
**PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA E BIODIVERSIDADE**

**THE EFFECT OF FOREST DEGRADATION ON ECOSYSTEM SERVICES
RELATED TO FRUGIVORY AND INSECTIVORY PROMOTED BY BIRDS AND
MAMMALS IN AMAZONIAN FORESTS**

LIANA CHESINI ROSSI

**Rio Claro – SP
2022**

PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA E BIODIVERSIDADE

THE EFFECT OF FOREST DEGRADATION ON ECOSYSTEM SERVICES
RELATED TO FRUGIVORY AND INSECTIVORY PROMOTED BY BIRDS AND
MAMMALS IN AMAZONIAN FORESTS

LIANA CHESINI ROSSI

Tese apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ecologia e Biodiversidade.

Orientador: Prof Dr. Marco Aurélio Pizo Ferreira

Co-orientador: Prof Dr. Alexander Charles Lees and Prof Dr. Bernard Josiah Barlow

Rio Claro – SP
2022

R832e Rossi, Liana Chesini
The effect of forest degradation on ecosystem services related to frugivory and insectivory promoted by birds and mammals in Amazonian forests / Liana Chesini Rossi. -- Rio Claro, 2022
206 p.

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientador: Marco Aurélio Pizo

1. ecologia. 2. funções ecológicas. 3. distúrbios antrópicos. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

Essa ficha não pode ser modificada.

CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: THE EFFECT OF FOREST DEGRADATION ON ECOSYSTEM SERVICES RELATED TO FRUGIVORY AND INSECTIVORY PROMOTED BY BIRDS AND MAMMALS IN AMAZONIAN FORESTS

AUTORA: LIANA CHESINI ROSSI

ORIENTADOR: MARCO AURELIO PIZO FERREIRA

COORIENTADOR: BERNARD JOSIAH BARLOW

COORIENTADOR: ALEXANDER CHARLES LEES

Aprovada como parte das exigências para obtenção do Título de Doutora em ECOLOGIA E BIODIVERSIDADE, área: Biodiversidade pela Comissão Examinadora:



Prof. Dr. MARCO AURELIO PIZO FERREIRA (Participação Virtual)
Departamento de Biodiversidade / IB Rio Claro

Profa. Dra. ELIANA CAZETTA (Participação Virtual)
Departamento de Ciências Biológicas / Universidade Estadual de Santa Cruz

Profa. Dra. MARINA CORREA CORTES (Participação Virtual)
Departamento de Biodiversidade / IB Rio Claro

Prof. Dr. MARIO COHN-HAFT (Participação Virtual)
Departamento de Biodiversidade (COBIO) e Coleções Zoológicas - Aves / Instituto Nacional de Pesquisas da Amazônia (INPA)

Prof. Dr. PAULO ROBERTO GUIMARÃES JUNIOR (Participação Virtual)
Departamento de Ecologia / Universidade de São Paulo

Rio Claro, 08 de setembro de 2022

AGRADECIMENTOS

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

A bolsa de doutorado foi financiada via Coordenação de Aperfeiçoamento de Pessoal de Nível Superior e Conselho Nacional de Desenvolvimento Científico e Tecnológico – CAPES/CNPq - 441573/2020-7 e a bolsa de doutorado sanduíche junto a Universidade Metropolitana de Manchester, Reino Unido através do Programa de Doutorado Sanduíche no Exterior - PDSE-CAPES 23038.000114/2020-80.

Agradeço imensamente a minha família paraense, **Josi, Xaxá (Xarope), Leca, Bega e Graveto** pelos dias intermináveis em campo que me fizeram uma pessoa bem feliz. Agradeço também pelo cuidado e carinho ao longo desses anos compartilhados, por me aguentarem até mesmo quando besuntada de andiroba, sem a dedicação dessas pessoas especiais esta tese não teria sido possível. À “paciência” de Xaxá em me ensinar sobre a Amazonia, olhar cuidadoso sobre a floresta que eu levo pra mim não importa onde eu esteja. À **Josi** pela amizade; minha admiração só cresce por essa mulher forte e guerreira! Agradeço de coração à comunidade do Branco que me acolheu e deu a esse trabalho um significado muito especial; ao **Peu** pela boniteza do ser, calmo e paciente; ao **Galo** pela ajuda e cuidado; **Yan** pelas conversas após o campo, quando o corpo cansado só queria repousar; à **Elaine** e seu abraço cada vez maior, com ela percebo o quanto o tempo está passando depressa. Agradeço ao **Louro**, amigo cheio de vida que, com seus encantamentos, cuida de todos. À **Bia**, mulher guerreira, um exemplo para mim; agradeço pela atenção e cuidado, pelas conversas e poemas.

Às amigas **Erika e Marina** por me apresentarem a Amazonia, sinto que as duas foram catalizadoras dessa força inexplicável que é essa floresta. Hoje, “amazonizada”, tenho a Amazônia meu lar. Erika, amiga muito especial, agradeço demais pela amizade, especialmente durante meu doutorado/pandemia, nossas discussões me ajudaram a manter a sanidade mental.

Aos meus pais, **Véra** e **José**, pelo amor de sempre, por me apoiarem nas minhas escolhas e estarem sempre perto de mim, ainda que distante; a minha irmã **Di**, por ser alegria, por ser vida! A minha **Dinda Carmem** e meu **Dindo Vicente** pelas conversas que me mantiveram aquecida durante a pandemia. Ao **Rafa** por ter compartilhado tanto amor e cuidado comigo durante essa caminhada da vida; por cuidar da **Mimi**, nossa mimi.

Pela presença e afeto das amizades de vida, **Bruna** e **Camila** e do **Thiago**, longe sim, mas cada dia mais perto. Às amigas rio-clarenses; **Ana**, por me acolher em sua casa, pelas conversas e incentivos; ao Salú e Filó pelos passeios necessários quando nada mais tinha jeito; **Raissa**, amiga que admiro muito e quero sempre perto, ainda que longe geograficamente; **Ju** querida, muito generosa e falante, compartilhamos bons momentos juntas; às lindas **Lais** e **Sara** pela dedicação e olhar atento às milhões de horas de vídeos que coletamos. À **Dona Beatriz** e **Maurem** por me acolherem em sua casa, nossas conversas amenizaram o peso das semanas intermináveis durante a quarentena.

Ao meu orientador **Marco** por me acolher e ter acreditado no meu trabalho mesmo sem muitas certezas se conseguiríamos. Muito grata pela confiança e ensinamentos, feliz com a aproximação e colaborações.

Aos meus coorientadores **Alex** e **Jos** por terem me recebido como aluna e me dado a oportunidade incrível de trabalhar na Amazônia. Agradeço também pelos incentivos na saga interminável para o estágio sanduíche.

Aos amigos que fiz no Laboratório de Ecologia de aves (LECAVE), UNESP – Rio Claro que estiveram sempre presentes e dispostos a ajudar. Aprendi muito com cada um e agradeço os momentos compartilhados; **Augusto** com os aninhamentos semanais, **Nati** e **Karlla** pelo trabalho lindo que fazem. Obrigada pelas discussões, aprendizados e pelos momentos compartilhados nos nossos encontros virtuais durante a quarentena, que tornaram esse período menos solitário.

Às pessoas especiais que me receberam durante o meu estágio na Inglaterra; **Alex**, **Nárgila** e **Sebastian** por me receberem no aconchego da sua casa durante o inverno inglês; feliz de compartilhar esse período importante pra mim com vocês. **Ollie** pela generosidade e parceria, também pelo bonito final de semana que passamos observando aves no litoral; **Ella**, amiga de espírito generoso, **Sadia** e sua magia com o chapati, **Francesca** e as boas pints que tomamos juntas, **Pelin**, **Dyuti**, **Elif**, **Andree** e **Mina** com quem compartilhei o dia a dia e aprendi muito.

Agradeço também a todos os coautores que colaboraram lendo e discutindo cuidadosamente os capítulos dessa tese. Em especial à **Joice**, professora cheia de boniteza, pela confiança e cuidado, sempre atenciosa; **Filipe** pelas discussões e palavras acolhedoras; e **Carine** pela sua paciência e ensinamentos compartilhados, feliz que estamos próximas novamente.

Às inúmeras pessoas que contribuíram para o desenvolvimento desta pesquisa muito antes de eu chegar lá. Um agradecimento especial aos parobotânicos **Jair**, **Ednaldo** e **Miguel**, importantes para a identificação das plantas. Aos **proprietários**, que nos deram a oportunidade de desenvolver esta pesquisa em suas florestas, especialmente à **Dona Célia** (pescadora profissional) e seu **Dalvino**, sempre tão amorosos comigo.

Ao grupo de **Ações Afirmativas da Unesp – Rio Claro**, pelas importantes reflexões e pelo bonito trabalho que vem desenvolvendo por uma educação mais diversa.

Ao **Programa de Pós-Graduação em Ecologia e Biodiversidade**, com todos seus professores e funcionários, que com dedicação formam esse curso de excelência; ao **Tadeu**, **Zé Paulo**, **Ivana**, **Felipe** pela disponibilidade em me ajudar e aconselhar. As representantes discentes **Ana** e **Juliana** pela ajuda de sempre nas dúvidas durante o processo burocrático que envolve o doutorado. Aos professores membros da banca de qualificação, **Marina Cortes**, **Laurence Culot** e **Marco Pizo** por fazerem parte e contribuírem para melhoria da tese. Aos

professores membros da banca avaliadora da defesa desta tese de doutorado **Eliana Cazetta**, **Marina Cortes**, **Paulo Guimarães Junior**, **Mario Cohn-Haft** e **Marco Pizo** e aos suplentes **Laurence Culot**, **Sérgio Henrique Borges** e **Mauro Galetti** por gentilmente aceitarem o convite.

RESUMO

Efeito da degradação florestal sobre os serviços ecossistêmicos relacionados à frugivoria e insetivoria promovido pelas aves na Floresta Amazônica

Florestas tropicais estão enfrentando ameaças impulsionadas por múltiplas atividades antrópicas, como extração seletiva de madeira e fogo. Em toda a Amazônia, as florestas afetadas por essas atividades cobrem cerca de 1 milhão de km², correspondendo a 17% das florestas remanescentes da região. Dada sua grande extensão, as florestas modificadas pelo homem desempenham um papel importante na conservação das espécies e na prestação de serviços ecossistêmicos. No entanto, distúrbios causados pelo homem afetam negativamente a biodiversidade e os processos ecológicos. Além disso, os impactos destes distúrbios sobre processos ecológicos, como controle da herbivoria e da dispersão de sementes, ainda são pouco compreendidos. Esta tese visa preencher esta lacuna do conhecimento avaliando como os distúrbios causados pelo homem, em particular a extração seletiva de madeira e incêndios florestais afetam comunidades biológicas e processos ecossistêmicos relacionados à regeneração florestal. Em 17 transectos florestais no centro-leste da Amazônia brasileira, usei seis metodologias para registrar 192 espécies frugívoras e 4.670 interações de frugivoria. Além disso, em 30 transectos florestais eu medi a incidência de predação em 4.500 lagartas artificiais. O objetivo do primeiro capítulo foi mensurar os efeitos da extração seletiva de madeira e dos incêndios florestais sobre as comunidades de espécies frugívoras. Os resultados indicam que, florestas queimadas há mais de 15 anos apresentaram baixo número de frugívoros obrigatórios (i.e., $\leq 80\%$ da dieta baseada em frutas) e de espécies de tamanho corporal grande, ao mesmo tempo que reduziram os valores de diversidade funcional. No segundo capítulo, avaliei os impactos da extração seletiva de madeira e dos incêndios florestais sobre as interações de

frugivoria. Descobri que, florestas que queimaram a mais de 15 anos tiveram uma menor diversidade de espécies e interações. Apesar desses efeitos, não encontrei diferenças na estrutura das redes de frugivoria; todas as redes foram altamente modulares e especializadas. Também registrei elevados valores de diversidade beta, resultado da alta dissimilaridade de interação entre as classes florestais. Por fim, no terceiro capítulo, examinei os efeitos dos distúrbios antrópicos sobre a incidência de predação de artrópodes folívoros. Os resultados mostraram uma surpreendente resiliência do processo de controle de artrópodes folívoros à degradação florestal; alta incidência de predação em florestas queimadas durante o El Niño de 2015-16. A incidência de predação em artrópodes folívoros foi realizada principalmente por artrópodes predadores. No geral, esses resultados sugerem que, embora os incêndios florestais recentes não tenham impactado fortemente os processos ecológicos, em longo prazo, incêndios florestais podem levar a mudanças significativas em comunidades ecológicas, reduzindo a ocorrência de frugívoros especialistas e de grande porte, bem como levando à perda da diversidade funcional e de interações de frugivoria na Florestas Amazônica. Portanto, a perda e as mudanças na diversidade taxonômica e funcional devido aos incêndios florestais, somadas as previsões de aumento na frequência desses incêndios, levam à vulnerabilidade dos processos ecológicos, como a frugivoria e da insetivoria –fundamentais para a manutenção e recuperação florestal, com possíveis consequências negativas sobre os serviços ecossistêmicos promovidos pelas florestas tropicais.

Palavras-chave: distúrbios antrópicos, funções ecológicas, florestas tropicais, interações ecológicas, incêndios florestais

ABSTRACT

The effect of forest degradation on ecosystem services related to frugivory and insectivory promoted by birds and mammals in Amazonian forests

Tropical forests are facing threats driven by multiple anthropogenic activities., such as selective logging and fires. Across Amazonia, forests affected by these activities cover c. 1 million km², corresponding to 17% of remaining forests in the region. Given its large extension, human-modified forests play an important role in species conservation and provision of ecosystem services. However, anthropogenic disturbances negatively affect biodiversity and ecological processes. Furthermore, the impacts of disturbances on ecological processes, such as herbivory control and seed dispersal, are still poorly understood. This thesis aims to fill these knowledge gaps by assessing how human-driven disturbances, in particular selective logging and forest fires, affect biological communities and ecosystems process related to forest regeneration, including insectivory and frugivory. Across 17 forest plots in central-eastern Brazilian Amazon, I combined six methodologies to record 192 frugivorous species; and 4,670 frugivory interactions. Additionally, across 30 plots, I measured predation incidence in 4,500 artificial caterpillars. My first Chapter aim was to measure the effects of selective logging and forest fires on frugivorous communities. The results indicate that forests burned more than 15 years in the past had a distinct frugivorous community composition in comparison to undisturbed forests, limiting the occurrence of obligate ($\leq 80\%$ diet based on fruits) and large-bodied frugivorous, while reduced the values of functional diversity. In the second Chapter, I assessed the impacts of selective logging and forest fires on frugivory interactions. I found that fires that occurred more than 15 years in the past reduced the number of species and unique interactions. Despite these effects, there were no impacts of neither selective logging or forest fires on the

structure of frugivory networks - all networks were highly modular and specialized. I also recorded a high beta-diversity of interactions in all forests, resulted from the high interaction dissimilarity among forest classes. Finally, in the third Chapter, I measured the effects of selective logging and forest fires on predation incidence on folivorous arthropods. Results showed a surprising resilience of predation incidence, which were similar between control plots and those affected by selective logging and forest fires. Arthropods were the main predators of caterpillars. Overall, these findings suggest that although fires that occurred <15 years ago have not strongly impacted frugivory and insectivory, fires can lead to significant changes on ecological communities, loss specialist and large frugivorous species as well as diversity of frugivory interactions and functions in Amazonian forests. Therefore, loss and changes in taxonomic and functional diversity due to forest fires, added to predictions of increases in fires frequency, rise up the vulnerability of frugivory and insectivory functions, both fundamental for forest maintenance and recovery, with implication on the services provided by tropical forests.

Keywords: anthropogenic disturbances, ecological functions, tropical forests, ecological interactions, forest fires

À Amazônia, centro do mundo

Na floresta, a ecologia somos nós, os humanos. Mas não também, tanto quanto nós, os 'xapiri', os animais, as árvores, os rios, os peixes, o céu, a chuva, o vento e o sol! É tudo o que veio à existência na floresta, longe dos brancos; tudo o que ainda não tem cerca.

Davi Kopenawa

PREFACE

This thesis has been written as papers and each of the data Chapters will be or has already been submitted for publication in peer-reviewed journals. Although the Chapters are standalone pieces of work, they are connected, introduced and discussed in an integrated way. Overlap between the Chapters is reduced as each has its own aims, but there is some small overlap in the introduction, site descriptions and methodology sections. Variable formatting between Chapters is a result of target journals requirements.

Even though the study presented in this thesis is largely my own, including literature review, methods design, data collection, statistical analysis and write up, it is integrated within a larger project (Rede Amazônia Sustentável – RAS). A number of researchers have been involved over the lifetime of this work and have provided substantial improvement in its content. Dr. Marco Aurelio Pizo, my lead supervisor, has played a significant role helping to guide fieldwork design and the content of all of the presented Chapters, with regard to refining research questions, methodological design, data analysis and structuring and proof reading of draft manuscripts. Dr. Alexander Charles Lees and Dr. Jos Barlow, my co-supervisors, have played similar roles to Marco in all Chapters. Dr. Alexander Charles Lees was my supervisor during my internship at the Manchester Metropolitan University, with an important contribution in Chapter 3. Additionally, Erika Berenguer, Joice Ferreira and Filipe França have all engaged in valuable discussions of the research topics, guiding fieldwork design, advising on statistical approaches and reviewing the manuscripts from all Chapters. A number of other individuals have made contributions to the content of this thesis in the following ways. Co-authors, Dr. Carine Emer providing significant contributions data analysis and structuring and proof reading of a draft of the Chapter 2; Msc. Yan Gabriel Ramos that contributed in data collection and identification, as well as Msc. Paulo Tavares, contributing for map design on Chapters 2 and 3.

Dr. Nárgila Gomes de Moura and Dr. Oliver C. Metcalf provided significant contributions, collecting data presented in Chapter 3.

This research was funded by the following: Conselho Nacional de Pesquisa (CNPq; grants CNPq-CAPES 441659/2016-0 and 441573/2020-7 [PELD-RAS], CAPES Foundation, an agency under the Ministry of Education of Brazil, PDSE - 88881.624387/2021-01, MCIC-CNPq 420254/2018-8 [RESFLORA] and CNPq-PrevFogo-IBAMA 441949/2018-5 [SEM-FLAMA]), Instituto Nacional de Ciência e Tecnologia – Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0) and Embrapa (SEG: 02.08.06.005.00), in Brazil; the Darwin Initiative (17-023), The Nature Conservancy, and Natural Environment Research Council (NERC; NE/F01614X/1, NE/G000816/1, NE/K016431/1 and NE/P004512/1).

PUBLICATION OUTPUTS FROM THIS THESIS

Published article

Rossi L.C., Berenguer E., Lees A.C., Barlow J., Ferreira J., França F.M., Tavares P., Pizo M.A. (2022). **Understorey fires affect predation on artificial caterpillars in human-modified tropical forests.** *Biotropica*, 54(3):754-763. DOI: 10.1111/btp.13097

Articles in preparation

Rossi L.C., Emer, C., Lees A.C., Berenguer E., Barlow J., Ferreira J., França F.M., Ramos, Y.G., Tavares P., Pizo M.A. **Fruit-frugivore interactions mediated by fires and logging in the Amazonian forests.** To be submitted to *Ecology*.

Rossi L.C., Lees A.C., Barlow J., Berenguer E., Ferreira J., França F.M., Metcalf O.C., Moura NG., Ramos, Y.G., Pizo M.A. **Amazonian frugivore community responses to disturbance in human-modified tropical forests.** To be submitted to *Proceedings of the Royal Society B: Biological Sciences*.

LIST OF TABLES

Table	Page
Table S2.1 Number of study plots in different forest disturbance classes.	87
Table S2.2 List of the eight ecological traits used to calculate the functional diversity indices. Measures followed Tobias <i>et al.</i> (2022) and Dunning (2008).	91
Table S2.3 Functional frugivore traits related to frugivory and seed dispersal. Frugivores were species that have fruits as a main dietary item based on Wilman <i>et al</i> (2014). Frugivore classification adapted from Kissling <i>et al.</i> (2007): Species that rely heavily on fruits were considered obligate frugivores (more than 80% of fruits on its diet), partial frugivores are species that include other major food items in their diet (20-79%), whereas opportunistic frugivores are species that only occasionally eat fruits as a supplementary food resource (up to 19%). Measurements were based on Tobias <i>et al.</i> (2022) and body mass on Dunning (2008). *Species that we saw eating fruits but were not considered as frugivores according to Wilman <i>et al.</i> (2014).	92
Table S2.4 Results of one-way variance test (ANOVA) testing the effects of human-forest disturbances on frugivore species in the Amazon Forest. Richness was based on rarefaction values (see detail for method in the mains text in 'Sampling frugivorous species section'). Frugivore classification: obligate frugivores – species with more than 80% of fruits on its diet; partial frugivores - fruits items range 20-79%; and opportunistic frugivores - eat fruits as a supplementary food resource (up to 19%).	100

Table S2.5	Pairwise comparison between forest classes on the richness of obligate frugivores based on Tukey test.	102
Table S2.6	Pairwise comparison based on Wilcox test between forest classes and the median of body mass values (g).	105
Table S2.7	Results of one-way variance test (ANOVA) for the effects of human-forest disturbances on Functional Diversity indexes in the Amazonian forests. FDis corresponds to functional dispersion (i.e., meaning the efficiency in using resources), while SESFRic corresponds to standardised values for functional richness (i.e., represents the niche space occupied by the community).	107
Table S2.8	Pairwise comparisons between forest classes of the functional dispersion (FDis) value indexes based on Tukey tests.	108
Table S2.9	Pairwise comparisons between forest classes of SESFRic values based on Tukey tests. SESFRic correspond to standardised values for functional richness index.	109
Table S3.1	Number of studies plots in different forest disturbance classes	148
Table S3.2	Description of the fruit-frugivore interaction in the Brazilian Amazon Forests. Seventeen transects sampled along distinct forest in the Amazon Forests: Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned). Samplings were based on hours. See methods in the main text for details of each network component.	152

Table S3.3	Frugivorous species recorded eating fruits. The numbers represent the frequencies of interaction involving the species.	154
Table S3.4	Plant morphotypes involved in the frugivory interaction. The numbers represent the frequencies of interaction involving the species.	158
Table S3.5	Results from Generalised Linear Models testing the effects of human-driven forest disturbances on frugivory networks in the Amazon Forest. Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned).	164
Table S3.6	The effect of fire and logging on the number of frugivorous species in the Amazonian forests, assessed using generalised linear mixed-effects models with <i>emmeans</i> test for post-hoc pairwise comparisons.	166
Table S3.7	The effect of fire and logging on the network size (frugivores and plants) in the Amazonian forests, assessed using generalised linear mixed-effects models with <i>emmeans</i> test for post-hoc pairwise comparisons.	167
Table S3.8	The effect of fire and logging on the number of unique frugivory interactions in the Amazonian forests, assessed using generalised linear mixed-effects models with <i>emmeans</i> test for post-hoc pairwise comparisons.	168
Table S3.9	Network metrics and null models for connectance, wNODEF, modularity and specialisation (see methods in the main text for details of each network component), of 17 transects sampled along distinct forest classes in the Amazonian forests: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior	171

sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned). First is the observed value in each network, second and third are the z-score of Patefield and Vaznull null models, respectively.

Table S3.10	Beta diversity of frugivores, plants and interactions of 17 ecological networks among distinct forest classes sampled in the Amazon Forests. Beta-diversity was estimated for the whole landscape (total) and within each forest class. β -total corresponds to the sum of species and interactions dissimilarity. β -turnover implies the replacement of some species and interactions by others and β -nestedness considers that a subset of species and interactions of sites with smaller numbers of species are subsets of the biotas at richer sites.	175
Table S4.1	Number of studies plots in different forest disturbance classes (pre-EN forest disturbance class), and of those affected by understorey fires during the 2015-16 El Niño (EN-fire-affected plots).	188
Table S4.2	Results of Models 1-6 (See Methods).	189
Table S4.3	The effect of El Niño 2015-16 understorey fires on total predation incidence artificial caterpillars along forest disturbance classes in Amazonian Forest, assessed using generalized linear mixed-effects models with <i>emmeans</i> test for post-hoc pairwise comparisons. Predation incidence in undisturbed forest served as baseline for comparisons. Pre-EN forest disturbance classes: UF – undisturbed forest; LF – logged forest; LBF – logged-and-burned forest; SF – Secondary forest. Forest that where affected understorey fires during	190

the 2015-16 El Niño are named EN-fire-affected. Significant results are highlighted in bold.

