effects Drive Tropical Forest Fragments Towards an Early-Successional System. *Biotropica* **40**, 657-661, doi:<https://10.1111/j.1744-7429.2008.00454.x> (2008).
- 62 Santos, B. A. *et al.* Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation* **141**, 249-260, doi:<https://doi.org/10.1016/j.biocon.2007.09.018> (2008).
- 63 Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. World map of the Koppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**, 259-263, doi:<http://dx.doi.org/10.1127/0941-2948/2006/0130> (2006).
- 64 ANA. *Sistema de Monitoramento Hidrológico (Hydrological Monitoring System)*. Agência Nacional de Águas[[nl]]National Water Agency, Available at <http://www.hidroweb.ana.gov.br>, 2017).
- 65 Norris, D. & Michalski, F. Socio-economic and spatial determinants of anthropogenic predation on Yellow-spotted River Turtle, *Podocnemis unifilis* (Testudines: Pelomedusidae), nests in the Brazilian Amazon: Implications for sustainable conservation and management. *Zoologia (Curitiba)* **30**, 482-490, doi:<http://dx.doi.org/10.1590/S1984-46702013000500003> (2013).
- 66 Yirdaw, E., Monge Monge, A., Austin, D. & Toure, I. Recovery of floristic diversity, composition and structure of regrowth forests on fallow lands: implications for conservation and restoration of degraded forest lands in Laos. *New Forests* **50**, 1007-1026, doi:<https://10.1007/s11056-019-09711-2> (2019).
- 67 McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* **218**, 1-24, doi:<https://doi.org/10.1016/j.foreco.2005.08.034> (2005).

- 68 Sist, P., Mazzei, L., Blanc, L. & Rutishauser, E. Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. *Forest Ecology and Management* **318**, 103-109, doi:<https://doi.org/10.1016/j.foreco.2014.01.005> (2014).
- 69 Phillips, O. L. *et al.* Species Matter: Wood Density Influences Tropical Forest Biomass at Multiple Scales. *Surveys in Geophysics* **40**, 913-935, doi:<https://10.1007/s10712-019-09540-0> (2019).
- 70 Bastin, J.-F. *et al.* Pan-tropical prediction of forest structure from the largest trees. *Global Ecology and Biogeography* **27**, 1366-1383, doi:<https://10.1111/geb.12803> (2018).
- 71 TEAM Network. 69 (Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science, Conservation International., Arlington, VA, USA., 2011).
- 72 Hortal, J., Borges, P. A. & Gaspar, C. Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology* **75**, 274-287, doi:<http://dx.doi.org/10.1111/j.1365-2656.2006.01048.x> (2006).
- 73 Magurran, A. E. & McGill, B. J. in *Biological diversity: frontiers in measurement and assessment* (eds A. E. Magurran & B. J. McGill) Ch. 1, 1-7 (Oxford University Press, 2011).
- 74 Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299-305, doi:<http://dx.doi.org/10.1890/08-2244.1> (2010).
- 75 FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. (2014).
- 76 Burnham, K. P. & Anderson, D. R. *Model selection and multi-model inference: A practical information-theoretic approach*. (Springer, 2002).
- 77 R: A language and environment for statistical computing. 3.6.3 (R Foundation for Statistical Computing, Vienna, Austria, 2020).
- 78 vegan: Community Ecology Package. R package version 2.4-0. <https://CRAN.R-project.org/package=vegan> (2016).
- 79 Wickham, H. *ggplot2: elegant graphics for data analysis*. (Springer, 2009).
- 80 MuMIn: multi-model inference. R package version 1.15.6. <https://CRAN.R-project.org/package=MuMIn> (2016).
- 81 Tweedie: Tweedie exponential family models. R package version 2.2.1. <https://cran.r-project.org/web/packages/tweedie> (2014).

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Author Contributions

D.N. conceived of the project; V.J.U.CR and A.A.S collected data. V.J.U.CR, A.A.S and D.N. performed data analysis and interpretation. A.A.S prepared figure 1. D.N. prepared figures 2-5. T.M.F.C and D.N. wrote the main manuscript text. All authors reviewed and revised the manuscript.

Competing Interests Statement

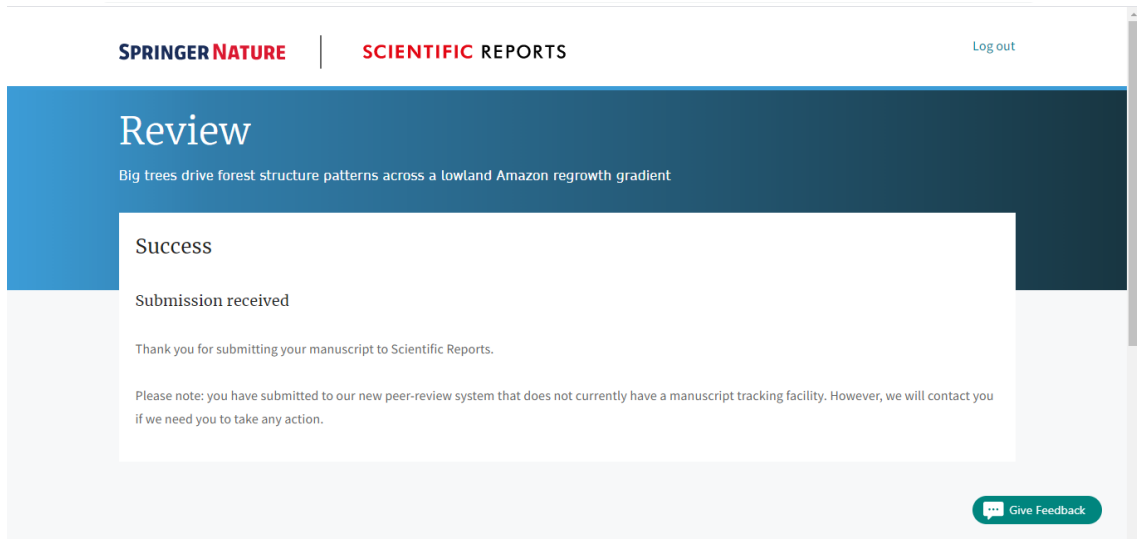
The authors declare that they have no competing interests as defined by Nature Research, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

6. CONCLUSÕES

- Nossos estudos mostram que embora a estrutura da floresta tenha se recuperado gradativamente, houve um declínio de área basal em áreas de floresta secundária de regeneração tardia associado a um declínio na proporção de árvores grandes.
- A presença de árvores pequenas está mais fortemente associada a condições ambientais como topografia e hidrografia enquanto a proporção de árvores grandes estão mais fortemente associadas classe de rebrota.
- Nossos estudos sugerem que há potencial para uma sucessão retrogressiva devido ao declínio da proporção de árvores grandes que se mostrou principal fator de diferença entre as áreas de rebrota e controle.
- Sugerimos que a presença de mamíferos dispersores de sementes, assim como a preservação de árvores de grande porte podem ser fatores vitais para a recuperação da estrutura florestal de áreas abandonadas.

ANEXO 1

Confirmação de submissão na revista Scientific Reports



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