Table S4.4 The effect of the El Niño 2015-16 fires on the incidence of vertebrates (i.e., birds, mammals and reptiles) predation on artificial caterpillars. Comparisons were made using generalized linear mixed-effects models with *emmeans* tests for post-hoc pairwise comparisons. The incidence of predation in undisturbed forest served as baseline for comparison. Pre-EN forest disturbance classes: UF – undisturbed forest; LF – logged forest; LBF – logged-and-burned forest; SF – Secondary Forest. Forests that were affected by understorey fires during the 2015-16 El Niño are named EN-fire-affected. Significant results are highlighted in bold. 192

LIST OF FIGURES

Figure	Page
Figure 1.1 Map of the study area in the Brazilian Amazon. (a) Location of Santarém within the Brazilian state of Pará; and (b) Santarém region. The white square corresponds to the study area. Map adapted from Withey <i>et al.</i> (2018).	33
Figure 1.2 Production systems in the Santarém region: (a) large-scale soybean and (b) corn plantations; (c) cattle ranching. First two photos were taken by L.C.R. and the last photo by Ester F. Oliveira.	34
Figure 1.3 Fire dynamic in the Amazonian forests. (a) Understory fires; (b) forest post-fire; (c) forest structure after three years of understory fires. First two photos were taken by Erika Berenguer, second and third by L.C.R	35
Figure 1.4 Selective logging in Brazilian Amazon. (a) Transport of legal wood; (b) and (c) illegal extraction. Photos were taken by L.C.R	36
Figure 2.1 Effects of logging and forest fires on (i) overall frugivore richness, and (ii) richness of obligate frugivorous species (> 79% fruits on the diet). Overall species richness was rarefied in order to control for differences in sampling effort among the forest classes. We used the proportion of obligate frugivores in each transect to measure the impact of forest disturbances. Different letters represent statistical differences among forest classes at $p < 0.05$. Non-significant pairwise differences between forest classes are indicated by the presence of the same letter (according to Tukey pairwise test). Black dots are potential outliers and lines inside box plots represent median values.	67

Figure 2.2	NMDS ordination of frugivore species in 17 sites sampled in the Amazonian forests. Points and ellipses represent transects and forest classes, respectively.	68
Figure 2.3	Effects of logging and fire on (a) Functional dispersion (FDis) and null model, and on (b) Raw functional richness (FRic) and standardized effect size of functional richness (SESFric) of frugivorous animals in 17 transects across four forest classes.	69
Figure S2.1	Spatial auto-correlation in frugivorous species sampled across 17 forest transects.	88
Figure S2.2	Accumulation curves of frugivore richness with increasing sampling effort (hours) in six sampling methods. Each method was sampled across 17 transects distributed in four forest classes (except for passive acoustic recorders sampled in seconds and minutes and point count, both sampled in 14 transects). Species number (dark lines) with the standard error (light lines).	90
Figure S2.3	Box plots comparing frugivore species richness between forest classes according to each sampling method. For the transect method, recently-burned forests had a higher number of species in comparison to other forest classes. Species richness was rarefied in order to control for differences in sampling effort among forest classes. Different letters represent statistical differences among forest classes at $P < 0.05$. Non-significant pairwise differences between forest classes are indicated by the same letter (according to Tukey pairwise test). Black dots are potential outliers and lines inside box plots represent median values.	101

- Figure S2.4** Effects of logging and forest fires on the richness of partial (20-79% of the diet composed of fruits) and opportunistic (up to 19%) frugivore species among forest classes. We used the proportion of obligate frugivores in each transect to assess the impact of forest disturbances. Black dots are potential outliers and lines inside box plots represent median values. 103
- Figure S2.5** NMDS ordination of frugivore species among six distinct sampling methods: (a) birds and mammals included, (b) only birds. Ellipses represent different forest classes. Methods correspond to focal plants, camera traps, passive acoustic recorders sampled in intervals of seconds and minutes, and points count. 104
- Figure S2.6** Effects of logging and forest fires on the body mass of frugivores (g). Different letters represent statistical differences among forest classes at $P < 0.05$. Non-significant pairwise differences between forest classes are indicated by the same letter (according to Wilcox pairwise test). Black dots are potential outliers and lines inside box plots represent median values. 106
- Figure 3.1.** Study area. (a) The inset shows the Amazon biome (light green) within Brazil (light grey) and the Santarém region (black). (b) Santarém region. (c) Numbers and points mark the locations of the 17 forest transects sampled in: undisturbed forest (undisturbed); logged forest (selective logged ≥ 30 years before sampling); historically-burned forest (selective logging ≥ 30 years before sampling and burned in the past ≥ 18 years before sampling), and recently-burned forest (selective logging 119

≥ 30 years before sampling and burned recently (three years before sampling).

Figure 3.2. The structure of the 17 frugivory networks from undisturbed and human- 126

modified forests in central-eastern Brazilian Amazon. Yellow and purple dots represent mammal and bird species, respectively, while plant species are the green dots. The size of the dots is proportional to the species degree, i.e., their number of pairwise frugivory interactions. fruit-frugivore interactions are denoted by the grey lines connecting two dots, the width of which represents the frequency of those interactions.

Figure 3.3. Effects of logging and fire on (a) network size (i.e., total number of 127

frugivore and plant species); (b) number of frugivores (birds and mammals); (c) number of plant species; (d) total number of interactions, and (e) number of unique pairwise interactions. Different letters represent statistical differences among forest classes at $p < 0.05$, black dots are potential outliers and lines inside box plots represent median values.

Figure 3.4. NMDS ordination of the 17 sites that were sampled in the Amazon 129

Forest: (a) size (i.e., total number of frugivore and plant species), and (b) number of unique pairwise interactions. Points represent the transects and ellipses of the forest classes.

Figure S3.1 Accumulation curves of interaction number with increasing sampling 151

effort (hours) in 17 transects distributed in four forest classes. Interactions number (dark lines) with the standard error (grey lines). Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior

sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned).

Figure S3.2 Spatial autocorrelation on frugivores, plants and interactions species sampled across 17 forest transects. 162

Figure S3.3 Distance from control forests (undisturbed forest) correlation on frugivores, plants and interactions composition. 163

Figure S3.4 The effect of selective logging and forest fires on the structure of frugivory networks: (a) connectivity; (b) Weighted-NODF; (c) Specialisation H_2' ; and (d) modularity, in the Amazonian forests. The first column shows the results of each metric from the observed values, second and third columns are the z-score obtained using Patefield and Vaznull null models, respectively (see Methods for details of each model). Black dots are potential outliers and lines inside box plots represent median values. Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned). 169

Figure S3.5 Differences on the number of modules among forest classes. Black dots are potential outliers and lines inside box plots represent median values. 173

Figure S3.6 The effect of selective logging and forest fires on the beta-diversity based on occurrence data of: (a) interactions; (b) frugivores; and (c) plant species. The first column box plot is the total of beta-diversity, second and third is the percentage contribution of the turnover and nestedness component to the total beta-diversity observed among forest 174

classes. Black dots are potential outliers and lines inside box plots represent median values.

Figure 4.1 (a) Our study region in relation to the Brazilian Amazon. (b) The location of our study plots. 180

Figure 4.2 Examples of artificial caterpillars used in our experiment. (a) Caterpillar placed on a twig. Caterpillars with (b – d) bird, (e - f) mammal, and (h - j) arthropod predation marks. 181

Figure 4.3 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015-16 El Niño (red) and those that remained unaffected (blue). Different letters indicate significant differences among forest classes following pairwise comparisons (Table S4.3). Pre-EN forest disturbance classes: UF - undisturbed forests, LF - logged forests, LBF - logged-and-burned forests, and SF - secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles). 182

Figure 4.4 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015-16 El Niño (red) and those that remained unaffected (blue). Predation incidence was divided into two groups: (a) caused by arthropods, (b) caused by vertebrates (birds, mammals, and reptiles). Different letters indicate significant differences among forest classes following pairwise comparisons 183

(Table S4.4). Pre-EN forest disturbance classes: UF - undisturbed forests, LF - logged forests, LBF - logged-and-burned forests, and SF - secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles).

Figure S4.1 Caterpillar recovered with unidentified marks – although we suspect it was a bird. 194

Figure S4.2 Ant predation during the installation process. 195

TABLE OF CONTENTS

1. INTRODUCTION	32
1.1 Tropical forests in a changing world	32
1.1.1 Forest degradation	35
1.1.1.1 Forest fires	35
1.1.1.2 Selective logging	36
1.1.1.3 Secondary forests	36
1.2 Ecological Functions	37
1.2.1 Ecological function in a changing world	38
1.3 Objectives	40
1.4 References	40
2. CHAPTER ONE: Responses of Amazonian frugivores to disturbance in human-modified tropical forests	54
2.1 Abstract	56
2.2 Introduction	57
2.3 Materials and methods	59
2.3.1 Study area and sampling design	59
2.3.2 Frugivore classification and sampling frugivorous species	60
2.3.3 Functional traits	63
2.3.4 Data Analysis	65
2.3.4.1 Species richness and composition	65
2.3.4.2 Functional traits and diversity measures and variation	66
2.4 Results	66
2.4.1 Species richness and composition	66

2.4.2 Functional traits and diversity	69
2.5. Discussion	70
2.5.1 Effects of logging and fires on frugivore richness and composition	70
2.5.2. Functional traits and diversity in logged and burned forests	72
2.5.3 Implications of the different survey methods	74
3.5.4 Conclusion	75
2.6 Acknowledgments	75
2.7 Author Contribution	76
2.8 References	76
2.9 Supporting information	87
2.9.1 Spatial auto-correlation	88
2.9.2 Sampling effectiveness	89
2.9.3 Bird traits used to calculate the functional diversity indices	91
2.9.4 References	110
3. CHAPTER TWO: Fruit-frugivore interactions mediated by fires and logging in Amazonian forests	112
3.1 Abstract	114
3.2 Introduction	115
3.3 Methods	118
3.3.1. Study area and sampling design	118
3.3.2. Fruit-frugivore interactions	120
3.3.3 Sampling methods	120
3.3.4 Interaction networks	121
3.3.5 Beta-diversity of interactions	122
3.3.6 Analyses	123

3.4 Results	125
3.4.1 Overview of fruit-frugivore interactions	125
3.4.2 Fire and logging effects on network components	127
3.4.3 Fire and logging effects on beta-diversity	128
3.5 Discussion	130
3.5.1 Fires and logging effects on frugivory networks	131
3.5.2 Fire and logging effects on beta-diversity	132
3.5.3 The limitation of the study	133
3.5.4 Conclusions	134
3.6 Acknowledgments	134
3.7 Author contribution	135
3.8 References	135
3.9 Supporting information	148
3.9.1 Frugivory interactions	149
3.9.2 Sampling completeness	150
3.9.3 Spatial auto-correlation	162
3.9.4 Distance measures	163
3.9.5 References	176
4. CHAPTER THREE: Predation on artificial caterpillars following understorey fires in human-modified Amazonian forests	177
4.1 Abstract	178
4.2 Introduction	179
4.3 Methods	179
4.3.1 Study area	179
4.3.2 Data collection	180

4.3.3 Data analysis	181
4.3.3.1 Predation incidence across pre-EN forest disturbance classes and EN-fire-affected plots	181
4.3.3.2 Effects of different predator groups across pre-EN forest disturbance classes and EN-fire-affected plots	181
4.2 Results	182
4.2.1 Effects of pre-EN forest disturbance classes and El Niño understorey fires on total predation incidence	182
4.2.2 Effects of pre-EN forest disturbance classes and El Niño understorey fires on the predation by different groups	182
4.3 Discussion	182
4.5.1 Predation incidence across pre-EN forest disturbance classes	182
4.5.2 Predation incidence in EN-fire-affected forests	183
4.5.3 The role of different predator groups	183
4.5.4 Caveats	184
4.5.5 Conclusion	184
4.6 Acknowledgments	184
4.7 Conflict of interest	184
4.8 Author contribution	184
4.9 References	185
4.10 Supporting information	188
5. CONCLUDING REMARKS	196
5.1 Key findings	197
5.1.2 Responses of Amazonian frugivores to disturbance in human-modified tropical forests (Chapter 1)	197

5.1.2 Fruit-frugivore interactions in burned and logged Amazonian forests (Chapter 2)	197
5.1.3 Predation on folivorous arthropods following forest degradation (Chapter 3)	198
5.2 The future of the forest	198
5.3 Future research priorities	199
5.3.1 Long-term monitoring of biodiversity in disturbed forests	200
5.3.2 Usage of different survey methods for sampling	200
5.3.3 Studies exploring the fruit-frugivore interactions	200
5.3.4 Exploring the responses of functional diversity to human-driven disturbances with a phylogenetic perspective	201
5.4 References	201

1. INTRODUCTION



1. INTRODUCTION

1.1 Tropical forests in a changing world

Tropical forests are important for the performance of numerous ecological and societal functions, such as carbon storage, biodiversity conservation, climate regulator, food and fuel provision, pest and disease control (BACCINI *et al.*, 2019; ERB *et al.*, 2018; MALHI, 2012). Despite this crucial importance, tropical forests face multiple threats driven by human activities and are especially vulnerable to economic and demographic pressures (MALHI *et al.*, 2014). The widespread degradation of forests can severely affect their biodiversity and associated ecosystem processes (BARLOW *et al.*, 2016; LAURANCE *et al.*, 2014; MARENGO *et al.*, 2018) and consequently the functions performed by these forests (CARDINALE *et al.*, 2012; EDWARDS *et al.*, 2014). For instance, Amazonian forests are vital as a climate controller, influencing rainfall patterns across the Americas (SPRACKLEN; GARCIA-CARRERAS, 2015).

The Amazon is the largest tropical forest in the world (6.5 million km²), spread across nine countries in South America of which Brazil holds 4.1 million km² (IBGE, 2004). Amazonian forests are facing threats driven by multiple anthropogenic activities. The most pervasive threat is deforestation, which has increased 47% in the last three years (11,088 km²) (SILVA JUNIOR *et al.*, 2021). Another threat is forest degradation, such as selective logging and fires (ASNER *et al.*, 2009; PIVELLO *et al.*, 2021), resulting in an increasing proportion of standing but degraded primary forests (e.g., currently, the area occupied by degraded forest surpasses deforested in the Brazilian Amazon; MATRICARDI *et al.*, 2020).

The state of Pará is the second largest Brazilian states including Amazonian territory (see Figure 1.1a) (IBGE, 2022). Owing to current and historically high levels of forest degradation and deforestation, the state of Pará is characterized by a mosaic of land-uses

including undisturbed and disturbed primary forests as well as regenerating secondary forests and a mosaic of different production systems (e.g., cattle ranching, large-scale soy bean and corn plantations, and small-scale manioc plantations; Figure 1.2). Therefore, Pará is a ‘natural laboratory’ with ideal conditions to study the effects of anthropogenic disturbances on forest ecosystems. This thesis focuses on Pará state, specifically the Santarém region of the central-eastern Brazilian Amazon (Figure 1.1b).

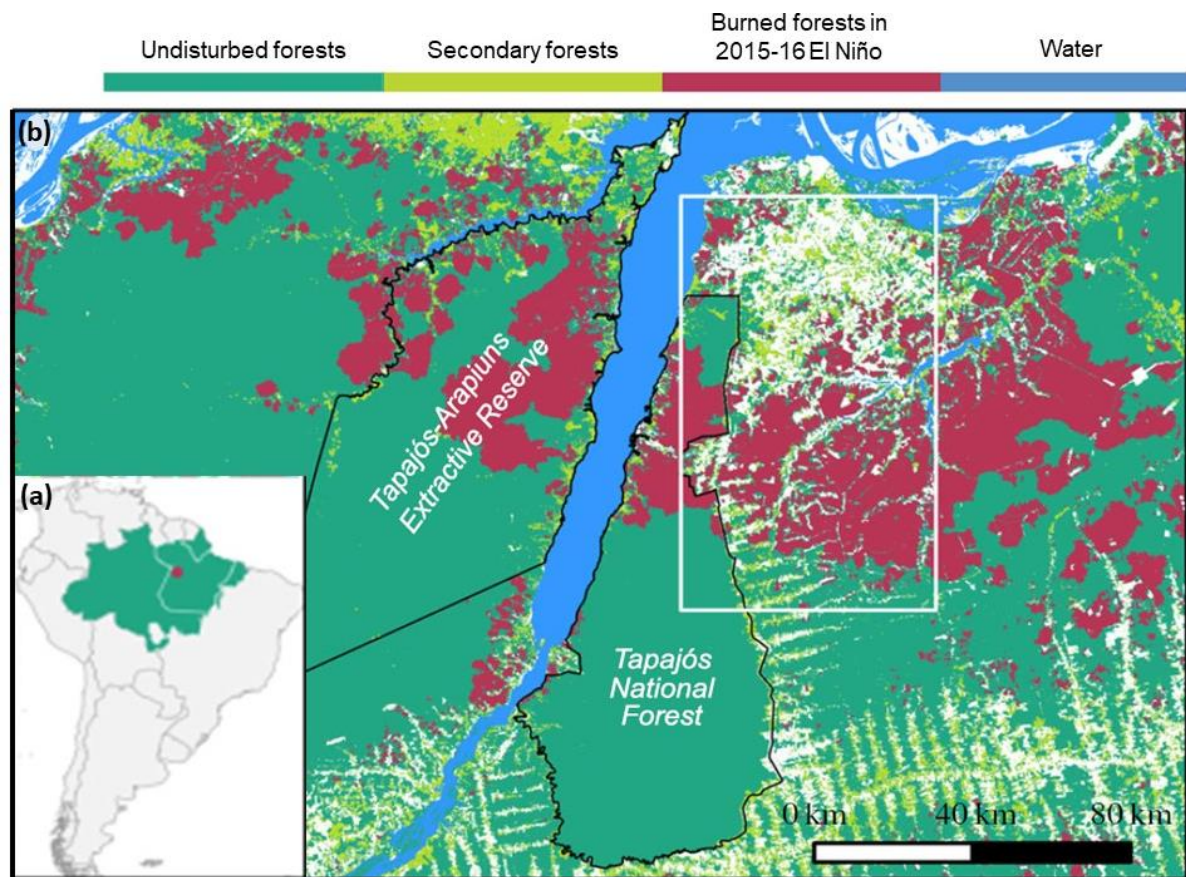


Figure 1.1 - Map of the study area in the Brazilian Amazon. (a) Location of Santarém within the Brazilian state of Pará; and (b) Santarém region. The white square corresponds to the study area. Map adapted from Withey *et al.* (2018).

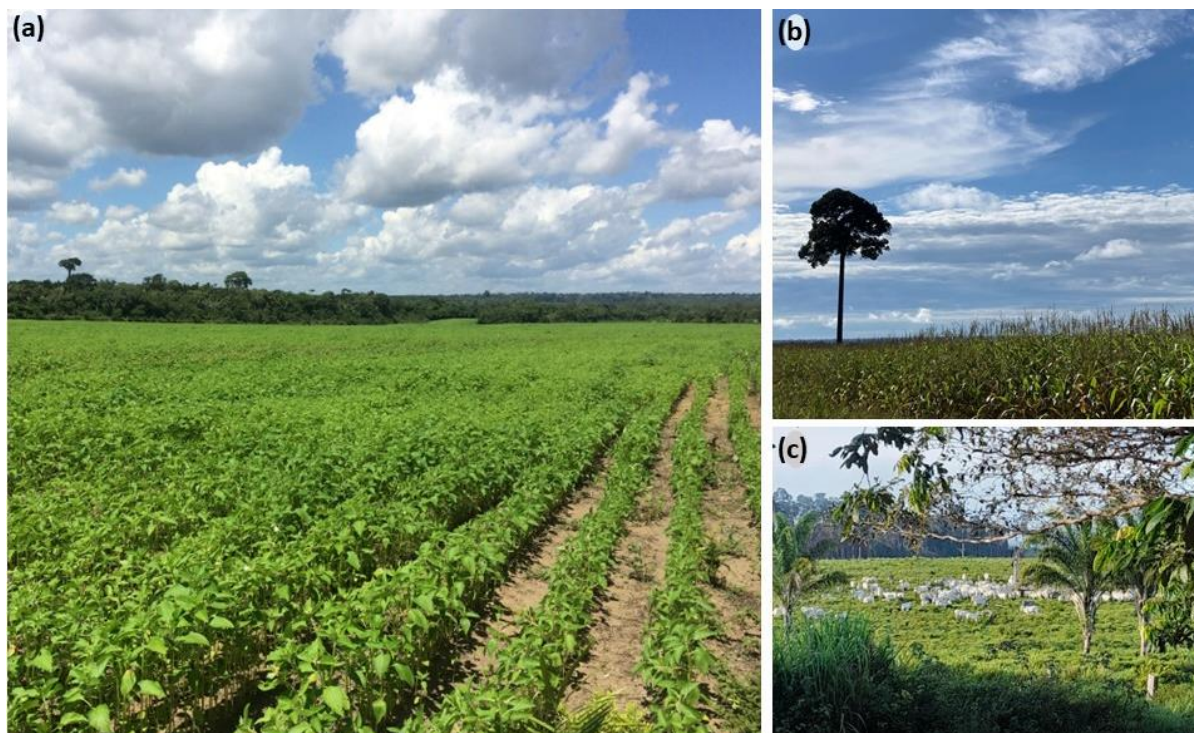


Figure 1.2 - Production systems in the Santarém region: (a) large-scale soybean and (b) corn plantations; (c) cattle ranching. First two photos were taken by L.C.R. and the last photo by Ester F. Oliveira.

The Santarém region is located 800 km west of Belém, the capital of Pará state (Figure 1a). Timber extraction increased substantially after the 1940s (LENTINI; VERÍSSIMO; PEREIRA, 2005) and reached the highest levels in the 1970s when the Brazilian government built a 3,467 km long road, connecting Santarém to Cuiabá, the capital of Mato Grosso state. Moreover, the combined the expansion of the city, the port and airport, the building of a hydroelectric dam and gold mining extraction led to a rapid increase in forest conversion rates (HOEFLE, 2013). Despite this, Santarém holds important areas of undisturbed forests, as well as a 5,491 km² national forest reserve, the Floresta Nacional do Tapajós (IBGE, 2022).

1.1.1 Forest degradation

1.1.1.1 Forest fires

Fire represents one of the greatest threats to tropical forests and its occurrence is directly linked to human activities (ANDERSON *et al.*, 2015; MALHI *et al.*, 2008; MARENGO *et al.*, 2018). For instance, Amazonian forests have recently been affected by the increase in frequency of extreme climatic events, and, consequently, the incidence of forest fires (BALCH *et al.*, 2015; Figure 1.3). Intense climatic events such as the 2015-16 El Niño caused an intense and long period of drought leading to a 48% increase in the incidence of forest fires compared to the year before the El Niño event (BETTS *et al.*, 2015; Figure 1.1b, 1.3).



Figure 1.3 - Fire dynamic in the Amazonian forests. (a) Understory fires; (b) forest post-fire; and (c) forest structure after three years of understory fires; First photo was taken by Erika Berenguer, second and third by L.C.R.

1.1.1.2 Selective logging

Another common human-driven disturbance in the tropics is selective logging. In Amazonian forests, logging operations tend to be selective, removing just a few valuable tree species from any given area. This practice is mainly conducted illegally and has already affected 20% of the remaining forests in the Brazilian Amazon (ASNER *et al.*; 2005; Figure 1.4).

1.1.1.3 Secondary forests

Human activities have resulted in an increasing number of secondary forests (HANSEN *et al.*, 2013). Secondary forests are forests that were totally deforested resulting in a distinct plant community composition and structure from primary forests. Commonly, secondary forests are found within degraded matrices with areas of agriculture and livestock (CHAZDON *et al.*, 2009; LAURANCE *et al.*, 2018). There are currently estimated to be 148,764 km² of secondary forests in the Amazon (JUNIOR *et al.*, 2020).



Figure 1.4 - Selective logging in Brazilian Amazon. (a) Transport of legal wood; (b) and (c) illegal extraction. Photos were taken by L.C.R.

1.2 Ecological Functions

Ecological functions are natural processes in the environment and support ecosystem functionality (SEKERCIOGLU; WENNY; WHELAN, 2016). Pollination, seed dispersal and biological control are examples of ecological functions. These processes involve fluxes of nutrients through food webs and the movement of propagules that keep ecosystems functioning (SRIVASTAVA *et al.*, 2012). Although numerous studies have described these process and their importance for the functioning of ecosystems (GARCÍA; MARTÍNEZ, 2012; MAAS *et al.*, 2016), they are still poorly understood, especially when they involve complex processes, such as the control of herbivorous insects performed by birds and bats – i.e., *top-down control* (VAN BAEL *et al.*, 2008; VIDAL *et al.*, 2018). There are numerous driving factors in herbivore control, such plant allelopathy (biochemicals produced by plants to avoid herbivory) – i.e., *bottom-up control*, which can also influence predation rates (VIDAL *et al.*, 2018).

Birds and mammals play key functional roles in many ecosystems, performing numerous ecological functions (LACHER *et al.*, 2019; MAAS *et al.*, 2016; SEKERCIOGLU; WENNY; WHELAN, 2016; SEKERCIOGLU, 2006; STOTZ *et al.*, 1996). Because of the great taxonomic diversity of most ecosystems around the world, animals are able to perform several functions, important for ecosystem dynamics, such as seed dispersal, pollination and herbivory control (WHELAN; WENNY; MARQUIS, 2008). Changes in animal communities (e.g., richness and composition) affect ecological function and consequently alter forest maintenance and regeneration (SEKERCIOGLU; DAILY; EHRLICH, 2004). In the last few decades, many studies have indicated the importance of the contribution of animals to ecosystem processes (see SEKERCIOGLU *et al.*, 2016), in particular, on seed dispersal (CARLO; MORALES, 2015; CARREIRA *et al.*, 2020; DARIO, 2014; STEVENSON *et al.*, 2015) and on the control of herbivorous insects (MAAS *et al.*, 2016; ROELS; PORTER; LINDELL, 2018). Both have received special attention, as they influence plant reproduction capacity and, consequently,

forest dynamics (HARRISON *et al.*, 2013; ROELS; PORTER; LINDELL, 2018; VIDAL *et al.*, 2014).

1.2.1 Ecological function in a changing world

Primary forests are irreplaceable in terms of their role in providing resources and maintaining biodiversity, especially for more specialist species, commonly more sensitive to human-driven disturbances (GIBSON *et al.*, 2011; LAURANCE *et al.*, 2018). However, degraded forests, such as secondary and burned forests represent a large part of the existing forests (MALHI *et al.*, 2014; MATRICARDI *et al.*, 2020; NEEFF *et al.*, 2006), thus playing an important role in species conservation (BARLOW *et al.*, 2016, 2007; CHAZDON *et al.*, 2009; MOURA *et al.*, 2013; NUNES *et al.*, 2022). Forest fires can directly impact animal communities by increasing mortality rates during the fire and smoke passage or indirectly by decreasing the availability of resources (BARLOW; PERES, 2004a, b). For instance, by increasing plant mortality (BERENGUER *et al.*, 2021), burned forests have an open canopy that lead to an increases in sunlight reaching the understory and, consequently leads to decreases in humidity, ultimately leading to changes in plant community composition (BARLOW *et al.*, 2003; HAWES *et al.*, 2020; PHILLIPS *et al.*, 2009; Figure 1.3). This may reduce the availability of fruits for frugivorous animals and in turn, resource availability - acting as a filter for some species, especially those with specific requirements as frugivores (PIGOT *et al.*, 2020).

Furthermore, the synergic effects of human-driven disturbances, such as hunting is na important driver of the decline of large animal abundance and cause of local extinctions, resulting in widespread losses of tropical biodiversity (LEWIS; EDWARDS; GALBRAITH, 2015; OSURI *et al.*, 2020). Hunting is a common practice in tropical forests and can strongly reduce the abundance and richness of several bird and mammal species, especially large-bodied species (SCABIN; PERES, 2021). In over-hunted tropical forests, the abundances of birds and

mammals can decline by 50% and 80%, respectively (BENÍTEZ-LÓPEZ *et al.*, 2017). The defaunation induced by hunting can limit the long-term ecological functions promoted by animals (BOMFIM *et al.*, 2018; HARRISON *et al.*, 2013). Although strong and pervasive, the effects of hunting are hard to detect through remote-sensing analysis, being much less well quantified than other human-driven disturbances (PERES; BARLOW; LAURANCE, 2006). Moreover, the effects of hunting on community processes are commonly exacerbated by synergistic factors, such as logging and fires (BRODIE *et al.*, 2015; PERES; BARLOW; HAUGAASEN, 2003).

Nonetheless, fires and logging lead to replacement of specialist species with widespread generalist species (BURIVALOVA; ŞEKERCIOĞLU; KOH, 2014; MOURA *et al.*, 2013). Given that animals deliver important ecological functions, changes in species composition may result in changes in ecological processes (HAWES *et al.*, 2020; MIRANDA; IMPERATRIZ-FONSECA; GIANNINI, 2019). For instance, reduction in frugivores may lead to reduction in seed removal, which may impact forest resilience and plant establishment, both important process in tropical forests (MASON *et al.*, 2013; PETCHEY *et al.*, 2004; SEBASTIÁN-GONZÁLEZ *et al.*, 2017). Even though previous studies have examined animal responses to human-driven disturbances (BARLOW *et al.*, 2006; BREGMAN *et al.*, 2016; MOURA *et al.*, 2014), our understanding of the impacts of these disturbances on the ecological functions promoted by animal species is limited in Amazonian forests (GARDNER *et al.*, 2009). Thus, the extreme importance and vulnerability of ecological functions to forest degradation, combined with a lack of studies in the Amazon and the El Niño event, provide a unique opportunity to understand the effects of fire and other human-driven forest degradation on ecological functions related to important ecosystem processes to forest regeneration.

1.3 Objectives

The main objective of this study is to measure the effect of forest degradation on the ecological functions of frugivory and biological control of folivorous insects promoted by animals in the Amazon forests. To achieve this, three Chapters were prepared:

Chapter 1: *Responses of Amazonian frugivores to disturbance in human-modified tropical forests.* Here we evaluated the impact of selective logging and forest fires on the richness, composition, body mass and functional diversity of frugivorous animals.

Chapter 2: *Fruit-frugivore interactions mediated by forest fires in Amazonian forests* where we assessed the impacts of selective logging and forest fires on frugivory networks.

Chapter 3: *Predation on artificial caterpillars following understory fires in human-modified Amazonian forests* where we evaluated the effect of human-driven forest degradation on predation rates of folivorous arthropods.

1.4 References

- ANDERSON, Liana Oighenstein; ARAGÃO, Luiz E.O.C. O. C.; GLOOR, Manuel; ARAI, Egídio; ADAMI, Marcos; SAATCHI, Sassan S.; MALHI, Yadvinder; SHIMABUKURO, Yosio E.; BARLOW, Jos; BERENGUER, Erika; DUARTE, Valdete. Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought. **Global Biogeochemical Cycles**, vol. 29, no. 10, p. 1739–1753, 2015. <https://doi.org/10.1002/2014GB005008>.
- ASNER, Gregory P.; KNAPP, David E.; BROADBENT, Eben N.; OLIVEIRA, Paulo J.C.; KELLER, Michael; SILVA, Jose N. Selective logging in the Brazilian Amazon. **Science**, vol. 310, no. 5747, p. 480–482, 2005. <https://doi.org/10.1126/science.1118051>.
- ASNER, Gregory P.; RUDEL, Thomas K.; AIDE, T. Mitchell; DEFRIES, Ruth; EMERSON, Ruth. A contemporary assessment of change in humid tropical forests. **Conservation**

- Biology**, vol. 23, no. 6, p. 1386–1395, 2009. <https://doi.org/10.1111/j.1523-1739.2009.01333.x>.
- BACCINI, A; WALKER, W; CARVALHO, L; FARINA, M; HOUGHTON, R A. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. **Science**, vol. 363, no. 6423, p. 230–234, 2019. <https://doi.org/10.1126/science.aat1205>.
- BALCH, Jennifer K.; BRANDO, Paulo M.; NEPSTAD, Daniel C.; COE, Michael T.; SILVÉRIO, Divino; MASSAD, Tara J.; DAVIDSON, Eric A.; LEFEBVRE, Paul; OLIVEIRA-SANTOS, Claudinei; ROCHA, Wanderley; CURY, Roberta T.S.; PARSONS, Amoreena; CARVALHO, Karine S. The Susceptibility of Southeastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment. **BioScience**, vol. 65, no. 9, p. 893–905, 2015. <https://doi.org/10.1093/biosci/biv106>.
- BARLOW, Jos; LENNOX, Gareth D.; FERREIRA, Joice; BERENGUER, Erika; LEES, Alexander C.; NALLY, Ralph Mac; THOMSON, James R.; FERRAZ, Silvio Frosini De Barros; LOUZADA, Julio; OLIVEIRA, Victor Hugo Fonseca; PARRY, Luke; RIBEIRO DE CASTRO SOLAR, Ricardo; VIEIRA, Ima C.G.; ARAGAÕ, Luiz E.O.C.; BEGOTTI, Rodrigo Anzolin; BRAGA, Rodrigo F.; CARDOSO, Thiago Moreira; JR, Raimundo Cosme De Oliveira; SOUZA, Carlos M.; ... GARDNER, Toby A. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. **Nature**, vol. 535, no. 7610, p. 144–147, 2016. DOI 10.1038/nature18326. Available at: <http://dx.doi.org/10.1038/nature18326>.
- BARLOW, Jos; MESTRE, Luiz A.M.; GARDNER, Toby A.; PERES, Carlos A. The value of primary, secondary and plantation forests for Amazonian birds. **Biological Conservation**, vol. 136, no. 2, p. 212–231, 2007. <https://doi.org/10.1016/j.biocon.2006.11.021>.
- BARLOW, Jos; PERES, C A; HENRIQUES, L. M.P.; STOUFFER, P C; WUNDERLE, J M. The responses of understorey birds to forest fragmentation, logging and wildfires: An

- Amazonian synthesis. **Biological Conservation**, vol. 128, no. 2, p. 182–192, 2006.
<https://doi.org/10.1016/j.biocon.2005.09.028>.
- BARLOW, Jos; PERES, Carlos. Avifaunal Responses to Single and Recurrent Wildfires in Amazonian Forests. **Ecological Applications**, vol. 14, no. 5, p. 1358–1373, 2004a. .
- BARLOW, Jos; PERES, Carlos A.; LAGAN, Bernard O.; HAUGAASEN, Torbjorn. Large tree mortality and the decline of forest biomass following Amazonian wildfires. **Ecology Letters**, vol. 6, no. 1, p. 6–8, 2003. <https://doi.org/10.1046/j.1461-0248.2003.00394.x>.
- BARLOW, Jos; PERES, Carlos A. Ecological responses to El Niño-induced surface fires
 Ecological responses to El Nin in central Brazilian Amazonia: management implications for flammable tropical forests. **Philosophical Transactions of the Royal Society B: Biological Sciences**, vol. 359, no. February, p. 367–380, 2004b.
<https://doi.org/10.1098/rstb.2003.1423>.
- BENÍTEZ-LÓPEZ, A; ALKEMADE, R; SCHIPPER, A M; INGRAM, D J; VERWEIJ, P A; EIKELBOOM, J A J; HUIJBREGTS, M A J. The impact of hunting on tropical mammal and bird populations. **Science**, vol. 356, p. 180–183, 2017. .
- BERENGUER, Erika; LENNOX, Gareth D.; FERREIRA, Joice; MALHI, Yadvinder; ARAGÃO, Luiz E.O.C.; BARRETO, Julia Rodrigues; DEL BON ESPÍRITO-SANTO, Fernando; FIGUEIREDO, Axa Emanuelle S.; FRANÇA, Filipe; GARDNER, Toby Alan; JOLY, Carlos A.; PALMEIRA, Alessandro F.; QUESADA, Carlos Alberto; ROSSI, Liana Chesini; DE SEIXAS, Marina Maria Moraes; SMITH, Charlotte C.; WITHEY, Kieran; BARLOW, Jos. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. **Proceedings of the National Academy of Sciences of the United States of America**, vol. 118, no. 30, 2021. <https://doi.org/10.1073/pnas.2019377118>.
- BETTS, R. A.; GOLDING, N.; GONZALEZ, P.; GORNALL, J.; KAHANA, R.; KAY, G.; MITCHELL, L.; WILTSHIRE, A. Climate and land use change impacts on global

- terrestrial ecosystems and river flows in the HadGEM2-ES Earth system model using the representative concentration pathways. **Biogeosciences**, vol. 12, no. 5, p. 1317–1338, 2015. <https://doi.org/10.5194/bg-12-1317-2015>.
- BOMFIM, Jamille de Assis; GUIMARÃES, Paulo R.; PERES, Carlos A.; CARVALHO, Gustavo; CAZETTA, Eliana. Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. **Ecography**, no. Levins 1970, p. 1–11, 2018. <https://doi.org/10.1111/ecog.03592>.
- BREGMAN, Tom P.; LEES, Alexander C.; MACGREGOR, Hannah E.A.; DARSKI, Bianca; DE MOURA, Nárgila G.; ALEIXO, Alexandre; BARLOW, Jos; TOBIAS, Joseph A. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests - ELECTRONIC SUPPLEMENTARY MATERIAL. **Proceedings of the Royal Society B: Biological Sciences**, vol. 283, no. 1844, 2016. <https://doi.org/10.1098/rspb.2016.1289>.
- BRODIE, Jedediah F.; GIORDANO, Anthony J.; ZIPKIN, Elise F.; BERNARD, Henry; MOHD-AZLAN, Jayasilan; AMBU, Laurentius. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. **Conservation Biology**, vol. 29, no. 1, p. 110–121, 2015. <https://doi.org/10.1111/cobi.12389>.
- BURIVALOVA, Zuzana; ŞEKERCIOĞLU, Çağan Hakkı; KOH, Lian Pin. Thresholds of logging intensity to maintain tropical forest biodiversity. **Current Biology**, vol. 24, no. 16, p. 1893–1898, 2014. <https://doi.org/10.1016/j.cub.2014.06.065>.
- CARDINALE, Bradley J.; DUFFY, J. Emmett; GONZALEZ, Andrew; HOOPER, David U.; PERRINGS, Charles; VENAIL, Patrick; NARWANI, Anita; MACE, Georgina M.; TILMAN, David; WARDLE, David A.; KINZIG, Ann P.; DAILY, Gretchen C.; LOREAU, Michel; GRACE, James B.; LARIGAUDERIE, Anne; SRIVASTAVA, Diane S.; NAEEM, Shahid. Biodiversity loss and its impact on humanity. **Nature**, vol. 486, no.

7401, p. 59–67, 2012. DOI 10.1038/nature11148. Available at:

<http://dx.doi.org/10.1038/nature11148>.

CARLO, Tomás A.; MORALES, Juan M. Generalist birds promote tropical forest regeneration and increase plant diversity via rare- biased seed dispersal. **Ecology**, vol. 97, no. 7, p. 1–5, 2015. <https://doi.org/10.1890/15-2147.1>.

CARREIRA, Daiane C; DÁTTILO, Wesley; BRUNO, Dáfini L; PERCEQUILLO, Alexandre Reis; FERRAZ, Katia M P M B; GALETTI, Mauro. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. **Scientific Reports**, , p. 1–11, 2020. DOI 10.1038/s41598-020-67326-6. Available at: <https://doi.org/10.1038/s41598-020-67326-6>.

CHAZDON, Robin L.; PERES, Carlos A.; DENT, Daisy; SHEIL, Douglas; LUGO, Ariel E.; LAMB, David; STORK, Nigel E.; MILLER, Scott E. The potential for species conservation in tropical secondary forests. **Conservation Biology**, vol. 23, no. 6, p. 1406–1417, 2009. <https://doi.org/10.1111/j.1523-1739.2009.01338.x>.

DARIO, Fabio Rossano. Frugivory and seed dispersal by mammals in the Amazon rainforest. **Asian Journal of Biological and Life Sciences**, vol. 3, no. 2, p. 137–142, 2014. .

EDWARDS, David P; TOBIAS, Joseph A; SHEIL, Douglas; MEIJAARD, Erik; LAURANCE, William F. Maintaining ecosystem function and services in logged tropical forests. **Trends in Ecology and Evolution**, vol. 29, no. 9, p. 511–520, 2014. DOI 10.1016/j.tree.2014.07.003. Available at: <http://dx.doi.org/10.1016/j.tree.2014.07.003>.

ERB, Karl Heinz; KASTNER, Thomas; PLUTZAR, Christoph; BAIS, Anna Liza S.; CARVALHAIS, Nuno; FETZEL, Tamara; GINGRICH, Simone; HABERL, Helmut; LAUK, Christian; NIEDERTSCHEIDER, Maria; PONGRATZ, Julia; THURNER, Martin; LUYSSAERT, Sebastiaan. Unexpectedly large impact of forest management and grazing on global vegetation biomass. **Nature**, vol. 553, no. 7686, p. 73–76, 2018.

<https://doi.org/10.1038/nature25138>.

GARCÍA, Daniel; MARTÍNEZ, Daniel. Species richness matters for the quality of ecosystem services: A test using seed dispersal by frugivorous birds. **Proceedings of the Royal Society B: Biological Sciences**, vol. 279, no. 1740, p. 3106–3113, 2012.

<https://doi.org/10.1098/rspb.2012.0175>.

GARDNER, Toby A.; BARLOW, Jos; CHAZDON, Robin; EWERS, Robert M.; HARVEY, Celia A.; PERES, Carlos A.; SODHI, Navjot S. Prospects for tropical forest biodiversity in a human-modified world. **Ecology Letters**, vol. 12, no. 6, p. 561–582, 2009.

<https://doi.org/10.1111/j.1461-0248.2009.01294.x>.

GIBSON, Luke; LEE, Tien Ming; KOH, Lian Pin; BROOK, Barry W; GARDNER, Toby A; BARLOW, Jos; PERES, Carlos A; BRADSHAW, Corey J.A.; LAURANCE, William F; LOVEJOY, Thomas E; SODHI, Navjot S. Primary forests are irreplaceable for sustaining tropical biodiversity. **Nature**, vol. 478, no. 7369, p. 378–381, 2011.

<https://doi.org/10.1038/nature10425>.

HANSEN, M. C.; POTAPOV, P. V.; MOORE, R.; HANCHER, M.; TURUBANOVA, S. A.; TYUKAVINA, A.; THAU, D.; STEHMAN, S. V.; GOETZ, S. J.; LOVELAND, T. R.; KOMMAREDDY, A.; EGOROV, A.; CHINI, L.; USTICE, C. O.; TOWNSHEND, J. R. G. High-Resolution Global Maps of 21st-Century Forest Cover Change. **Science**, vol. 342, p. 850–853, 2013. .

HARRISON, Rhett D.; TAN, Sylvester; PLOTKIN, Joshua B.; SLIK, Ferry; DETTO, Matteo; BRENES, Tania; ITOH, Akira; DAVIES, Stuart J. Consequences of defaunation for a tropical tree community. **Ecology Letters**, vol. 16, no. 5, p. 687–694, 2013.

<https://doi.org/10.1111/ele.12102>.

HAWES, Joseph E.; VIEIRA, Ima C.G.; MAGNAGO, Luiz F.S.; BERENGUER, Erika; FERREIRA, Joice; ARAGÃO, Luiz E.O.C.; CARDOSO, Amanda; LEES, Alexander C.;

- LENNOX, Gareth D.; TOBIAS, Joseph A.; WALDRON, Anthony; BARLOW, Jos. A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. **Journal of Ecology**, vol. 108, no. 4, p. 1373–1385, 2020. <https://doi.org/10.1111/1365-2745.13358>.
- HOEFLE, Scott William. Santarém, Cidade Portal de Fronteiras Históricas do Oeste do Pará. **Espaço Aberto**, vol. 3, no. 1, p. 45–76, 2013. <https://doi.org/10.36403/espacoaberto.2013.2100>.
- IBGE. IBGE Cidades. Available at: <http://cidades.ibge.gov.br/>. 2022. Available at: <https://cidades.ibge.gov.br/>.
- IBGE. Mapa de Biomas do Brasil. 2004. .
- JUNIOR, Celso H. L. Silva; HEINRICH, Viola H. A.; FREIRE, Ana T. G.; BROGGIO, Igor S.; ROSAN, Thais M.; DOBLAS, Juan; ANDERSON, Liana O.; ROUSSEAU, Guillaume X.; SHIMABUKURO, Yosio E.; SILVA, Carlos A.; HOUSE, Joanna I.; ARAGÃO, Luiz E. O. C. Benchmark maps of 33 years of secondary forest age for Brazil. **scientific Data**, vol. 7, no. 269, p. 1–9, 2020. <https://doi.org/10.1038/s41597-020-00600-4>.
- LACHER, Thomas E.; DAVIDSON, Ana D.; FLEMING, Theodore H.; GÓMEZ-RUIZ, Emma P.; MCCracken, Gary F.; OWEN-SMITH, Norman; PERES, Carlos A.; VANDER WALL, Stephen B. The functional roles of mammals in ecosystems. **Journal of Mammalogy**, vol. 100, no. 3, p. 942–964, 2019. <https://doi.org/10.1093/jmammal/gyy183>.
- LAURANCE, William F.; CAMARGO, José L.C.; FEARNside, Philip M; LOVEJOY, Thomas E; WILLIAMSON, G Bruce; MESQUITA, Rita C.G.; MEYER, Christoph F.J.; BOBROWIEC, Paulo E.D.; LAURANCE, Susan G.W. An Amazonian rainforest and its fragments as a laboratory of global change. **Biological Reviews**, vol. 93, no. 1, p. 223–247, 2018. <https://doi.org/10.1111/brv.12343>.
- LAURANCE, William F; LOVEJOY, Thomas E; VASCONCELOS, Heraldo L; BRUNA,

- Emilio M; DIDHAM, Raphael K; STOUFFER, Philip C; GASCON, Claude; BIERREGAARD, Richard O; SUSAN, G; SAMPAIO, Erica. Ecosystem Decay of Amazonian Forest Fragments. vol. 16, no. 3, p. 605–618, 2014. .
- LENTINI, Marco; VERÍSSIMO, Adalberto; PEREIRA, Denys. **A Expansão Madeireira na Amazônia (Expansion of the Logging Frontier in the Brazilian Amazon)**. [S. l.: s. n.], 2005.
- LEWIS, Simon L; EDWARDS, David P; GALBRAITH, David. Increasing human dominance of tropical forests. **Science**, vol. 349, no. 6250, p. 827–832, 2015.
<https://doi.org/10.1126/science.aaa9932>.
- MAAS, Bea; KARP, Daniel S.; BUMRUNGSRI, Sara; DARRAS, Kevin; GONTHIER, David; HUANG, Joe C.C.; LINDELL, Catherine A.; MAINE, Josiah J.; MESTRE, Laia; MICHEL, Nicole L.; MORRISON, Emily B.; PERFECTO, Ivette; PHILPOTT, Stacy M.; ŞEKERCIOĞLU, Çagan H.; SILVA, Roberta M.; TAYLOR, Peter J.; TSCHARNTKE, Teja; VAN BAEL, Sunshine A.; WHELAN, Christopher J.; WILLIAMS-GUILLÉN, Kimberly. Bird and bat predation services in tropical forests and agroforestry landscapes. **Biological Reviews**, vol. 91, no. 4, p. 1081–1101, 2016. <https://doi.org/10.1111/brv.12211>.
- MALHI, Yadvinder. The productivity, metabolism and carbon cycle of tropical forest vegetation. **Journal of Ecology**, vol. 100, no. 1, p. 65–75, 1 Jan. 2012. DOI 10.1111/j.1365-2745.2011.01916.x. Available at:
<https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2745.2011.01916.x>. Accessed on: 29 Jun. 2022.
- MALHI, Yadvinder; GARDNER, Toby A.; GOLDSMITH, Gregory R.; SILMAN, Miles R.; ZELAZOWSKI, Przemyslaw. Tropical Forests in the Anthropocene. **Annual Review of Environment and Resources**, vol. 39, no. 1, p. 125–159, 2014.
<https://doi.org/10.1146/annurev-environ-030713-155141>.

- MALHI, Yadvinder; ROBERTS, J. Timmons; BETTS, Richard A.; KILLEEN, Timothy J.; LI, Wenhong; NOBRE, Carlos A. Climate change, deforestation, and the fate of the Amazon. **Science**, vol. 319, no. 5860, p. 169–172, 2008.
<https://doi.org/10.1126/science.1146961>.
- MARENGO, Jose A; SOUZA, Carlos M.; THONICKE, Kirsten; BURTON, Chantelle; HALLADAY, Kate; BETTS, Richard A; ALVES, Lincoln M; SOARES, Wagner R. Changes in Climate and Land Use Over the Amazon Region: Current and Future Variability and Trends. **Frontiers in Earth Science**, vol. 6, no. December, p. 1–21, 2018.
<https://doi.org/10.3389/feart.2018.00228>.
- MASON, Norman W.H.; DE BELLO, Francesco; MOUILLOT, David; PAVOINE, Sandrine; DRAY, Stéphane. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. **Journal of Vegetation Science**, vol. 24, no. 5, p. 794–806, 2013. <https://doi.org/10.1111/jvs.12013>.
- MATRICARDI, Eraldo Aparecido Trondoli; SKOLE, David Lewis; COSTA, Olívia Bueno; PEDLOWSKI, Marcos Antonio; SAMEK, Jay Howard; MIGUEL, Eder Pereira. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. **Science**, vol. 369, no. 6509, p. 1378–1382, 1 Sep. 2020. <https://doi.org/10.1126/SCIENCE.ABB3021>.
- MIRANDA, Leonardo S.; IMPERATRIZ-FONSECA, Vera L.; GIANNINI, Tereza C. Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. **PLoS ONE**, vol. 14, no. 4, p. 1–17, 2019.
<https://doi.org/10.1371/journal.pone.0215229>.
- MOURA, Nárgila G.; LEES, Alexander Charles; ANDRETTI, Christian B.; DAVIS, Bradley J.W.; SOLAR, Ricardo R.C.; ALEIXO, Alexandre; BARLOW, Jos; FERREIRA, Joice; GARDNER, Toby A. Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. **Biological Conservation**, vol. 167, p. 339–348, 2013.

<https://doi.org/10.1016/j.biocon.2013.08.023>.

- MOURA, Nárgila G; LEES, Alexander C; ALEIXO, Alexandre; BARLOW, Jos; DANTAS, Sidnei M; FERREIRA, Joice; LIMA, Maria De Fátima C.; GARDNER, Toby A. Two hundred years of local avian extinctions in eastern Amazonia. **Conservation Biology**, vol. 28, no. 5, p. 1271–1281, 2014. <https://doi.org/10.1111/cobi.12300>.
- NEEFF, Till; LUCAS, Richard M.; SANTOS, João Roberto Dos; BRONDIZIO, Eduardo S.; FREITAS, Corina C. Area and age of secondary forests in Brazilian Amazonia 1978-2002: An empirical estimate. **Ecosystems**, vol. 9, no. 4, p. 609–623, 2006. <https://doi.org/10.1007/s10021-006-0001-9>.
- NUNES, Cássio Alencar; BERENGUER, Erika; FRANÇA, Filipe; FERREIRA, Joice; LEES, Alexander C.; LOUZADA, Julio; SAYER, Emma J.; SOLAR, Ricardo; SMITH, Charlotte C.; ARAGÃO, Luiz E. O. C.; BRAGA, Danielle de Lima; DE CAMARGO, Plinio Barbosa; CERRI, Carlos Eduardo Pellegrino; DE OLIVEIRA, Raimundo Cosme; DURIGAN, Mariana; MOURA, Nárgila; OLIVEIRA, Victor Hugo Fonseca; RIBAS, Carla; VAZ-DE-MELLO, Fernando; ... BARLOW, Jos. Linking land-use and land-cover transitions to their ecological impact in the Amazon. **Proceedings of the National Academy of Sciences**, vol. 119, no. 27, 5 Jul. 2022. DOI 10.1073/pnas.2202310119. Available at: <https://pnas.org/doi/full/10.1073/pnas.2202310119>.
- OSURI, Anand M; MENDIRATTA, Uttara; NANIWADEKAR, Rohit; VARMA, Varun; NAEEM, Shahid. Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds. **Frontiers in Forests and Global Change**, vol. 2, p. 87, 2020. DOI 10.3389/ffgc.2019.00087. Available at: <https://www>.
- PERES, Carlos A.; BARLOW, Jos; LAURANCE, William F. Detecting anthropogenic disturbance in tropical forests. **Trends in Ecology and Evolution**, vol. 21, no. 5, p. 227–229, 2006. <https://doi.org/10.1016/j.tree.2006.03.007>.

- PERES, Carlos A; BARLOW, Jos; HAUGAASEN, Torbjørn. Vertebrate responses to surface wildfires in a central Amazonian forest. **ORYX**, vol. 37, no. 1, p. 97–109, 2003.
<https://doi.org/10.1017/S0030605303000188>.
- PETCHEY, Owen L; HECTOR, Andy; GASTON, Kevin J; ECOLOGY, Source; MAR, No. How Do Different Measures of Functional Diversity Perform? **Ecology**, vol. 85, no. 3, p. 847–857, 2004. .
- PHILLIPS, L. E. O.; LEWIS, S. L.; FISHER, J. B.; LLOYD, J.; LOPEZ-GONZALEZ, G.; MALHI, Y.; MONTEAGUDO, A.; PEACOCK, J.; QUESADA, C. A.; VAN DER HEIJDEN, G.; ALMEIDA, S.; AMARAL, I.; ARROYO, L.; AYMARD, G.; BAKER, T. R.; BANKI, O.; BLANC, L.; BONAL, D.; ARAGAO, O L. Drought sensitivity of the Amazon rainforest TT - Drought sensitivity of the Amazon rainforest. **Science**, vol. 323, no. March, p. 1344–1347, 2009. Available at:
<http://www.sciencemag.org/content/323/5919/1344.short>.
- PIGOT, Alex L.; SHEARD, Catherine; MILLER, Eliot T.; BREGMAN, Tom P.; FREEMAN, Benjamin G.; ROLL, Uri; SEDDON, Nathalie; TRISOS, Christopher H.; WEEKS, Brian C.; TOBIAS, Joseph A. Macroevolutionary convergence connects morphological form to ecological function in birds. **Nature Ecology and Evolution**, vol. 4, no. 2, p. 230–239, 2020. <https://doi.org/10.1038/s41559-019-1070-4>.
- PIVELLO, Vânia R.; VIEIRA, Ima; CHRISTIANINI, Alexander V.; RIBEIRO, Danilo Bandini; DA SILVA MENEZES, Luciana; BERLINCK, Christian Niel; MELO, Felipe P.L.; MARENGO, José Antonio; TORNQUIST, Carlos Gustavo; TOMAS, Walfrido Moraes; OVERBECK, Gerhard E. Understanding Brazil’s catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. **Perspectives in Ecology and Conservation**, vol. 19, no. 3, p. 233–255, 2021. DOI 10.1016/j.pecon.2021.06.005.
Available at: <https://doi.org/10.1016/j.pecon.2021.06.005>.

- ROELS, Steven M.; PORTER, Jade L.; LINDELL, Catherine A. Predation pressure by birds and arthropods on herbivorous insects affected by tropical forest restoration strategy. **Restoration Ecology**, vol. 26, no. 6, p. 1203–1211, 1 Nov. 2018. DOI 10.1111/rec.12693. Available at: <https://onlinelibrary.wiley.com/doi/full/10.1111/rec.12693>. Accessed on: 4 Feb. 2022.
- SCABIN, Andressa B; PERES, Carlos A. Hunting pressure modulates the composition and size structure of terrestrial and arboreal vertebrates in Amazonian forests. **Biodiversity and Conservation**, 2021. DOI 10.1007/s10531-021-02266-9. Available at: <https://doi.org/10.1007/s10531-021-02266-9>.
- SEBASTIÁN-GONZÁLEZ, Esther; PIRES, Mathias M.; DONATTI, Camila I.; GUIMARÃES, Paulo R.; DIRZO, Rodolfo. Species traits and interaction rules shape a species-rich seed-dispersal interaction network. **Ecology and Evolution**, vol. 7, no. 12, p. 4496–4506, 2017. <https://doi.org/10.1002/ece3.2865>.
- SEKERCIOGLU, C. H.; DAILY, G. C.; EHRLICH, P. R. Ecosystem consequences of bird declines. **Proceedings of the National Academy of Sciences**, vol. 101, no. 52, p. 18042–18047, 2004. DOI 10.1073/pnas.0408049101. Available at: <http://www.pnas.org/cgi/doi/10.1073/pnas.0408049101>.
- SEKERCIOGLU, Ç.H.; WENNY, D.G.; WHELAN, C.J. **Why Birds Matter**. [S. l.: s. n.], 2016. <https://doi.org/10.7208/chicago/9780226382777.001.0001>.
- SEKERCIOGLU, Cagan H. Increasing awareness of avian ecological function. **Trends in Ecology and Evolution**, vol. 21, no. 2, p. 464–471, 2006. <https://doi.org/10.1016/j.tree.2006.05.007>.
- SILVA JUNIOR, Celso H.L.; PESSÔA, Ana C.M.; CARVALHO, Nathália S; REIS, João B.C.; ANDERSON, Liana O; ARAGÃO, Luiz E.O.C. The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. **Nature Ecology and Evolution**, vol. 5, no. 2, p.

- 144–145, 2021. DOI 10.1038/s41559-020-01368-x. Available at:
<https://doi.org/10.1038/s41559-020-01368-x>.
- SPRACKLEN, D. V.; GARCIA-CARRERAS, L. The impact of Amazonian deforestation on Amazon basin rainfall. **Geophysical Research Letters**, vol. 42, no. 21, p. 9546–9552, 2015. <https://doi.org/10.1002/2015GL066063>.
- SRIVASTAVA, Diane S.; CADOTTE, Marc W.; MACDONALD, A. Andrew M.; MARUSHIA, Robin G.; MIROTECHNICK, Nicholas. Phylogenetic diversity and the functioning of ecosystems. **Ecology Letters**, vol. 15, no. 7, p. 637–648, 2012. <https://doi.org/10.1111/j.1461-0248.2012.01795.x>.
- STEVENSON, Pablo R.; LINK, Andrés; GONZÁLEZ-CARO, Sebastian; TORRES-JIMÉNEZ, María Fernanda. Frugivory in canopy plants in a western Amazonian forest: Dispersal systems, phylogenetic ensembles and keystone plants. **PLoS ONE**, vol. 10, no. 10, p. 1–22, 2015. <https://doi.org/10.1371/journal.pone.0140751>.
- STOTZ, D.F.; FITZPATRICK, F.W.; PARKER, T.A.; MOSKOVITS, D.K. **Neotropical birds. Univ. of Chicago Press, Chicago**. [S. l.: s. n.], 1996.
- VAN BAEL, Sunshine A.; PHILPOTT, Stacy M.; GREENBERG, Russell; BICHER, Peter; BARBER, Nicholas A.; MOONEY, Kailen A.; GRUNER, Daniel S. Birds as predators in tropical agroforestry systems. **Ecology**, vol. 89, no. 4, p. 928–934, 2008. <https://doi.org/10.1890/06-1976.1>.
- VIDAL, Mariana M.; HASUI, Erica; PIZO, Marco A.; TAMASHIRO, Jorge Y.; SILVA, Wesley R.; GUIMARÃES, Paulo R. Frugivores at higher risk of extinction are the key elements of a mutualistic network. **Ecology**, vol. 95, no. 12, p. 3440–3447, 2014. <https://doi.org/10.1890/13-1584.1.sm>.
- VIDAL, Mayra C.; MURPHY, Shannon M. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. **Ecology Letters**, vol. 21, no. 1, p. 138–150, 2018.

<https://doi.org/10.1111/ele.12874>.

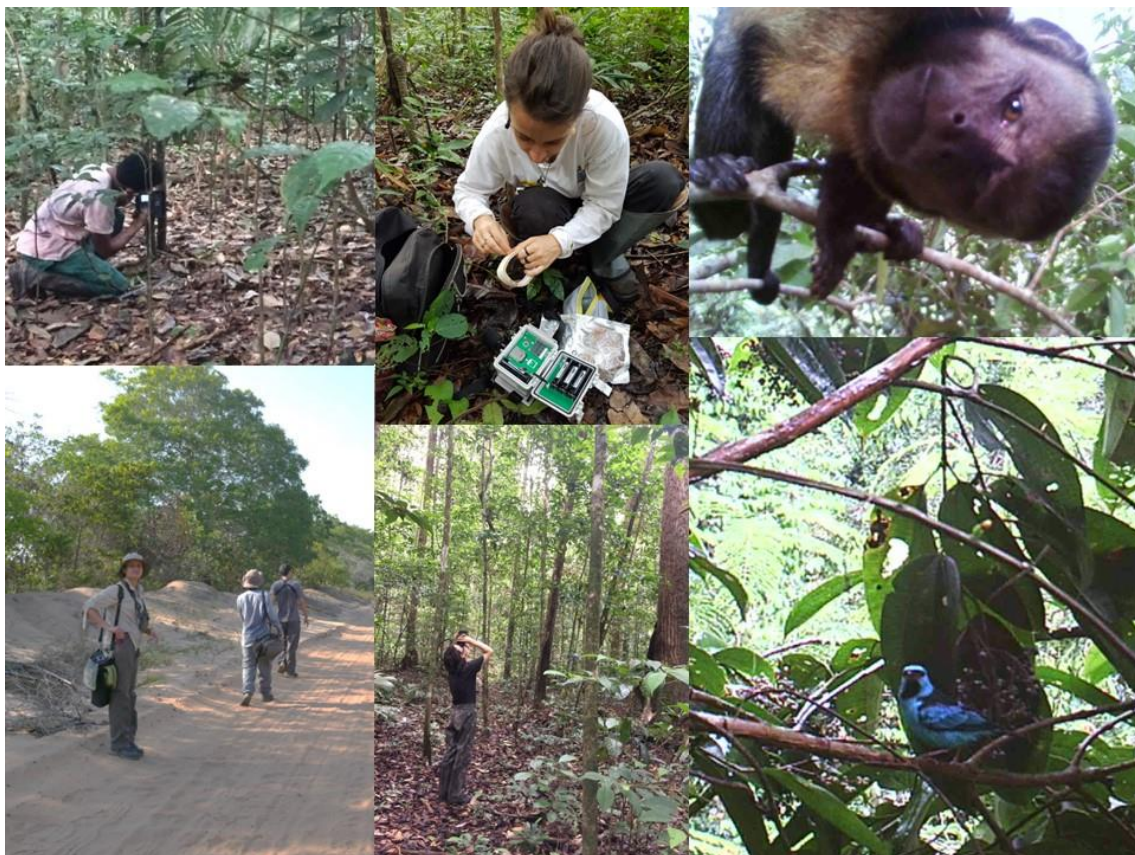
WHELAN, Christopher J; WENNY, Daniel G; MARQUIS, Robert J. Ecosystem services provided by birds. **Annals of the New York Academy of Sciences**, vol. 1134, p. 25–60, 2008. <https://doi.org/10.1196/annals.1439.003>.

WILMAN, Hamish; BELMAKER, Jonathan; SIMPSON, Jennifer; DE LA ROSA, Carolina; RIVADENEIRA, Marcelo M.; JETZ, Walter. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. **Ecology**, vol. 95, no. 7, p. 2027–2027, 2014. DOI 10.1890/13-1917.1. Available at: <http://doi.wiley.com/10.1890/13-1917.1>.

WITHEY, Kieran; BERENGUER, Erika; PALMEIRA, Alessandro Ferraz; ESPÍRITO-SANTO, Fernando D.B.; LENNOX, Gareth D.; SILVA, Camila V.J.; ARAGÃO, Luiz E.O.C.; FERREIRA, Joice; FRANÇA, Filipe; MALHI, Yadvinder; ROSSI, Liana Chesini; BARLOW, Jos. Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. **Philosophical Transactions of the Royal Society B: Biological Sciences**, vol. 373, no. 1760, 2018. <https://doi.org/10.1098/rstb.2017.0312>.

CHAPTER ONE

Responses of Amazonian frugivores to disturbance in human-modified tropical forests



Responses of Amazonian frugivores to disturbance in human-modified tropical forests

Liana Chesini Rossi^{1,2}, Alexander Charles Lees^{2,3}, Jos Barlow⁴, Erika Berenguer^{4,5}, Joice Ferreira^{6,7}, Filipe M. França⁸, Oliver, C. Metcalf², Nárgila Gomes de Moura³, Yan Gabriel Ramos⁹, Marco Aurélio Pizo¹

¹ Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil

² Division of Biology and Conservation Ecology, School of Science and the Environment, Manchester Metropolitan University, Manchester, UK

³ Cornell Lab of Ornithology, Cornell University, Ithaca, USA

⁴ Lancaster Environment Centre, Lancaster University, Lancaster, UK

⁵ Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

⁶ Embrapa Amazônia Oriental, Belém, PA, Brazil

⁷ Programa de Pós-Graduação em Ecologia (PPGECO) e Programa de Pós-Graduação em Ciências Ambientais (PPGCA), Universidade Federal do Pará, Belém, PA, Brazil

⁸ School of Biological Sciences, University of Bristol, Bristol, UK

⁹ Instituto Espaço Silvestre, Itajaí, SC, Brazil

Correspondent author: lianachesinibio@gmail.com

2.1 Abstract

Tropical forests are subject to high rates of forest degradation driven by anthropogenic disturbances, with severe consequences for frugivorous species - central to seed dispersal, a fundamental process for forest resilience. Here, by combining six different sampling methods, we used the richness, composition, body size and functional diversity of frugivorous Amazonian birds and mammals to explore the impacts of selective logging and forest fires on the ecosystem processes of seed dispersal. We show that, although the overall frugivorous richness was similar across all forest classes, the richness of obligate frugivores and the body mass was lower in historically-burned than in undisturbed forests. Historically-burned resented lower values of functional diversity than expected by chance. Nonetheless, burned forests also had the most distinct species composition from undisturbed forests. We demonstrate that, in the long-term, fires can lead to changes in community composition, limiting the occurrence of specialist and large body frugivores, while exerting negative effects on functional diversity which was low almost 20 years after fire events. Thus, we highlight the importance of long-term monitoring studies as well as the usage of different sampling methods to better understand the impacts of human-driven disturbances on frugivores and in the ecological function they promote.

Keywords: forest fire, functional diversity, sampling methods, seed dispersal, selective logging, tropical forests.

2.2 Introduction

Wildfires are one of the greatest threats to tropical forests globally [1]. Extreme climatic events such as the *El Niño* of 2015-2016, which lead to prolonged dry seasons, dramatically increase fire incidence in Amazonian forests [2]. Forest fires result in diverse ecological impacts, including increasing tree mortality [3] and changes in species composition [4,5]. These changes may have important consequences for ecological processes, such as seed dispersal and hence the rate of forest regeneration and their resilience [6,7]. In addition to fire, predatory logging practices can also have negative impacts on biodiversity and are ubiquitous in many tropical forest landscapes [8]. The combined effects of multiple stressors, such as fire and logging can heighten the severity of impacts, leading to drastic loss of forest biodiversity [6,9,10]. Moreover, the increased accessibility of logged and burned forests is often associated with an increase in hunting activity, which disproportionately affects large-bodied species [11].

Tracking trends in species occurrence have become important to understand the consequences of human impacts on biodiversity and in monitoring the outcomes results of forest management interventions [12]. Currently, 13.5% of all birds and 25% of all mammal species are threatened with global extinction [13,14]. Brazil is one of the countries with the highest number of threatened species (11.54% of birds [15] and 10.6% of mammals [16]). Investigating changes in vertebrate biodiversity is even more crucial for such species of conservation concern, which include many frugivores which are key in maintaining many ecosystem processes [17]. By eating fruits, frugivores might disperse seeds affecting seedling success and ultimately forest maintenance and regeneration [18]. Despite the huge importance of frugivorous species, they are one of the most sensitive functional group; loss of 46% of frugivorous species due to forest loss [19], which may negatively impact ecosystem function in these forests [20].

Sampling tropical frugivores can be challenging because many of them live in the forest canopy, some are nocturnal, whilst others (e.g., cotingas) can be very quiet. Several species are also highly vagile and may make regional scale movements questing for fruits, thus leading to unpredictable absences [21,22]. In recent years, many studies have included the usage of new technologies, such as camera traps and automatic recorders to improve the efficiency of sampling biological communities. These methods have proved to be efficient in filling in the gaps left by traditional methods (e.g., increasing the detection of shy, nocturnal and rare species [23,24]). Furthermore, automatic equipment allows the continuous data collection with almost no human interference and accessing difficult areas, such as forest canopies [24].

To address the challenges of preventing biodiversity loss and maintaining ecosystem functionality, it is crucial to evaluate the effects of habitat modification on forest frugivores communities [25]. Here we aim to assess the impact of fires and selective logging on frugivore communities by comparing: (1) overall richness, (2) richness of obligate, partial and opportunistic frugivores, (3) community composition, (4) body mass, and (5) functional diversity, all between different forest classes. We sampled frugivores in undisturbed, selectively logged, historically and recently-burned forest transects using six methodologies: line transects, focal observations, point counts, passive acoustic recordings sampling in second and minutes interval, and camera trap. We tested five hypotheses: (i) That overall frugivore richness will not be affected by forest disturbances given the high species turnover – e.g., replacement of specialist core forest species by open areas species [17,26]. However, since recent fires can differentially impact the functional groups, we hypothesized (ii) that specialist species – i.e., obligate frugivores will show negative response to fires, while generalist frugivores (partial and opportunistic frugivores) will respond positively [10,27]. (iii) That the negative impacts of fires (e.g., high mortality

rates) will limit the occurrence of frugivores species, especially the large-bodied frugivores. In this line, (iv) the non-random impact of fires on specialist and large frugivores will translate in a distinct species composition in burned forests, especially those recently-burned [28], which in turn will result in (iv) lower values of functional diversity [29]. On the other hand, we expect logged and historically-burned forests to have similar species richness, composition and functional diversity to undisturbed forests, as they have had almost two decades to recover.

2.3 Materials and methods

2.3.1 Study area and sampling design

We collected data on frugivorous birds and non-volant mammals in the central-eastern Brazilian Amazon in the municipalities of Belterra, Mojuí dos Campos and Santarém, state of Pará. Sampled forest areas were located in *terra firme* forests nested within a wider matrix of one million hectares of undisturbed and disturbed forests immersed in an agriculture matrix comprising both large and small private landholdings [30]. In 2015 and 2016 a major El Niño event caused a prolonged dry season, which resulted in multiple understorey fires covering c. one million hectares of the study region [1,31].

Forest areas were stratified in transects to capture the main forest disturbance classes and important internal heterogeneities in forest structure [30]. We sampled 17 forest transects distributed in the following forest classes: nominally undisturbed forests with no logging and fire effects but some pressure from subsistence hunting (hereafter called undisturbed forests, $n = 5$), forests where selective logging occurred ≥ 30 years prior to sampling (hereafter called logged forests, $n = 4$), forests where selective logging occurred ≥ 30 years and burned in ≥ 18 years before the study (hereafter called historically-burned forests, $n = 4$), and finally forests where selective logging occurred ≥ 30 years prior

sampling, while fires occurred 3 years prior sampling in consequence of the 2015-16 El Niño (hereafter called recently-burned forests, $n = 4$) (Table S2.1). At each forest transect and according to different methodologies, frugivorous animals were sampled along two types of transects: 300 m and 1000 m transects (except for a logged and two undisturbed plots, which were only sampled along the 1000 m transect, see below for more details). To ensure spatial independence between transects, they were separated by a minimum distance of 1.5 km.

2.3.2 Frugivore classification and sampling frugivorous species

The frugivorous species were determined from a comprehensive literature survey (see Supporting information) and correspond to birds and mammals species that consume fruits as part of their diet [32]. We also included species we saw consuming fruits during the sampling (i.e., at focal, transect and camera trap surveys), but were not considered as a frugivore [32] (Table S2.2).

To assess the diet flexibility and species resilience to environmental changes, we classified frugivorous birds into three classes: obligate, partial and opportunistic [33]. We refer to *obligate frugivores* species who rely heavily on fruits as (80% or more of their diet is based on fruits), *partial frugivores* for species that include other major food items in their diet (20-79%) or *opportunistic frugivores* for species that only occasionally eat fruits as a supplementary food resource (up to 19%, Table S2.3).

Frugivorous birds and non-volant mammals were recorded using six sampling methods: (i) transects, (ii) focal watches at fruiting plants, (iii) camera traps (arboreal and terrestrial), passive acoustic recording at intervals of (iv) seconds and (v) minutes, and (vi) point counts by human observers. Avian taxonomy follows Pacheco et al (2021), while mammalian follows Abreu-Jr et al (2020)^[35].

Line transects: between February 2019 and March 2020 we walked along 1000 m transects (17 transects) recording frugivores (birds and mammals) through direct observations [36]. Surveys were done by LCR between 0600 and 1800, covering the whole diurnal cycle of frugivore activities, except on days with heavy rain. We sampled one transect per day (N = 227), except for 22 days when we sampled two, one transect in the morning and another in the afternoon. All transects were visited at least twice monthly.

Focal: Simultaneously during the line transect surveys, we carried out frugivore (birds and mammal) sampling through focal observations. Along the 1000 m transects, we made direct observation of frugivorous species on selected fruiting plants with zoochoric dispersal syndrome and ripe fruit availability. Focal observations increase the probability of detecting rare animal species [37,38].

Camera traps: We sampled frugivores (birds and mammals) with camera traps installed in fruiting trees, both at the ground level (30 cm off the ground) near fallen fruits and in the subcanopy (at a height of 5–15 m). For both (ground and subcanopy), trees were selected based on ripe fruit availability and ease of climbing. Cameras were installed simultaneously during the line transect surveys.

Camera traps (APEMAN - 16MP with Infrared Night Vision up to 20 m) were installed along 1000 m transect (17 transects). Camera traps were set to be active 24 h daily to record 20-second videos with 20-second intervals between recordings. The number of cameras varied across the transects depending on fruit availability (3-6 each transect). The exposure time of each camera ranged from 2-35 days, also depending on fruit availability. Logistical constraints did not allow us to monitor more trees or to standardize sampling

efforts across transects. Consecutive detection of the same frugivore species was considered independent if more than an hour passed between detections [39,40]. Sampling effort was calculated as the sum of days in which each camera trap was active.

Point counts: In 2016, between 15 and 26 November 2016 frugivorous birds were sampled through point counts by NGM, ACL and SD. In each 300-m transect (14 transects), three points separated by 150 m were sampled. At these points, all bird species seen or heard were recorded for 15 minutes [41]. We sampled each point twice to partially capture temporal variation in avian vocal activity.

Passive acoustic recorders: Between June and August 2018, we collected acoustic data in 14 transects. Frugivorous birds were sampled using Frontier Labs Bioacoustic Audio Recorder Units (16-bit 44.1 kHz, Frontier Labs, 2015). One recorder per transect were placed in trees at a height of 7–10 m in the same 150 m stretch of transects used for point counts (see details in Metcalf et al., 2022[43]). The continuous acoustic recordings were divided into two sampling methods: *high temporal resolution* – frugivores were sampled during four survey periods per transect - 15 min in duration each, totalling 1 h of data from each transect (see Supporting information); and *Low temporal resolution* - again 1 h of recordings was taken from each transect but the survey periods lasted 15 s (see Supporting information). Samples for both survey methods were taken in the beginning of the day (a two-and-a-half-hour period starting 30 min before sunrise), corresponding to a period of high avian activity [43, 44]. Bird vocalizations recorded were identified by NGM.

2.3.3 Functional traits

For all frugivorous bird species, we considered morphological traits related to frugivory and seed dispersal. We selected wing, tarsus, and tail length as traits related to long-distance dispersal capacity [45,46], beak length, width and depth correspond to trophic traits and reflect the maximum fruit size that can be ingested [47], while Kipp's distance is related to dispersal ability and provide further insight into wing shape and flight ability, thus capturing traits related to dispersal limitation and gap-crossing ability [48,49]. The wing and beak measurements were taken from Tobias et al. (2022), while body mass as a measure of size was based on Dunning (2008). All trait measurements are provided in the electronic supplementary material (Table S2.2, S2.3).

To mitigate strong correlations among functional traits with body size, we used ordination techniques to generate independent trait axes related to different morphological traits linked to the ecological process of seed dispersal. Using two-step principal component analysis (PCA) on morphological trait data, we created four trait axes [29]. Initially, we standardized the data using the *decostand* function in the *vegan* package [52]. The first PCA axis was created based on PCAs undertaken on locomotory (wing, tarsus, tail length) and trophic traits (beak length, width and depth). As in both PCAs the first components were strongly correlated with body size, we combined them both in a second PCA and used the first axis as a size measure [29]. For the second and third axes, we used the second axis of locomotory and trophic PCAs. Lastly, a fourth axis – i.e., dispersal traits, consisted of the log-transformed hand-wing index, a standard measure of flight ability computed from wing length and Kipp's distance [29].

To evaluate how selective logging and forest fire may influence community assembly processes, we calculated two functional diversity indexes for frugivorous bird communities [53,54]. We chose to combine feeding and locomotion traits because they are directly related to seed dispersal functions performed by birds [55] and the species

resilience to forest disturbances [56]. Functional dispersion (FDis) describes the mean distance of one species to the centroid of all species in the community, weighted by their abundance [57]. FDis is related to the efficiency in using diet resources [58]. Functional richness (FRic) represents the niche space occupied by the community, with higher values indicating a greater diversity of resources used [58].

We standardised the effect size (SES) for FRic to minimize the influence of species richness [20]. The SESFRic was calculated based on: $\text{observed FRic} - \text{mean of expected FRic} / \text{SD of expected FRic}$. Communities that are more functionally rich than would be expected by chance (given their species richness) have positive values of SESFRic, and those which are less functionally rich have negative values - positive and negative values indicate higher and lower functional diversities. To calculate the functional diversity indexes, we initially constructed a dissimilarity matrix based on our matrix of species *versus* traits based on the Gower Distance, then we calculated the functional diversity indexes using the *FD* package [59,60].

We used null models to estimate whether the functional diversity of frugivorous bird communities is above or below that expected by chance [60]. Expected FRic was calculated with a null model based on the permutation of the presence/ absence matrix (samples (rows) x species (columns)), with the trait matrix maintained as originally. Null models were calculated using the *independent swap* algorithm that randomizes the data matrix maintaining occurrence and sample richness [60].

2.3.4 Data Analysis

2.3.4.1 Species richness and composition

We first tested for spatial auto-correlation effects on frugivore species by performing a Mantel test [52] between the geographical distance and all frugivore species dissimilarity matrices among pairs of sampling transects. Our results showed no spatial correlation on frugivore species occurrence (see Supplementary material, Figure S2.1). Then, to evaluate the sampling completeness of frugivores communities, we built species accumulation curves (see Supplementary material, Figure S2.2). Although asymptotes were not achieved for most methods, sampling was consistent among forest classes, with $84.99\% \pm 0.09$ of species recorded (Figure S2.2).

To explore the effects of forest fires and selective logging on overall frugivore richness, we rarefied the species richness obtained with each method in each forest class given differences in sampling effort. We then tested for differences in species richness among different sampling methods. Lastly, we check for the effects of forest fires and selective logging on the frugivory specialisation using the proportion of each frugivory category (obligate, partial and opportunistic) recorded in each forest class. We carried out both analyses using one-way ANOVAs with a Tukey HSD test for pairwise comparisons between forest classes in the *vegan* package.

To visualise the response of frugivore community composition to disturbances (logging and fire) and sampling method we used nonmetric multidimensional scaling (NMDS) to map the similarities in the composition of frugivore communities in two-dimensional space [52]. Differences in composition among forest classes and sampling methods were tested with permutational multivariate analysis of variance (PERMANOVA) [61]. We first used NMDS across all methods and then separated different sampling methods. Both NMDSs and PERMANOVAs analyses were performed using the frequency

of occurrences and calculating the Bray-Curtis index to measure the similarity between pairs of sites. The NMDS ordination was performed using the *metaMDS* function, while the PERMANOVA test was conducted with the *adonis* function, both in the *vegan* package [52].

2.3.4.2 Functional traits and diversity measures and variation

To account for the effect of forest classes on body mass of birds and mammals, we constructed a non-parametric test (Kruskal-Wallis) in the *vegan* package with a Wilcox test performed using the *rstatix* package [62] for pairwise comparisons.

We calculated functional diversity (FD) indexes on the basis of relative abundance data for all bird communities. To test whether functional diversity changed with levels of forest degradation, we first assessed the raw functional distance (FDis) variation across forest classes. Then, we assessed whether these changes in FDis deviated from random using null models. Second, we measured how functional richness varied with impacts from logging and forest fires by testing the differences in the raw functional richness (FRic) and the standardized values (SESFRic) among forest classes. The functional diversity differences were also tested using a variance test (ANOVAs) with a Tukey HSD test for pairwise comparisons.

2.4 Results

2.4.1 Species richness and composition

Overall, we recorded 190 frugivore species from a dataset of 17,809 records: 162 birds ($n = 13,826$ records) and 28 mammals ($n = 3,983$) (Table S2.3). Among them, 69 species occurred in all forest classes, 56 birds and 13 mammals. Combining all methods, there were no differences in frugivore richness among forest classes (Figure 2.1a, Table S2.4), with

133 species recorded in undisturbed and logged, 119 in historically-burned, and 148 in recently-burned forests. Exploring results from each method separately, we found consistency in the number of species except for transect lines, for which recently-burned forests exhibited the highest species richness in comparison with other forest classes (Figure S2.3, Table S2.4).

Considering only obligate frugivores (>80% fruits in the diet), we recorded a lower number of species in historically-burned forests in comparison with undisturbed and logged forests (Figure 2.1b, Table S2.4 and S2.5). However, the richness of partial and opportunistic frugivores did not differ among forest classes (Figure S2.4, Table S2.4).

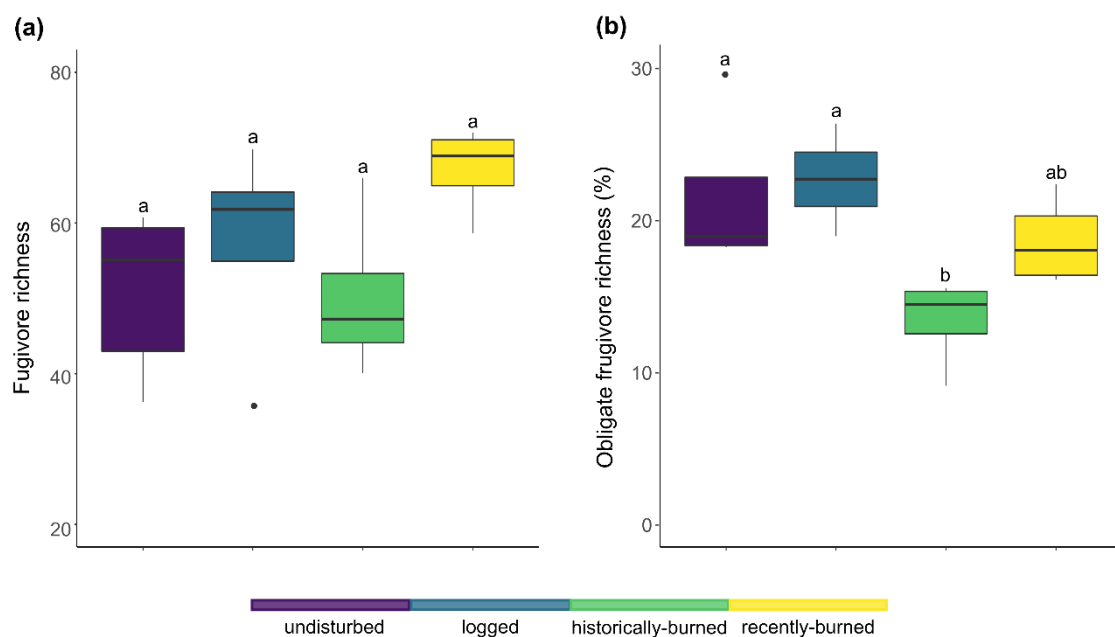


Figure 2.1 Effects of logging and forest fires on (i) overall frugivore richness, and (ii) richness of obligate frugivorous species (>79% fruits on the diet). Overall species richness was rarefied in order to control for differences in sampling effort among the forest classes. We used the proportion of obligate frugivores in each transect to measure the impact of forest disturbances. Different letters represent statistical differences among forest classes at $p < 0.05$. Non-significant pairwise differences between forest classes are indicated by

the presence of the same letter (according to Tukey pairwise test). Black dots are potential outliers and lines inside box plots represent median values.

We also found that burned forests had the most distinct frugivore assemblages, especially when compared with undisturbed forest sites ($R^2 = 0.32$, $P < 0.01$, Figure 2.2). Frugivore community composition was also significantly distinct between methods, both considering overall community composition ($R^2 = 0.60$, $P < 0.01$, Figure S2.5a) and when considering only birds ($R^2 = 0.53$, $P < 0.01$, Figure S2.5b). Camera traps recorded the most idiosyncratic species assemblages, followed by line transects and focal points – both had more similar species composition in comparison with other methods (Figure S2.5). Lastly, passive acoustic recorders, either sampled in intervals of seconds or minutes, and points count share more species with each other than to the other methods (Figure S2.5).

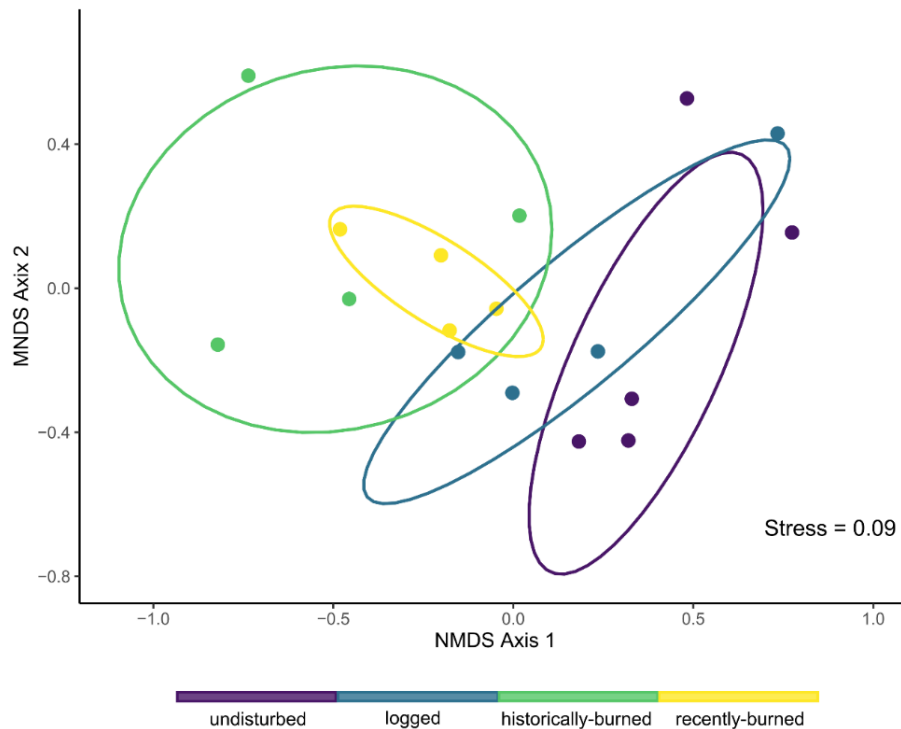


Figure 2.2 NMDS ordination of frugivore species in 17 sites sampled in the Amazonian forests. Points and ellipses represent transects and forest classes, respectively.

2.4.2 Functional traits and diversity

The mean of community body mass (birds and mammals) was significantly lower in historically-burned forests in comparison to other forest classes (Chi-squared-value = 10.50, $P = 0.01$, Table S2.6, Figure S2.6).

Regarding the functional diversity of frugivorous birds, we found that historically-burned forests had lower values of SESFRic and FDis. Using a null-model approach, we found that FDis was lower in historically-burned forests than in undisturbed forests (Table S2.7, S2.8, Figure 2.3a). Although the raw FRich did not change with forest degradation, when the effect size was standardized (SES) SESFRic had a lower value in historically-burned than in primary forest (Table S2.7, S2.9, Figure 2.3b).

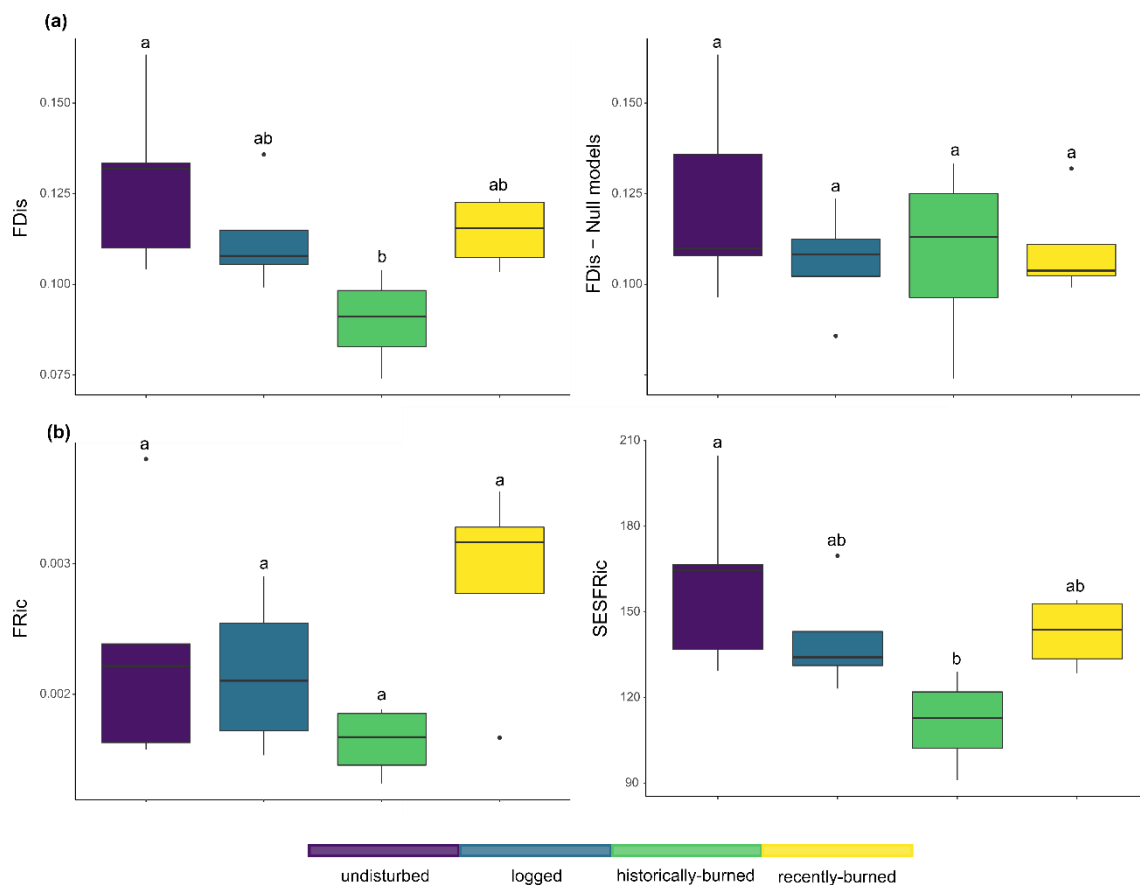


Figure 2.3 Effects of logging and fire on (a) Functional dispersion (FDis) and null model, and on (b) Raw functional richness (FRic) and standardized effect size of functional

richness (SESFRic) of frugivorous animals in 17 transects across four forest classes. Different letters represent statistical differences among forest classes at $p < 0.05$. Non-significant pairwise differences between forest classes are indicated by the presence of the same letter (according to Tukey pairwise test). Black dots are potential outliers and lines inside box plots represent median values.

2.5. Discussion

Our findings reveal that although fires did not affect overall frugivore species richness, they negatively affected the richness of specialist and large-bodied frugivores. Historically-burned forests had lower richness of obligates as well as fewer large-sized frugivores in comparison to undisturbed forests. Fires also affected community frugivore structure in Amazonian forests since burned forests had different species composition from undisturbed forests. By combining a wide set of ecological traits and robust functional diversity metrics in our study, we revealed that in the long-term, fires can have pervasive impacts on the functional diversity of frugivores birds, with historically-burned forests having lower functional diversity, which may have negative consequences for seed dispersal.

2.5.1 Effects of logging and fires on frugivore richness and composition

According to our expectations, our results revealed similar frugivore richness between undisturbed, logged and burned forests. The lack of evidence of human-driven disturbances was also reported by other studies in the Amazonian forests [63–65], and can be a result of the greater resilience of frugivore species richness in tropical forests, especially those with high dispersal capacity to move through human-modified landscapes [22]. It may also be associated with higher dietary plasticity in some frugivorous species, giving them some

advantages in human-modified forests. Developing second growth in logged and burned forests, especially after fires, provide small fruits (e.g., Melastomataceae) used by these species - increased abundance of fruit availability, is commonly associated with the proliferation of some frugivorous birds [66,67]. Meanwhile, the high habitat heterogeneity created by logging and fires can increase the occurrence of habitat generalist or gap specialist species (i.e., species adapted to live in more open and edge areas) maintaining total frugivore richness levels despite community turnover [28,68].

On the other hand, fires significantly reduced the richness of obligate frugivores, but did not affect the richness of partial and opportunistic frugivores. Although the vulnerability of obligate frugivores to human-driven disturbances was expected [69], especially to fire [28,70], we surprisingly recorded a stronger effect of historically rather than recently-burned forests (i.e., historically-burned forests had the lowest richness of obligate frugivore richness). The decline in frugivore richness due to fires can be a result of the high mortality of key food species [3]. In turn, even though fruit productivity can be maintained right after fires [67], historically-burned forests led to impoverishment of fruit availability due to ongoing plant mortality [71]. Indeed, fires can induce tree mortality even for long periods (e.g., 10 years after the events, Silva et al., 2018) leading to important losses of fruiting plants, affecting the diversity and abundance of fruits available to frugivores, especially large-sized species [17,73].

We found consistent differences in frugivore composition between burned (historically and recently-burned) and unburned forests (undisturbed and logged). Although high dissimilarities of bird [64,74] and mammal [70] communities were expected between recently-burned and undisturbed forests due to the direct impacts of fire, they run contrary to that expected for historically-burned forests. Our findings suggest that frugivore communities are still distinct even 20 years after fire events. Rather than showing a

recovery toward a primary forest community, frugivore assemblages in historically-burned forests have drifted and remain composed of generalist adapted to live in edge and gaps areas suggesting that fires may favour certain frugivorous species while limiting the occurrence of other species more reliant on undisturbed forests [74,75].

2.5.2. Functional traits and diversity in logged and burned forests

Historically-burned forests had low values of functional diversity, whilst logged and recently-burned ones had similar levels to undisturbed forests. The trait structure of communities in historically-burned forests was dispersed around mean trait values – i.e., in the long-term, fires decreased avian functional dispersion, implying a reduction of ecosystem function in these forests [57]. On the other hand, we detected no effect of logging and fires on raw functional richness. The lack of differences may be confounded by similar species richness in logged, burned and undisturbed forests [76]. In turn, as raw functional richness is influenced by species richness, then each additional species increases the space occupied by the community [53]. However, when we controlled for the effects of species richness, we found that historically-burned forests had significantly lower values of functional richness than undisturbed forests - i.e., less standardized functional richness than expected given their species richness. Yet, positive standardize functional richness values were associated with undisturbed forests, indicating low functional redundancy, which may be a result of the great niche differentiation due to the high taxonomic, phylogenetic, and functional diversity of tropical forests [13,77,78].

The low functional diversity found in historically-burned forests contradicts our prediction that these ecosystems would recover functionality 18 years after fires events [29,79]. Indeed, changes in species composition reported in historically-burned forests certainly affected the functional diversity [80]. The prevalence of species such as

Chiroxiphia pareola and *Dancis cayana* in such forests may change ecological trait distribution toward medium-small sized species, thus reducing overall functional diversity [55]. On the other hand, un-burned forests offer a more diverse range of fruit sizes (i.e., small to large fruits) favouring a great range of frugivore body sizes, including large-bodied species [71]. Therefore, besides limiting the occurrence of some frugivores, fires reduced the functional diversity, which in the long-term may have implications for ecosystem processes, such as the seed dispersal [81,82].

Furthermore, the reduction in functional diversity in historically-burned forests may be associated with the loss of large-bodied species. Large-bodied frugivores play a key function in the tropical forests by dispersing large seeds for long distances [83]. Loss of large frugivores is commonly associated with other synergistic factors beyond forest degradation, such as hunting [84]. Hunting is common in the study region and can depress the abundance of several frugivores, especially large-bodied species [85,86]. In turn, some species such as *Pecari tajacu* and *Tapirus terrestris* were only recorded in undisturbed or minimally disturbed forests (i.e., logged). Furthermore, we did not record *Tayassu pecari* at all, which is indicative of sub-regional impacts of hunting on this highly mobile and highly social species. On the other hand, the gap of difference in community structure and richness of recently-burned forests can be explained by the distinct forest structure post-fire. Although right after fires hunting practices can be exacerbated [70], in the medium-term (after three years), the rapid regeneration of early pioneer trees may discourage hunters due to a reduction in hunter access and visibility within the forest while simultaneous providing additional fruit resources for terrestrial animals and time for frugivore communities to recover [28].

2.5.3 Implications of the different survey methods

The differences in the structure among forest classes may influence the detectability of frugivores. For instance, the accumulation curves for five of the six methods (excepted for focal) are steeper in recently-burned forest, which may be explained by the open areas created by the high tree mortality due to fires - there is essentially no mid-storey [3], which may increase the sound range and sighting lines for visual methods. Nonetheless, the higher frugivorous richness detectable by focal plants method in undisturbed forests may be explained by the greater concentration of frugivores around fruiting trees - food resources are scarcer, so each resource (plants) ought to have a greater concentration of visitors for camera traps and focal plants.

Due to high diversity in life histories within frugivores, different sampling methods provide a means to maximise detection of all members of the frugivore community (Figure S2.5). The use of passive-acoustic recorders permits high temporal resolution sampling, which increases the proportion of the frugivore community detected [43,87]. Further, visual methods (transect and focal) provided a complementary approach for sampling frugivore by contributing to the detection of some groups that rarely vocalised, such as cotingas. Furthermore, camera trapping is a well-established method to sample nocturnal species, such as *Tapirus terrestris* and small mammals, as well as cryptic or difficult-to-record ones, such as *Psophia dextralis* and *Dasyprocta leporina* [24,88]. Camera trapping has proven also to be extremely important when extended to the forest canopy [24]. In turn, our survey detected poorly-known species, such as *Pyrilia vulturina* and *Potos flavus*. Thus, we highlight the importance of combining multiple methods, allowing the detection of species not detected by traditional ones (e.g., point count), thus contributing to a more complete frugivore survey.

3.5.4 Conclusion

The loss of obligate and large-bodied frugivores, as well as the shift in community composition toward a distinct species than found in undisturbed forests may negatively affect the functional diversity which persists for at least 18 years after fire events. Therefore, we highlight the importance of long-term monitoring to measure the responses of frugivorous species and functional diversity in human-modified forests, especially in forests that experienced (often recurrent) fires. Nonetheless, we encourage other studies to use different methods to sample frugivore communities, allowing a broader taxonomic sample to give a more ample wider perspective on the effects of human-driven impacts on frugivores. Understanding the pervasive consequences of human drive disturbances is crucial to reveal impacts on the provision of seed dispersal processes which are essential for tropical forest maintenance and recovery.

2.6 Acknowledgments

We thank the Large Scale Biosphere-Atmosphere Program (LBA) for logistical and infrastructure support during field measurements. We are deeply grateful to our field and laboratory assistants: Gilson Oliveira, Joni Oliveira, Josué Oliveira, Josiane Oliveira, Marcos Oliveira and Renilson Freitas, as well as all collaborating private land owners for their support and access to their land. We also thank Lais Lautenschlager Rodrigues and Sara Moreira for the screening camera trap data, also to Carlos Rodrigo Brocardo and Rodrigo Fadini for helping in mammal identification and Juliana Teixeira for assistance during the analysis. We are grateful to multiple funding agencies for financial support: Conselho Nacional de Pesquisa (CNPq, grants CNPq-CAPES 441659/2016-0 and 441573/2020-7 [PELD-RAS], MCIC-CNPq 420254/2018-8 [RESFLORA] and CNPq-PrevFogo-IBAMA 441949/2018-5 [SEM-FLAMA]), Instituto Nacional de Ciência e

Tecnologia – Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0) and Embrapa (SEG: 02.08.06.005.00), in Brazil, the Darwin Initiative (17-023), The Nature Conservancy, and Natural Environment Research Council (NERC, NE/F01614X/1, NE/G000816/1, NE/K016431/1 and NE/P004512/1), in the UK. E.B. and J.B. were also funded by H2020-MSCA-RISE (691053-ODYSSEA). F.F. and J.B. acknowledge funding provided by BNP Paribas Foundation (Climate and Biodiversity Initiative, BioClimate project). MAP thanks the CNPq for a research grant (304742/2019-8).

2.7 Author Contribution

LCR and ACL conceived the original idea of this study. LCR, ACL, EB, NGM and OCM conceived the study design, conducted the sampling and organized the database. LCR and ACL conducted the data analyses with input from MAP. LCR wrote the manuscript, with significant contributions of all co-authors. All authors discussed the results and revised the manuscript before submission.

2.8 References

1. Aragão LEOC *et al.* 2018 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nat. Commun.* **9**, 1–12.
(doi:10.1038/s41467-017-02771-y)
2. Betts RA, Golding N, Gonzalez P, Gornall J, Kahana R, Kay G, Mitchell L, Wiltshire A. 2015 Climate and land use change impacts on global terrestrial ecosystems and river flows in the HadGEM2-ES Earth system model using the representative concentration pathways. *Biogeosciences* **12**, 1317–1338.
(doi:10.5194/bg-12-1317-2015)
3. Berenguer E *et al.* 2021 Tracking the impacts of El Niño drought and fire in

- human-modified Amazonian forests. *Proc. Natl. Acad. Sci. U. S. A.* **118**, 1–8.
(doi:10.1073/pnas.2019377118)
4. França FM *et al.* 2020 El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes. *Biotropica* **52**, 252–262. (doi:10.1111/btp.12756)
 5. Barlow J, Peres CA, Lagan BO, Haugaasen T. 2003 Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* **6**, 6–8.
(doi:10.1046/j.1461-0248.2003.00394.x)
 6. Miranda LS, Imperatriz-Fonseca VL, Giannini TC. 2019 Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. *PLoS One* **14**, 1–17. (doi:10.1371/journal.pone.0215229)
 7. Rogers HS, Donoso I, Traveset A, Fricke EC. 2021 Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. *Annu. Rev.* **52**, 641–666.
 8. Matricardi EAT, Skole DL, Costa OB, Pedlowski MA, Samek JH, Miguel EP. 2020 Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science (80-.).* **369**, 1378–1382. (doi:10.1126/SCIENCE.ABB3021)
 9. Fontúrbel FE, Candia AB, Malebrán J, Salazar DA, González-Browne C, Medel R. 2015 Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Glob. Chang. Biol.* **21**, 3951–3960.
(doi:10.1111/gcb.13025)
 10. Symes WS, Edwards DP, Miettinen J, Rheindt FE, Carrasco LR. 2018 Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nat. Commun.* **9**. (doi:http://dx.doi.org/10.1038/s41467-018-06579-2)
 11. Brodie JF, Giordano AJ, Zipkin EF, Bernard H, Mohd-Azlan J, Ambu L. 2015

- Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conserv. Biol.* **29**, 110–121. (doi:10.1111/cobi.12389)
12. Brooks TM, Wright SJ, Sheil D. 2009 Evaluating the Success of Conservation Actions in Safeguarding Tropical Forest Biodiversity. *Conserv. Biol.* **23**, 1448–1457. (doi:10.1111/J.1523-1739.2009.01334.X)
 13. Lees AC, Haskell L, Allinson T, Bezeng SB, Burfield IJ, Renjifo LM, Rosenberg K V, Viswanathan A, Butchart SHM. 2022 State of the World’s Birds. *Annu. Rev. Environ. Resour.* **47**, 1–30. (doi:10.1146/annurev-environ-112420-014642)
 14. Schipper J *et al.* 2008 The Status of the World’s Land. *Science (80-.).* **322**, 225–230.
 15. Pacheco JF, Silveira LF, Aleixo A, Agne CE, Bencke GA, Bravo GA, Brito GRR. 2021 *Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee—second edition.*
 16. Quintela FM, Da Rosa CA, Feijó A. 2020 Updated and annotated checklist of recent mammals from Brazil. *An. Acad. Bras. Cienc.* **92**, 1–57. (doi:10.1590/0001-3765202020191004)
 17. Morante-Filho JC, Arroyo-Rodríguez V, Pessoa M de S, Cazetta E, Faria D. 2018 Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. *Ecol. Appl.* **28**, 2024–2032. (doi:http://dx.doi.org/10.1002/eap.1791)
 18. Fleming TH, Kress JW. 2011 A brief history of fruits and frugivores. *Acta Oecologica* **37**, 521–530. (doi:10.1016/j.actao.2011.01.016)
 19. Morante-Filho JC, Faria D, Mariano-Neto E, Rhodes J. 2015 Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. *PLoS One* **10**, 1–18. (doi:10.1371/journal.pone.0128923)

20. Laliberté AE, Legendre P, Shipley B. 2015 Package FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. <http://cran.r-project.org/web/packages/FD/>. *Ecology* **91**, 1–28.
21. Loiselle BA, Blake JG. 1991 Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* **72**, 180–193. (doi:10.2307/1938913)
22. Lees AC, Peres CA. 2009 Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* **118**, 280–290. (doi:10.1111/j.1600-0706.2008.16842.x)
23. Wearn OR, Glover-Kapfer P. 2019 Snap happy: Camera traps are an effective sampling tool when compared with alternative methods. *R. Soc. Open Sci.* **6**. (doi:10.1098/rsos.181748)
24. Moore JF *et al.* 2021 The potential and practice of arboreal camera trapping. *Methods Ecol. Evol.* **12**, 1768–1779. (doi:10.1111/2041-210X.13666)
25. Sekergioglu C, Whelan C, Wenny D, Floyd C. 2016 Bird Ecosystem Services Promote Biodiversity and Support Human Well-Being. *Why Birds Matter Avian Ecol. Funct. Ecosyst. Serv.* , 341–364.
26. Solar RR de C *et al.* 2015 How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol. Lett.* **18**, 1108–1118. (doi:10.1111/ele.12494)
27. Moura NG, Lees AC, Aleixo A, Barlow J, Berenguer E, Ferreira J, Mac Nally R, Thomson JR, Gardner TA. 2016 Idiosyncratic responses of Amazonian birds to primary forest disturbance. *Oecologia* **180**, 903–916. (doi:10.1007/s00442-015-3495-z)
28. Barlow J, Peres CA. 2004 Ecological responses to El Niño-induced surface fires

- Ecological responses to El Nin in central Brazilian Amazonia: management implications for flammable tropical forests. *Philos. Trans. R. Soc. B Biol. Sci.* **359**, 367–380. (doi:10.1098/rstb.2003.1423)
29. Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, Barlow J, Tobias JA. 2016 Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. B Biol. Sci.* **283**, 20161289. (doi:10.1098/rspb.2016.1289)
 30. Gardner TA *et al.* 2013 A social and ecological assessment of tropical land uses at multiple scales: The Sustainable Amazon Network. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 20120166–20120166. (doi:10.1098/rstb.2012.0166)
 31. Withey K *et al.* 2018 Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20170312. (doi:10.1098/rstb.2017.0312)
 32. Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027. (doi:10.1890/13-1917.1)
 33. Kissling WD, Böhning-Gaese K, Jetz W. 2009 The global distribution of frugivory in birds. *Glob. Ecol. Biogeogr.* **18**, 150–162. (doi:10.1111/j.1466-8238.2008.00431.x)
 34. Pacheco JF *et al.* 2021 Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee—second edition. *Ornithol. Res.* **29**, 94–105. (doi:10.1007/s43388-021-00058-x)
 35. Abreu-Jr EF *et al.* 2021 Lista de Mamíferos do Brasil. *Com. Taxon. da Soc. Bras. Mastozool.* (doi:10.5281/zenodo.5590639)
 36. Ribeiro da Silva F, Montoya D, Furtado R, Memmott J, Pizo MA, Rodrigues RR.

- 2015 The restoration of tropical seed dispersal networks. *Restor. Ecol.* **23**, 852–860. (doi:10.1111/rec.12244)
37. Pizo MA, Galetti M. 2010 Métodos e Perspectivas da Frugivoria e Dispersão de Sementes por Aves. *Biologia (Bratisl)*. , 492–504.
 38. Jordano P. 2016 Chasing Ecological Interactions. *PLoS One* **14**, 2–5. (doi:10.1371/journal.pbio.1002559)
 39. Acevedo-Quintero JF, Zamora-Abrego JG, García D. 2020 From structure to function in mutualistic interaction networks: Topologically important frugivores have greater potential as seed dispersers. *J. Anim. Ecol.* **89**, 2181–2191. (doi:10.1111/1365-2656.13273)
 40. Rivas-Romero JA, Soto-Shoender JR. 2015 Filling in the Gaps: Evaluating the Use of Camera Traps in the Canopy to Examine Frugivore Visits to *Oreopanax echinops* in the Highlands of Guatemala. *Southwest. Nat.* **60**, 366–397. (doi:10.1894/0038-4909-60.4.366)
 41. Moura NG, Lees AC, Andretti CB, Davis BJW, Solar RRC, Aleixo A, Barlow J, Ferreira J, Gardner TA. 2013 Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. *Biol. Conserv.* **167**, 339–348. (doi:10.1016/j.biocon.2013.08.023)
 42. Frontier Labs. 2015 Bioacoustic Audio Recorder User Guide.
 43. Metcalf OC, Barlow J, Marsden S, Gomes de Moura N, Berenguer E, Ferreira J, Lees AC. 2022 Optimizing tropical forest bird surveys using passive acoustic monitoring and high temporal resolution sampling. *Remote Sens. Ecol. Conserv.* **8**, 45–56. (doi:10.1002/rse2.227)
 44. Wimmer J, Towsey M, Roe P, Williamson I. 2013 Sampling environmental acoustic recordings to determine bird species richness. *Ecol. Appl.* **23**, 1419–1428.

(doi:10.1890/12-2088.1)

45. Weiss KCB, Ray CA. 2019 Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. *Ecography (Cop.)*. **42**, 2012–2020. (doi:10.1111/ecog.04387)
46. Miles DB, Ricklefs RE. 1984 The Correlation Between Ecology and Morphology in Deciduous Forest Passerine. *Ecology* **65**, 1629–1640.
47. Wheelwright NT. 1985 Fruit-Size, Gape Width, and the Diets of Fruit-Eating Birds. *Ecology* **66**, 808–818.
48. Dawideit BA, Phillimore AB, Laube I, Leisler B, Böhning-Gaese K. 2009 Ecomorphological predictors of natal dispersal distances in birds. *J. Anim. Ecol.* **78**, 388–395. (doi:10.1111/j.1365-2656.2008.01504.x)
49. Claramunt S, Derryberry EP, Remsen J V., Brumfield RT. 2012 High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc. R. Soc. B Biol. Sci.* **279**, 1567–1574. (doi:10.1098/rspb.2011.1922)
50. Tobias JA *et al.* 2022 AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581–597. (doi:10.1111/ele.13898)
51. Dunning JBJ. 2008 *Avian Body Masses Second Edition*.
52. Oksanen J *et al.* 2015 Vegan: Community Ecology Package R Package. version 2.3-1.
53. Mason NWH, De Bello F, Mouillot D, Pavoine S, Dray S. 2013 A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *J. Veg. Sci.* **24**, 794–806. (doi:10.1111/jvs.12013)
54. Mammola S, Carmona CP, Guillaume T, Cardoso P. 2021 Concepts and applications in functional diversity. *Funct. Ecol.* **35**, 1869–1885. (doi:10.1111/1365-2435.13882)

55. Pigot AL *et al.* 2020 Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.* **4**, 230–239.
(doi:10.1038/s41559-019-1070-4)
56. Luck GW, Lavorel S, McIntyre S, Lumb K. 2012 Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *J. of Animal Ecology*. **81**, 1065–1076. (doi:10.1111/j.1365-2656.2012.01974.x)
57. Laliberté E, Legendre P. 2010 A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305. (doi:10.1890/08-2244.1)
58. Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005 Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118. (doi:10.1111/j.0030-1299.2005.13886.x)
59. Podani J, Schmera D. 2006 On dendrogram-based measures of functional diversity. *Oikos* **115**, 179–185. (doi:10.1111/j.2006.0030-1299.15048.x)
60. Gotelli NJ. 2000 Null model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621. (doi:10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2)
61. Anderson MJ. 2001 A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* , 32–46.
62. Kassambara A. 2021 ‘rstatix’: Pipe-Friendly Framework for Basic Statistical tests. R package version 0.7.0, <<https://CRAN.R-project.org/package=rstatix>>.
63. Lee JS, Cornwell WK, Kingsford RT. 2022 Rainforest bird communities threatened by extreme fire. *Glob. Ecol. Conserv.* **33**, e01985.
(doi:10.1016/j.gecco.2021.e01985)
64. Slik JWF, Van Balen S. 2006 Bird community changes in response to single and repeated fires in a lowland tropical rainforest of eastern Borneo. *Biodivers.*

- Conserv.* **15**, 4425–4451. (doi:10.1007/s10531-005-4385-1)
65. Stouffer PC *et al.* 2021 Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. *Ecol. Lett.* **24**, 186–195. (doi:10.1111/ele.13628)
66. Menezes GSC, Cazetta E, Dodonov P. 2019 Vegetation structure across fire edges in a Neotropical rain forest. *For. Ecol. Manage.* **453**, 117587. (doi:10.1016/j.foreco.2019.117587)
67. Rocha JI da S, Menezes GSC, Cazetta E, Dodonov P, Talora DC. 2022 Seed rain across fire-created edges in a neotropical rainforest. *Plant Ecol.* **223**, 247–261. (doi:10.1007/s11258-021-01205-6)
68. Barlow J, Peres CA, Henriques LMP, Stouffer PC, Wunderle JM. 2006 The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biol. Conserv.* **128**, 182–192. (doi:10.1016/j.biocon.2005.09.028)
69. Newbold T, Scharlemann JPW, Butchart SHM, Sekercioglu CH, Alkemade R, Booth H, Purves DW. 2013 Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B Biol. Sci.* **280**. (doi:10.1098/rspb.2012.2131)
70. Peres CA, Barlow J, Haugaasen T. 2003 Vertebrate responses to surface wildfires in a central Amazonian forest. *ORYX* **37**, 97–109. (doi:10.1017/S0030605303000188)
71. Hawes JE *et al.* 2020 A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. *J. Ecol.* **108**, 1373–1385. (doi:10.1111/1365-2745.13358)
72. Silva CVJ *et al.* 2018 Drought-induced Amazonian wildfires instigate a decadal-

- scale disruption of forest carbon dynamics. *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20180043. (doi:10.1098/rstb.2018.0043)
73. Kissling WD, Rahbek C, Böhning-Gaese K. 2007 Food plant diversity as broad-scale determinant of avian frugivore richness. *Proc. R. Soc. B Biol. Sci.* **274**, 799–808. (doi:10.1098/rspb.2006.0311)
 74. Mestre LAM, Cochrane MA, Barlow J. 2013 Long-term Changes in Bird Communities after Wildfires in the Central Brazilian Amazon. *Biotropica* **45**, 480–488. (doi:10.1111/btp.12026)
 75. Barlow J, Peres C. 2004 Avifaunal Responses to Single and Recurrent Wildfires in Amazonian Forests. *Ecol. Appl.* **14**, 1358–1373.
 76. Prescott GW, Gilroy JJ, Haugaasen T, Medina Uribe CA, Foster WA, Edwards DP. 2016 Reducing the impacts of Neotropical oil palm development on functional diversity. *Biol. Conserv.* **197**, 139–145. (doi:10.1016/j.biocon.2016.02.013)
 77. Peña R, Schleuning M, Donoso I, Rodríguez-Pérez J, Dalerum F, García D. 2020 Biodiversity components mediate the response to forest loss and the effect on ecological processes of plant-frugivore assemblages. *Funct. Ecol.* **34**, 1257–1267. (doi:10.1111/1365-2435.13566)
 78. Gibson L *et al.* 2011 Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381. (doi:10.1038/nature10425)
 79. Dunn RR. 2004 Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.* **18**, 302–309. (doi:10.1111/j.1523-1739.2004.00151.x)
 80. Petchey OL, Gaston KJ. 2002 Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411. (doi:10.1046/j.1461-0248.2002.00339.x)
 81. Sebastián-González E, Pires MM, Donatti CI, Guimarães PR, Dirzo R. 2017

- Species traits and interaction rules shape a species-rich seed-dispersal interaction network. *Ecol. Evol.* **7**, 4496–4506. (doi:10.1002/ece3.2865)
82. Bomfim J de A, Guimarães PR, Peres CA, Carvalho G, Cazetta E. 2018 Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. *Ecography (Cop.)*. **41**, 1–11. (doi:10.1111/ecog.03592)
 83. Culot L, Bello C, Batista JLF, Do Couto HTZ, Galetti M. 2017 Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. *Sci. Rep.* **7**, 1–8. (doi:10.1038/s41598-017-08222-4)
 84. Ripple WJ *et al.* 2016 Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* **3**. (doi:10.1098/rsos.160498)
 85. Scabin AB, Peres CA. 2021 Hunting pressure modulates the composition and size structure of terrestrial and arboreal vertebrates in Amazonian forests. *Biodivers. Conserv.* **30**, 3613–3632. (doi:10.1007/s10531-021-02266-9)
 86. Osuri AM, Mendiratta U, Naniwadekar R, Varma V, Naeem S. 2020 Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds. *Front. For. Glob. Chang.* **2**, 87. (doi:10.3389/ffgc.2019.00087)
 87. Darras K, Batáry P, Furnas BJ, Grass I, Mulyani YA, Tschardt T. 2019 Autonomous sound recording outperforms human observation for sampling birds: a systematic map and user guide. *Ecol. Appl.* **29**. (doi:10.1002/eap.1954)
 88. Palmeirim AF, Benchimol M, Peres CA, Vieira MV. 2019 Moving forward on the sampling efficiency of neotropical small mammals: insights from pitfall and camera trapping over traditional live trapping. *Mammal Res.* **64**, 445–454. (doi:10.1007/s13364-019-00429-2)

2.9 Supporting information

Table S2.1 Number of study plots in different forest disturbance classes.

Forest class	Forest description	N° transects
undisturbed forest	pristine forest with no logging and fire effects	5
logged forest	selective logging occurred ≥ 30 years prior sampling	4
historically-burned forest	≥ 30 years selective logged and ≥ 18 years burned forests prior sampling	4
recently-burned forests	≥ 30 years selective logged and 3 years burned forests prior sampling	4

2.9.1 Spatial auto-correlation

We tested for the influence of spatial auto-correlation on frugivore richness using Mantel tests based on Pearson coefficient index with 1,000 permutations run using *mantel* function on *vegan* Package [1]. We used UTM (Universal Transverse Mercator) coordinates and the abundance of frugivores at each forest transect to build the dissimilarity matrix based on Bray-Curtis index. However, no variable exhibited spatial dependency frugivores ($r = 0.04$, $P = 0.30$) (Figure S2.1).

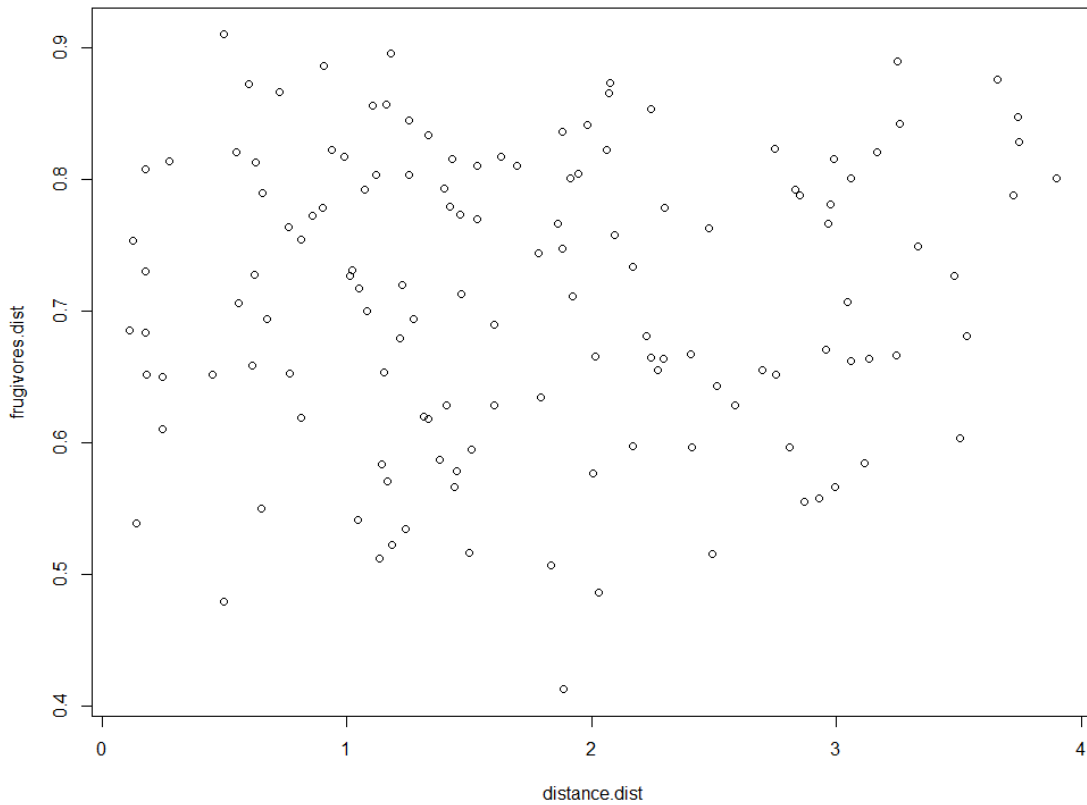


Figure S2.1 Spatial auto-correlation in frugivorous species sampled across 17 forest transects.

2.9.2 Sampling effectiveness

Rarefaction curves were used to evaluate sampling effectiveness with each method in each forest class using the *vegan* package [1]. We created multiple accumulation curves for each sampling method where the frugivore richness observed was related to sampling effort (measured as the number of hours/ days/ samplings, Figure S2.2). The curves were generated using the *specaccum* function and the species richness estimator Chao1 was calculated with the *estimateR* function in the *vegan* package [1].

Although asymptotes were not reached for most methods, according to our sampling effort, sampling was consistent among forest class (Figure S2.2). The average of species richness was $84.99\% \pm 0.09$ among transects (mean $\pm$ SD), while passive acoustic recorders sampled at second intervals and camera traps had the highest values (94.45 ± 2.26 and 91.2 ± 5.13 , respectively). The sampling effectiveness was similar among forest classes, varying from $88.41\% \pm 4.82$ in undisturbed forest to $81.2\% \pm 9.76$ in logged forests of species richness recorded. The consistent sampling among forest classes suggests that our sampling effectiveness was adequate to estimate species richness in each method and forest class.

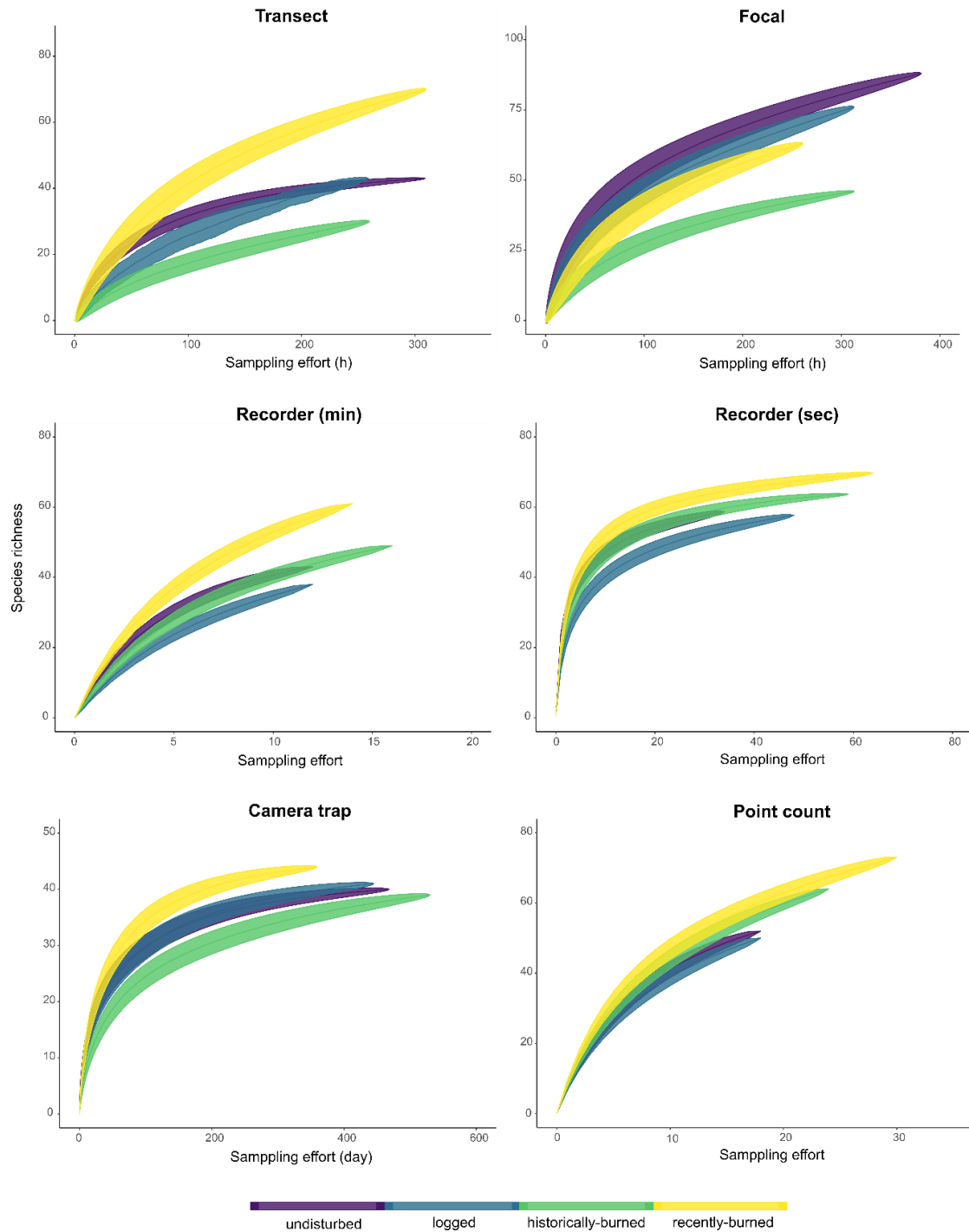


Figure S2.2 Accumulation curves of frugivore richness with increasing sampling effort (hours) in six sampling methods. Each method was sampled across 17 transects distributed in four forest classes (except for passive acoustic recorders sampled in seconds and minutes and point count, both sampled in 14 transects). Species number (dark lines) with the standard error (light lines).

2.9.3 Bird traits used to calculate the functional diversity indices

Functional diversity is directly related to morphological traits [2,3]. Therefore, we selected bird traits that are mainly related to feeding habits, which is directly related to the ecological functions performed by species, such as seed dispersal (Table S2.2) [4–6]. Additionally, these traits are also sensitivity to environmental disturbances [7]. By combining categorical traits extracted we measure the functional diversity through forest classes.

Table S2.2 List of the eight ecological traits used to calculate the functional diversity indices. Measures followed Tobias *et al.* (2022), and body mass Dunning (2008).

Trait	Ecological function
Beak length - Culmen Beak depth Beak width	Trophic traits - reflect the maximum fruit size that can be ingested or handle by the animal
Tarsus length Wing length Tail length Kipp's distance	Locomotory traits - indicators of the movement/dispersal capability (e.g., flight ability), providing information about dispersal limitation and gap-crossing ability and foraging behaviour of bird species
Body mass	Home range, locomotory capacity, and range of fruit size ingestion capacity

Table S2.3 Functional frugivore traits related to frugivory and seed dispersal. Frugivores were species that have fruits as a main dietary item based on Wilman *et al.* (2014)[10]. Frugivore classification adapted from Kissling, Rahbek, & Böhning-Gaese (2007)[11]: Species that rely heavily on fruits were considered obligate frugivores (more than 80% of fruits on its diet), partial frugivores are species that include other major food items in their diet (20 - 79%), whereas opportunistic frugivores are species that only occasionally eat fruits as a supplementary food resource (up to 19%). Measurements were based on Tobias *et al.* (2022) and body mass Dunning (2008)[12]. *Species that we saw eating fruits but were not considered as frugivores according to Wilman *et al.* (2014).

Species	Group	Fruit dependence	Body mass	Tail length	Tarsus length	Wing length	Beak length - Culmen	Beak width	Beak depth	Kipps distance
<i>Aburria kujubi</i>	bird	facultative	1195.82	299.60	66.40	347.80	36.10	9.00	10.90	53.70
<i>Alouatta belzebul</i>	mammal	facultative	6400	-	-	-	-	-	-	-
<i>Amazona amazonica</i>	bird	obligate	370	99.20	21.40	202.20	37.10	18.40	29.10	56.90
<i>Amazona farinosa</i>	bird	facultative	625.99	135.00	26.60	244.90	42.30	20.50	35.40	68.70
<i>Amazona ochrocephala</i>	bird	facultative	476.94	116.50	22.00	212.90	38.30	19.70	32.90	60.80
<i>Ara chloropterus</i>	bird	facultative	1214	486.40	34.30	402.10	76.70	35.20	75.10	167.40
<i>Ara macao</i>	bird	facultative	1015	554.50	31.60	393.70	67.20	31.80	63.50	127.50
<i>Ara severus</i>	bird	facultative	343	242.60	20.70	239.40	39.70	20.50	36.90	86.30
<i>Aramides cajaneus</i>	bird	opportunistic	397	62.80	63.00	178.70	51.30	5.30	11.10	20.80
<i>Arremon taciturnus</i>	bird	facultative	24.8	61.30	23.80	72.00	14.60	5.50	7.30	7.90
<i>Ateles marginatus</i>	mammal	facultative	5999.98	-	-	-	-	-	-	-
<i>Attila cinnamomeus</i>	bird	facultative	38.8	81.20	22.70	87.20	22.70	6.80	6.20	7.80
<i>Attila spadiceus</i>	bird	opportunistic	39.1	67.80	24.90	85.60	22.30	7.30	6.50	12.30
<i>Baryphthengus martii</i>	bird	facultative	165.02	250.80	32.60	150.70	49.30	11.70	14.00	24.30
<i>Brotogeris chrysoptera</i>	bird	obligate	54.5	57.40	11.30	106.60	23.00	9.60	14.30	40.70

<i>Brotogeris versicolurus</i>	bird	facultative	71.53	76.20	11.80	114.00	21.80	9.40	14.50	44.70
<i>Cacicus cela</i>	bird	facultative	85.45	97.80	29.80	145.30	33.70	7.90	11.80	39.50
<i>Cacicus haemorrhous</i>	bird	facultative	83.71	101.10	29.80	161.80	34.00	8.50	11.40	41.20
<i>Caluromys philander</i>	mammal	facultative	229.25	-	-	-	-	-	-	-
<i>Camptostoma obsoletum</i>	bird	facultative	8.1	40.90	13.90	52.30	9.80	3.20	3.10	8.70
<i>Campylorhynchus turdinus</i>	bird	facultative	32.6	86.60	26.70	85.40	25.10	4.10	4.90	11.10
<i>Cebus apella</i>	mammal	facultative	2500	-	-	-	-	-	-	-
<i>Celeus elegans</i>	bird	facultative	134.97	99.90	23.70	161.30	33.00	8.90	8.40	28.80
<i>Celeus flavus</i>	bird	opportunistic	147.33	91.00	25.80	140.20	28.50	8.30	8.90	26.40
<i>Celeus grammicus</i>	bird	facultative	64.5	71.00	20.60	122.80	24.80	6.90	6.40	27.70
<i>Ceratopipra rubrocapilla</i>	bird	obligate	12	31.40	12.60	61.20	10.40	3.80	4.10	11.50
<i>Cerdocyon thous</i>	mammal	opportunistic	5239.98	-	-	-	-	-	-	-
<i>Chiropotes albinasus</i>	mammal	facultative	2900.01	-	-	-	-	-	-	-
<i>Chiroxiphia pareola</i>	bird	facultative	16.84	34.40	17.80	69.40	11.40	4.40	4.90	8.20
<i>Chlorophanes spiza</i>	bird	facultative	19	48.20	18.90	68.30	15.90	4.50	4.60	16.70
<i>Coereba flaveola*</i>	bird	opportunistic	10.0	34.10	16.90	54.60	13.20	3.60	3.90	11.00
<i>Columbina passerina</i>	bird	facultative	35.36	59.60	15.20	81.60	13.90	2.50	3.20	21.60
<i>Columbina talpacoti</i>	bird	opportunistic	46.0	65.80	16.40	86.80	14.20	3.10	3.60	17.70
<i>Cotinga cayana</i>	bird	obligate	61.8	64.00	20.30	106.20	16.50	5.50	4.90	23.10
<i>Cotinga cotinga</i>	bird	obligate	54	78.30	20.60	110.60	21.60	6.20	5.00	22.40
<i>Crypturellus cinereus</i>	bird	obligate	506.63	55.90	49.80	162.40	31.00	5.20	5.40	30.10
<i>Crypturellus soui</i>	bird	facultative	216.16	47.90	36.40	127.50	24.20	4.20	3.90	32.90
<i>Crypturellus strigulosus</i>	bird	facultative	430.58	47.90	46.40	160.90	32.30	5.30	5.30	30.10
<i>Crypturellus variegatus</i>	bird	obligate	378	44.60	41.10	155.40	33.60	5.30	5.00	50.10
<i>Cuniculus paca</i>	mammal	facultative	8172.55	-	-	-	-	-	-	-
<i>Cyanerpes caeruleus</i>	bird	facultative	12	32.10	13.80	56.70	19.50	3.40	3.30	14.40
<i>Cyanerpes cyaneus</i>	bird	facultative	14	34.80	13.70	60.90	19.40	3.80	3.60	15.70
<i>Cyanocompsa cyanoides</i>	bird	facultative	32.5	66.80	21.10	79.60	19.60	10.20	13.90	10.80
<i>Cyanoloxia rothschildii</i>	bird	facultative	32.5	68.10	19.50	77.60	19.10	9.30	12.30	11.80

<i>Cymbilaimus lineatus</i>	bird	opportunistic	35.8	71.50	25.80	75.80	24.70	8.50	8.90	7.70
<i>Cyphorhinus arada</i>	bird	facultative	20.9	39.00	24.00	64.40	17.70	3.60	5.00	6.50
<i>Dacnis cayana</i>	bird	facultative	13	43.90	15.50	61.80	13.70	3.70	4.20	15.50
<i>Dacnis lineata</i>	bird	obligate	11	40.80	14.10	59.50	12.90	3.40	3.50	15.30
<i>Daptorius ater</i>	bird	opportunistic	351.75	199.40	48.30	310.70	33.10	12.00	15.00	98.50
<i>Dasyprocta leporina</i>	mammal	facultative	3020.02	-	-	-	-	-	-	-
<i>Dendrexetastes rufigula</i>	bird	opportunistic	69.6	104.00	23.60	105.20	33.70	8.50	9.20	15.50
<i>Deroptus accipitrinus</i>	bird	facultative	246	144.00	19.20	192.70	37.00	20.40	33.10	65.70
<i>Didelphis marsupialis</i> *	mammal	opportunistic	1091.16	-	-	-	-	-	-	-
<i>Dryocopus lineatus</i>	bird	opportunistic	183.19	122.00	28.60	184.70	41.30	11.00	10.20	41.00
<i>Eira barbara</i>	mammal	opportunistic	3910.03	-	-	-	-	-	-	-
<i>Elaenia flavogaster</i>	bird	facultative	24.8	70.60	21.40	77.40	12.70	5.00	4.00	12.70
<i>Empidonomus varius</i>	bird	facultative	27.1	80.60	15.30	96.80	17.50	6.30	5.50	23.50
<i>Euphonia chlorotica</i>	bird	obligate	11	32.90	12.90	56.70	9.20	4.10	4.00	13.70
<i>Euphonia minuta</i>	bird	facultative	10	27.70	12.40	51.40	10.60	4.10	3.60	11.80
<i>Euphonia rufiventris</i>	bird	obligate	14	34.10	15.50	58.50	12.00	4.70	4.90	12.10
<i>Euphonia violacea</i>	bird	obligate	15	33.20	13.90	57.90	10.00	4.80	5.20	16.20
<i>Fropus passerinus</i>	bird	facultative	23	37.70	9.80	79.50	15.90	8.30	12.80	31.90
<i>Formicarius analis</i>	bird	opportunistic	62.19	56.80	32.40	89.30	21.80	5.60	6.00	14.80
<i>Geotrygon montana</i>	bird	facultative	133.86	76.30	26.90	136.50	19.50	3.50	4.40	36.70
<i>Gymnoderus foetidus</i>	bird	obligate	275.49	121.70	31.90	201.40	29.30	9.50	8.80	42.10
<i>Habia rubica</i>	bird	facultative	32.46	84.00	23.70	92.50	18.10	6.90	8.30	15.90
<i>Hemithraupis guira</i>	bird	opportunistic	103.1	52.20	16.00	63.50	13.50	4.10	4.80	13.70
<i>Herpsilochmus rufimarginatus</i>	bird	opportunistic	12	46.70	18.10	48.30	14.90	3.70	4.00	3.70
<i>Hylexetastes uniformis</i> *	bird	opportunistic	10.58	112.60	32.00	126.00	40.70	9.20	11.20	17.80
<i>Icterus cayanensis</i> *	bird	opportunistic	35.4	97.40	23.20	98.60	23.20	4.30	5.80	15.30
<i>Iodopleura isabellae</i>	bird	facultative	20	37.20	13.70	74.20	11.50	5.20	4.10	19.40
<i>Lamprospiza melanoleuca</i>	bird	facultative	34	64.50	21.00	92.70	19.10	6.60	8.30	21.50
<i>Lanio cristatus</i>	bird	facultative	18.8	70.40	18.20	76.20	15.90	5.60	6.90	14.20

<i>Lanio luctuosus</i>	bird	facultative	13	54.00	17.30	62.10	14.00	4.90	5.50	10.80
<i>Lanio surinamus</i>	bird	facultative	19	70.10	18.00	79.90	16.40	5.30	5.50	16.30
<i>Lanio versicolor</i>	bird	facultative	17	67.60	15.30	76.70	15.20	4.90	5.40	15.50
<i>Laniocera hypopyrra</i>	bird	facultative	51	84.90	20.40	105.50	21.80	6.10	6.20	24.70
<i>Lathrotriccus euleri*</i>	bird	opportunistic	11.3	48.50	14.50	62.20	14.40	5.30	3.80	12.60
<i>Legatus leucophaeus</i>	bird	facultative	22.2	55.20	15.10	78.50	13.00	6.30	4.60	20.10
<i>Lepidothrix iris</i>	bird	obligate	8	27.00	13.60	51.70	11.20	4.60	4.20	9.90
<i>Leptotila rufaxilla</i>	bird	opportunistic	157	94.30	27.30	135.50	20.30	3.40	4.50	32.90
<i>Leptotila verreauxi</i>	bird	facultative	146.88	102.10	27.70	136.70	19.50	3.60	4.00	29.80
<i>Lipaugus vociferans</i>	bird	facultative	75.42	110.20	21.40	123.10	26.90	8.00	7.30	20.90
<i>Makalata didelphoides</i>	mammal	facultative	398.66	-	-	-	-	-	-	-
<i>Manacus manacus</i>	bird	obligate	16.7	32.80	20.90	52.20	11.50	4.40	4.20	8.40
<i>Marmosa demerarae</i>	mammal	facultative	75.75	-	-	-	-	-	-	-
<i>Marmosops sp</i>	mammal	facultative	33.91	-	-	-	-	-	-	-
<i>Mazama americana*</i>	mammal	opportunistic	227990.8	-	-	-	-	-	-	-
<i>Mazama nemorivaga</i>	mammal	facultative	16633.17	-	-	-	-	-	-	-
<i>Megarynychus pitangua</i>	bird	opportunistic	69.91	85.80	19.20	113.50	33.70	13.90	10.40	26.60
<i>Melanerpes cruentatus</i>	bird	facultative	58.1	56.10	18.60	113.80	26.30	6.70	6.60	31.70
<i>Mesomys sp</i>	mammal	facultative	129.4625	-	-	-	-	-	-	-
<i>Metachirus nudicaudatus</i>	mammal	facultative	375	-	-	-	-	-	-	-
<i>Mico argentatus</i>	mammal	facultative	440	-	-	-	-	-	-	-
<i>Milvago chimachima</i>	bird	opportunistic	315.21	198.40	49.40	285.90	30.50	11.30	14.50	85.50
<i>Mionectes macconnelli</i>	bird	facultative	13.5	49.80	16.00	60.70	13.70	4.10	3.40	10.20
<i>Mionectes oleagineus</i>	bird	obligate	11.17	48.20	16.00	60.50	11.80	4.20	3.40	10.50
<i>Mitu tuberosum</i>	bird	facultative	2769.46	329.50	109.60	385.40	59.70	16.40	42.70	39.10
<i>Momotus momota</i>	bird	facultative	114.96	253.90	28.40	142.30	42.50	9.70	12.60	26.40
<i>Monasa morphoeus</i>	bird	opportunistic	87.9	114.30	19.20	125.50	37.00	9.10	11.20	27.60
<i>Myiarchus tuberculifer</i>	bird	opportunistic	17.7	76.50	20.10	80.40	21.10	7.10	5.20	15.50
<i>Myiodynastes maculatus</i>	bird	facultative	43.2	85.50	19.60	106.90	26.30	10.60	8.40	22.30

<i>Myiopagis gaimardii</i>	bird	facultative	12.02	52.80	17.80	57.30	11.30	3.90	3.20	10.30
<i>Myiornis ecaudatus*</i>	bird	opportunistic	5.3	16.60	11.50	32.00	10.20	3.10	3.00	4.70
<i>Myiozetetes cayanensis</i>	bird	facultative	25.9	71.40	20.40	84.10	14.40	5.40	4.60	12.80
<i>Nasua nasua</i>	mammal	facultative	3793.85	-	-	-	-	-	-	-
<i>Odontophorus gujanensis</i>	bird	facultative	314.06	71.30	37.20	143.40	19.70	7.90	11.50	18.80
<i>Ornithion inerme*</i>	bird	opportunistic	7.0	31.60	12.80	43.70	9.60	3.10	3.10	8.10
<i>Ortalis motmot</i>	bird	obligate	520	237.30	61.50	206.80	30.20	9.90	12.10	31.70
<i>Pachyramphus castaneus</i>	bird	opportunistic	19.5	59.90	18.30	74.10	14.30	6.20	5.10	14.00
<i>Pachyramphus marginatus</i>	bird	facultative	18.4	50.40	18.50	67.70	14.70	6.90	5.20	15.00
<i>Pachyramphus minor</i>	bird	facultative	36.6	65.10	20.90	89.20	19.30	8.40	7.60	18.00
<i>Pachyramphus polychopterus</i>	bird	facultative	20.8	55.70	18.70	72.00	14.90	7.00	5.70	16.40
<i>Pachyramphus rufus</i>	bird	facultative	18.8	48.40	17.50	67.60	14.60	6.60	5.40	14.20
<i>Parkerthraustes humeralis</i>	bird	obligate	37	71.50	20.90	83.90	19.70	8.20	10.00	19.80
<i>Patagioenas cayennensis</i>	bird	facultative	229	112.70	23.40	180.30	24.50	4.60	5.50	62.80
<i>Patagioenas plumbea</i>	bird	facultative	178.77	141.60	23.10	177.80	23.10	4.30	5.10	61.90
<i>Patagioenas speciosa</i>	bird	obligate	258.47	98.30	23.70	184.70	24.50	4.80	6.00	65.50
<i>Patagioenas subvinacea</i>	bird	obligate	162.48	114.40	20.80	156.30	18.80	3.80	4.10	53.60
<i>Pecari tajacu</i>	mammal	opportunistic	21266.69	-	-	-	-	-	-	-
<i>Penelope pileata</i>	bird	obligate	1249.79	358.30	85.50	322.00	40.70	9.60	11.80	31.00
<i>Penelope supercilialis</i>	bird	obligate	894.99	286.80	71.80	248.60	34.80	9.90	11.00	34.10
<i>Philander opossum</i>	mammal	opportunistic	585.5	-	-	-	-	-	-	-
<i>Phoenicircus carnifex</i>	bird	obligate	82.87	85.80	25.20	101.10	19.90	5.90	6.40	9.30
<i>Pionites leucogaster</i>	bird	facultative	155	69.50	16.90	138.30	28.00	13.60	24.90	44.40
<i>Pionus fuscus</i>	bird	obligate	206	64.80	18.10	164.00	31.20	14.50	24.40	53.20
<i>Pionus menstruus</i>	bird	facultative	251	75.00	16.10	178.50	26.90	14.60	23.60	53.10
<i>Piprites chloris</i>	bird	opportunistic	16	50.30	16.80	66.20	11.70	4.20	4.70	16.70
<i>Pitangus sulphuratus</i>	bird	facultative	62.85	84.80	25.80	111.90	29.30	10.10	9.10	20.60
<i>Plecturocebus moloch</i>	mammal	facultative	854.73	-	-	-	-	-	-	-
<i>Potos flavus</i>	mammal	obligate	3000	-	-	-	-	-	-	-

<i>Proechimys sp</i>	mammal	facultative	293.9532	-	-	-	-	-	-	-
<i>Psarocolius bifasciatus</i>	bird	facultative	335.7	165.50	50.60	231.70	64.10	11.50	16.80	52.80
<i>Psarocolius decumanus</i>	bird	facultative	286.95	170.30	46.50	198.60	51.80	11.20	17.80	49.10
<i>Psarocolius viridis</i>	bird	facultative	206.3	152.80	50.30	219.70	57.40	10.20	15.10	51.70
<i>Psittacara leucophthalmus</i>	bird	facultative	158.0	145.60	15.40	172.30	25.70	16.50	29.70	71.30
<i>Psophia dextralis</i>	bird	facultative	1071	115.90	118.70	285.50	37.10	8.20	13.30	15.60
<i>Pteroglossus aracari</i>	bird	obligate	250.16	147.00	34.50	143.10	99.10	27.70	32.60	22.40
<i>Pteroglossus bitorquatus</i>	bird	obligate	142	123.20	29.50	117.50	78.80	21.00	27.90	21.70
<i>Pteroglossus inscriptus</i>	bird	obligate	125.82	129.40	29.10	119.70	83.10	21.30	27.30	21.40
<i>Pyrilia vulturina</i>	bird	obligate	151.5	68.20	14.90	149.80	25.40	10.30	16.80	52.80
<i>Pyrrhura amazonum</i>	bird	facultative	58.9	94.30	12.80	116.20	17.80	9.50	16.10	47.20
<i>Querula purpurata</i>	bird	facultative	107.35	117.60	24.30	178.20	28.80	12.50	9.70	31.70
<i>Ramphastos tucanus</i>	bird	facultative	659.58	156.80	52.50	237.00	169.10	38.10	51.70	34.70
<i>Ramphastos vitellinus</i>	bird	facultative	360.36	157.10	46.00	195.70	121.00	31.40	41.20	25.50
<i>Ramphocelus carbo</i>	bird	facultative	25.92	79.90	21.60	78.10	18.30	7.40	7.90	12.40
<i>Ramphotrigon ruficauda</i>	bird	facultative	18.4	70.90	16.30	75.40	17.10	6.50	4.30	11.00
<i>Rhytipterna simplex</i>	bird	facultative	31.8	95.30	21.30	96.80	22.70	7.10	6.40	16.00
<i>Saimiri sciureus</i>	mammal	facultative	743.24	-	-	-	-	-	-	-
<i>Saltator coerulescens</i>	bird	opportunistic	54.9	95.50	26.80	100.70	22.30	8.80	11.00	14.60
<i>Saltator grossus</i>	bird	facultative	44.2	87.40	23.70	96.10	21.40	10.30	13.70	17.90
<i>Saltator maximus</i>	bird	facultative	47.62	88.90	25.30	96.10	20.70	8.90	10.40	16.10
<i>Sapajus apella</i>	mammal	facultative	2500	-	-	-	-	-	-	-
<i>Schiffornis turdina</i>	bird	facultative	31.7	67.70	22.10	92.10	17.00	4.90	6.00	14.10
<i>Sciurus aestuans</i>	mammal	facultative	185	-	-	-	-	-	-	-
<i>Selenidera gouldii</i>	bird	obligate	180.9	106.80	33.00	127.20	62.60	20.10	24.10	23.50
<i>Sublegatus obscurior</i>	bird	opportunistic	16	62.00	16.90	65.60	11.70	4.50	3.00	11.00
<i>Tachyphonus luctuosus</i>	bird	facultative	13	54.00	17.30	62.10	14.00	4.90	5.50	10.80
<i>Tangara mexicana</i>	bird	facultative	20.5	49.60	16.40	70.20	13.00	4.30	5.00	16.20
<i>Tangara nigrocincta</i>	bird	obligate	17	47.50	15.30	68.30	12.30	4.70	4.70	14.60

<i>Tangara punctata</i>	bird	facultative	15	45.70	17.10	61.90	12.30	4.10	4.40	12.40
<i>Tangara varia</i>	bird	facultative	10	39.60	14.90	55.40	10.50	3.70	3.80	11.50
<i>Tangara velia</i>	bird	obligate	21	51.20	16.20	72.30	14.40	3.80	5.00	16.90
<i>Tapirus terrestris</i> *	mammal	opportunistic	207500.9	-	-	-	-	-	-	-
<i>Thraupis episcopus</i>	bird	facultative	35	64.00	22.30	87.30	14.20	6.40	6.70	20.70
<i>Thraupis palmarum</i>	bird	facultative	39	70.40	20.70	92.50	15.00	5.90	6.50	20.40
<i>Tinamus guttatus</i>	bird	facultative	686.18	75.60	57.60	195.40	33.10	5.00	5.30	50.90
<i>Tinamus major</i>	bird	facultative	1026.21	83.20	64.40	241.00	38.50	5.20	5.90	51.30
<i>Tinamus tao</i>	bird	facultative	1600.1	125.60	79.70	278.70	45.50	6.50	6.80	47.30
<i>Tityra cayana</i>	bird	obligate	68.1	71.00	24.50	116.70	28.20	11.40	10.60	31.00
<i>Tityra semifasciata</i>	bird	facultative	79.3	71.70	25.60	120.50	28.00	10.40	10.70	30.70
<i>Tolmomyias assimilis</i>	bird	opportunistic	17	50.30	17.50	63.10	15.90	5.70	3.80	10.10
<i>Tolmomyias flaviventris</i>	bird	facultative	12.2	51.20	16.30	59.40	13.30	5.10	3.90	8.80
<i>Touit huetii</i>	bird	obligate	60	50.40	9.90	111.20	18.20	9.20	13.80	46.10
<i>Trogon collaris</i>	bird	facultative	65.43	132.70	13.40	121.20	20.30	8.20	9.10	46.30
<i>Trogon curucui</i>	bird	facultative	54	129.00	12.40	122.50	19.70	8.80	9.40	44.30
<i>Trogon melanurus</i>	bird	facultative	114	150.10	14.00	153.50	24.80	10.20	12.00	54.10
<i>Trogon ramonianus</i>	bird	facultative	43.4	122.70	11.70	115.50	19.40	10.40	8.60	42.00
<i>Trogon rufus</i>	bird	facultative	53.8	130.90	13.10	113.10	19.90	8.90	9.80	42.80
<i>Trogon viridis</i>	bird	facultative	89.69	158.40	14.20	146.10	25.20	10.10	11.70	50.60
<i>Tunchiornis ochraceiceps</i>	bird	facultative	11.6	43.90	16.80	57.10	15.60	3.60	4.20	7.50
<i>Turdus albicollis</i>	bird	facultative	54	90.00	30.00	110.80	23.50	4.60	6.00	23.60
<i>Turdus fumigatus</i>	bird	facultative	75.7	90.80	31.00	113.50	24.20	5.00	6.70	23.90
<i>Turdus leucomelas</i>	bird	facultative	69.1	92.10	32.40	111.60	22.20	5.10	6.00	24.80
<i>Tyranneutes stolzmanni</i>	bird	obligate	7.2	23.20	11.50	47.20	10.30	3.70	3.10	13.60
<i>Tyrannulus_ latus</i>	bird	facultative	7	40.70	13.70	48.20	8.30	3.20	3.10	8.70
<i>Tyrannus melancholicus</i> *	bird	opportunistic	37.4	91.90	18.70	108.80	23.50	9.70	7.40	25.50
<i>Veniliornis affinis</i>	bird	facultative	34.83	62.50	16.20	91.90	22.10	5.60	6.70	18.90
<i>Vireo chivi</i>	bird	facultative	16.1	52.10	18.30	68.00	14.00	4.40	4.30	14.10

<i>Xipholena lamellipennis</i>	bird	obligate	53.8	74.20	20.90	109.80	19.80	6.10	5.40	18.70
<i>Zimmerius acer</i>	bird	facultative	7.13	40.90	14.70	50.60	9.70	2.90	2.90	8.90

Table S2.4 Results of one-way variance test (ANOVA) testing the effects of human-forest disturbances on frugivore species in the Amazon Forest. Richness was based on rarefaction values (see detail for method in the mains text in 'Sampling frugivorous species section'). Frugivore classification: obligate frugivores – species with more than 80% of fruits on its diet; partial frugivores - fruits items range 20 - 79%; and opportunistic frugivores - eat fruits as a supplementary food resource (up to 19%) [11].

Models	Df	Sum Sq	Mean Sq	F-value	P-value
Overall frugivores richness ~ forest class	3	744.9	248.3	1.78	0.19
Focal ~ forest class	3	123.0	41.01	3.32	0.05
Transect ~ forest class	3	112.64	37.55	7.11	<0.01
Recorders - min ~ forest class	3	10.94	3.64	2.34	0.13
Recorders - sec ~ forest class	3	217.0	72.35	3.35	0.06
Point count ~ forest class	3	35.72	11.9	1.38	0.30
Camera trap ~ forest class	3	12.12	4.04	1.74	0.20
Obligate frugivores ~ forest class	3	212.6	70.85	5.21	0.01
Partial frugivores ~ forest class	3	88.92	29.64	1.682	0.22
Opportunistic frugivores ~ forest class	3	75.79	25.26	2.61	0.10

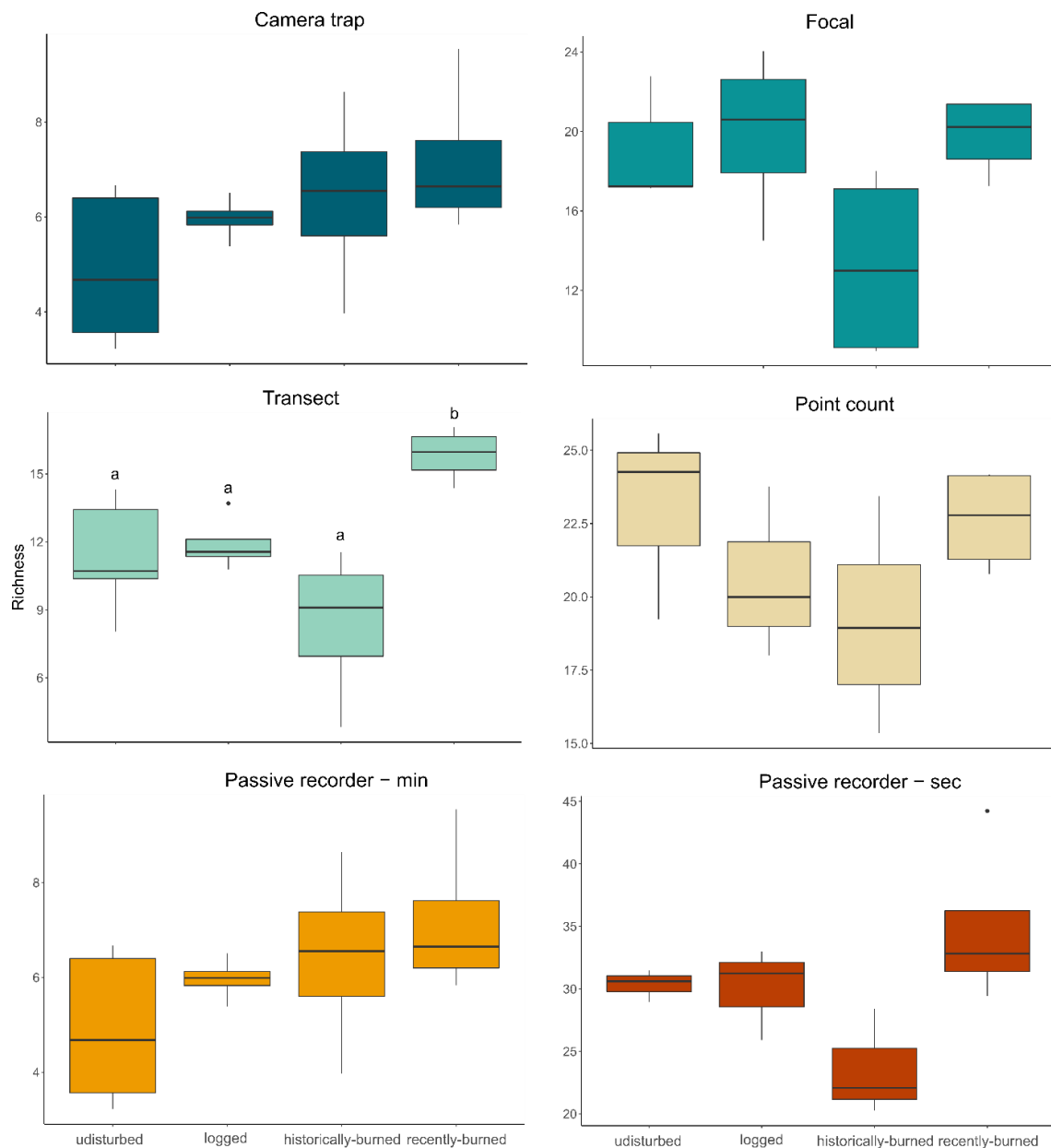


Figure S2.3 Box plots comparing frugivore species richness between forest classes according to each sampling method. For the transect method, recently-burned forests had a higher number of species in comparison to other forest classes. Species richness was rarefied in order to control for differences in sampling effort among forest classes. Different letters represent statistical differences among forest classes at $P < 0.05$. Non-significant pairwise differences between forest classes are indicated by the same letter (according to Tukey pairwise test). Black dots are potential outliers and lines inside box plots represent median values.

Table S2.5 Pairwise comparison between forest classes on the richness of obligate frugivores based on Tukey test.

Forest class	Differences	Lower	Upper	<i>P</i>-value
undisturbed - logged	-1.09	-8.35	6.17	0.97
undisturbed - historically-burned	8.18	0.92	15.44	0.03
undisturbed - recently-burned	2.95	-4.31	10.21	0.64
logged - historically-burned	9.28	1.62	16.93	0.02
logged - recently-burned	-4.05	-11.70	3.61	0.44
recently-burned - historically-burned	5.23	-2.42	12.88	0.24

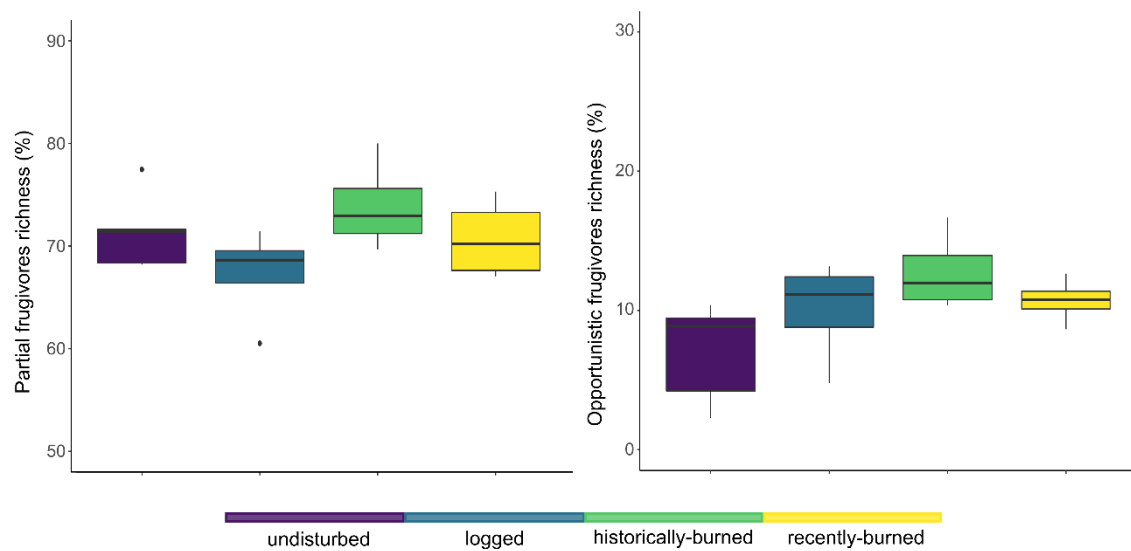


Figure S2.4 Effects of logging and forest fires on the richness of partial (20 - 79% of the diet composed of fruits) and opportunistic (up to 19%) frugivore species among forest classes. We used the proportion of obligate frugivores in each transect to assess the impact of forest disturbances. Black dots are potential outliers and lines inside box plots represent median values.

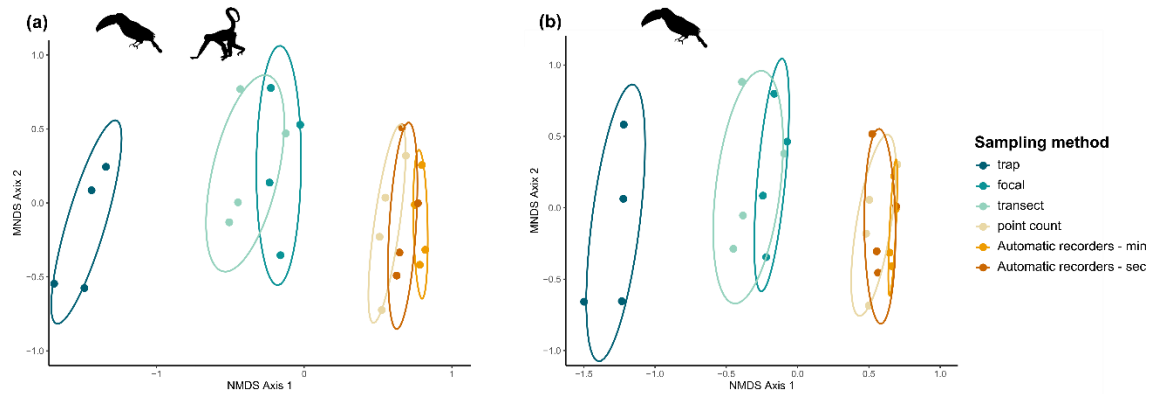


Figure S2.5 NMDS ordination of frugivore species among six distinct sampling methods: (a) birds and mammals included, (b) only birds. Ellipses represent different forest classes. Methods correspond to focal plants, camera traps, passive acoustic recorders sampled in intervals of seconds and minutes, and points count.

Table S2.6 Pairwise comparison based on Wilcox test between forest classes and the median of body mass values (g).

Forest class	Statistic	<i>P</i>-adj
undisturbed ~ historically-burned	20	0.01
undisturbed ~ logged	15	0.28
undisturbed ~recently-burned	17	0.11
logged ~ historically-burned	0	0.02
logged ~ recently-burned	7	0.88
historically-burned ~ recently-burned	0	0.02

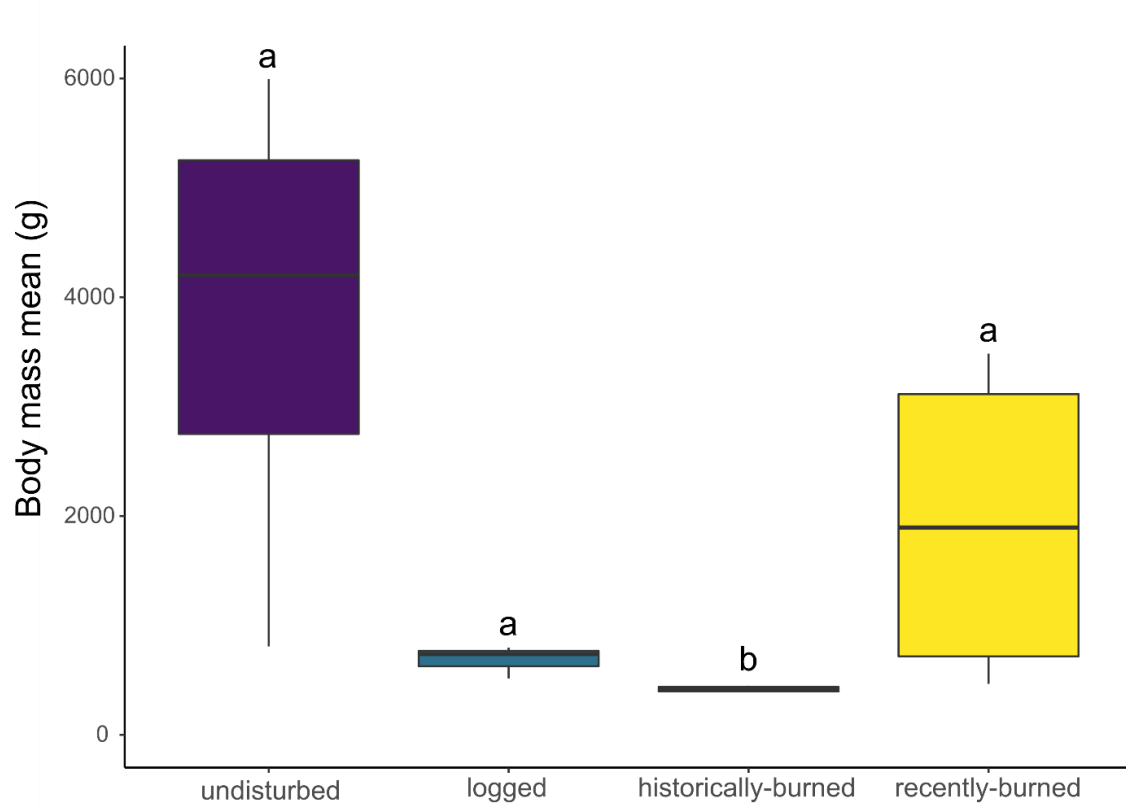


Figure S2.6 Effects of logging and forest fires on the body mass of frugivores (g). Different letters represent statistical differences among forest classes at $P < 0.05$. Non-significant pairwise differences between forest classes are indicated by the same letter (according to Wilcox pairwise test). Black dots are potential outliers and lines inside box plots represent median values.

Table S2.7 Results of one-way variance test (ANOVA) for the effects of human-forest disturbances on Functional Diversity indexes in the Amazonian forests. FDis corresponds to functional dispersion (i.e., meaning the efficiency in using resources), while SESFRic corresponds to standardised values for functional richness (i.e., represents the niche space occupied by the community).

Models	Df	Sum Sq	Mean Sq	F-value	P-value
FDis ~ forest class	3	0.003	0.001	3.833	0.03*
FDis null models ~ forest class	3	0.001	0.0001	0.192	0.90
FRic ~ forest class	3	0.0000032	0.00000107	2.059	0.15
SESFRic ~ forest class	3	5368	1789.2	3.833	0.03**

Table S2.8 Pairwise comparisons between forest classes of the functional dispersion (FDis) value indexes based on Tukey tests.

Forest class	Differences	Lower	Upper	<i>P</i> -value
undisturbed - logged	-0.016	-0.049	0.018	0.526
undisturbed - historically-burned	-0.039	-0.072	-0.005	0.022
undisturbed - recently-burned	-0.014	-0.048	0.019	0.620
logged - historically-burned	0.023	-0.013	0.058	0.281
logged - recently-burned	0.002	-0.033	0.037	0.999
recently-burned - historically-burned	0.025	-0.011	0.060	0.225

Table S2.9 Pairwise comparisons between forest classes of SESFRic values based on Tukey tests. SESFRic correspond to standardised values for functional richness index.

Forest class	Differences	Lower	Upper	<i>P</i> -value
undisturbed - logged	-20.16	-62.70	22.37	0.52
undisturbed - historically-burned	-48.94	-91.48	-6.40	0.02
undisturbed - recently-burned	-17.82	-60.36	24.71	0.62
logged - historically-burned	28.78	-16.05	73.62	0.28
logged - recently-burned	2.33	-42.50	47.17	0.99
recently-burned - historically-burned	31.12	-13.72	75.96	0.22

2.9.4 References

1. Oksanen J *et al.* 2015 Vegan: Community Ecology Package R Package. version 2.3-1.
2. Petchey OL, Gaston KJ. 2002 Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411. (doi:10.1046/j.1461-0248.2002.00339.x)
3. Villéger S, Mason NWH, Mouillot D. 2008 New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301. (doi:10.1890/07-1206.1)
4. Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, Barlow J, Tobias JA. 2016 Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. B Biol. Sci.* **283**, 20161289. (doi:10.1098/rspb.2016.1289)
5. Dehling DM, Jordano P, Schaefer HM, Böhning-Gaese K, Schleuning M. 2016 Morphology predicts species' functional roles and their degree of specialization in plant–Frugivore interactions. *Proc. R. Soc. B Biol. Sci.* **283**. (doi:10.1098/rspb.2015.2444)
6. Pigot AL, Bregman T, Sheard C, Daly B, Etienne RS, Tobias JA. 2016 Quantifying species contributions to ecosystem processes: A global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Proc. R. Soc. B Biol. Sci.* **283**. (doi:10.1098/rspb.2016.1597)
7. Sekercioglu CH. 2006 Increasing awareness of avian ecological function. *Trends Ecol. Evol.* **21**, 464–471. (doi:10.1016/j.tree.2006.05.007)
8. Tobias JA *et al.* 2022 AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581–597. (doi:10.1111/ele.13898)

9. Dunning JBJ. 2008 *CRC handbook of avian body masses*.
10. Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027. (doi:10.1890/13-1917.1)
11. Kissling WD, Rahbek C, Böhning-Gaese K. 2007 Food plant diversity as broad-scale determinant of avian frugivore richness. *Proc. R. Soc. B Biol. Sci.* **274**, 799–808. (doi:10.1098/rspb.2006.0311)
12. Dunning JBJ. 2008 *Avian Body Masses Second Edition*.

CHAPTER TWO

Fruit-frugivore interactions mediated by fires and logging in Amazonian forests



Fruit-frugivore interactions mediated by fires and logging in Amazonian forests

Liana Chesini Rossi^{1,2}, Carine Emer^{1,3}, Alexander Charles Lees^{2,4}, Erika Berenguer^{5,6}, Jos Barlow⁶, Joice Ferreira^{7,8}, Filipe M. França⁹, Yan Gabriel Ramos¹⁰, Paulo Tavares⁸, Marco Aurélio Pizo¹

¹ Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil

² Division of Biology and Conservation Ecology, School of Science and the Environment, Manchester Metropolitan University, Manchester, UK

³ Research Department, Rio de Janeiro Botanical Garden, RJ, Brazil

⁴ Cornell Lab of Ornithology, Cornell University, Ithaca, USA

⁵ Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

⁶ Lancaster Environment Centre, Lancaster University, Lancaster, UK

⁷ Embrapa Amazônia Oriental, Belém, PA, Brazil

⁸ Programa de Pós-Graduação em Ecologia (PPGECO) e Programa de Pós-Graduação em Ciências Ambientais (PPGCA), Universidade Federal do Pará, Belém, PA, Brazil

⁹ School of Biological Sciences, University of Bristol, Bristol, UK

¹⁰ Instituto Espaço Silvestre, Itajaí, SC, Brazil

Correspondent author: lianachesinibio@gmail.com

3.1 Abstract

Besides great advances in the last decades, our knowledge about frugivory interactions in tropical forests is still limited to a few locations. This is an important knowledge gap, as frugivory interactions define important ecological processes related to forest resilience to multiple anthropogenic disturbances. We assessed the consequences of human disturbances on fruit-frugivore interactions by assessing the effects of selective logging and fires on frugivory networks in Amazonian forests. Fruit consumption by birds and mammals were monitored throughout a year in 17 forest transects within a mosaic landscape, including: five undisturbed, four selective logged (≥ 30 years prior sampling), four historically-burned (burned more than 18 years and logged ≥ 30 years prior sampling) and four recently-burned forests (burned three years and logged ≥ 30 years before the study). We tested how such forest disturbances affect the structural properties of networks as well as the variation of beta-diversity components at the landscape level. We found a significantly smaller number of species and unique interactions in historically-burned in comparison to undisturbed forests. In contrast, there were no effects of fire and logging on network components; all networks had high modularity and specialisation when compared to null models, suggesting the frugivory network structure can be resilient to the human disturbances assessed. Furthermore, beta-diversity remained high in all forest classes and was explained by the high turnover of species and interactions. In turn, historically-burned had almost entirely distinct interaction composition from unburned forests. Our study provides empirical evidence of the effects of historic fires on frugivory interaction in Amazonian forests, in the long-term, fires associated with logging are likely to lead to significant changes in fruit-frugivore interactions influencing the future of forest dynamics.

Key words: Beta-diversity, frugivory networks, interaction composition, logged forests, network metrics, seed dispersal, seed predation, understorey fires, tropical forests

3.2 Introduction

Tropical forests are increasingly threatened by human disturbances (Bullock et al. 2020, Matricardi et al. 2020). For instance, forest fires are increasing in frequency due to climate change, extreme climatic events and human-driven forest disturbances (Fonseca et al. 2019, Barlow et al. 2020). Indeed, in comparison to the 1970s, the central-eastern of the Amazonian basin is 1.9C hotter and c. 34% drier during the dry season (Gatti et al. 2021). These changes in climate can exacerbate extreme climatic events (Cai et al. 2014), leading into megafires, as seen in Eastern Amazonia during the 2015-2016 El Niño, when over 1 million hectares of forests burned and killed 2.5 billion trees (Berenguer et al. 2021). Another common threat is selective logging, widespread across 20% of the Brazilian Amazon, mostly illegally exploited (Asner et al. 2009). The combined effects of these stressors have clear and increasingly well-known effects on many aspects of ecosystem condition, including biodiversity, soil, above ground carbon (Nunes et al. 2022).

Beyond assessments of stocks and states, there is growing evidence that tropical forest disturbance also has a major influence on forest functioning and ecosystem processes - including seed dispersal and predation, key functions for forest resilience (Dennis et al. 2007, Boissier et al. 2020). For example, we know that frugivory interaction is likely to be very important in tropical forests, where up to 90% of plant species are dispersed by vertebrates (Howe et al. 1982). Moreover, frugivore communities change after disturbance. Degraded forests, such as burned, limit the occurrence of some birds (Slik and Van Balen 2006, Mestre et al. 2013) and mammals species (Barlow and Peres 2004), which may impact the diversity of these communities (Solar et al. 2015). It is also known that seed size and dispersal mode change after disturbance (Hawes et al. 2020). The elevated tree mortality due to forest fires added to the selective removal of commercial plant species lead to a dominance of plants with low wood density (Berenguer et al. 2018) associated with small fruits and high level of zoochory (Hawes

et al. 2020). Therefore, these changes depict impacts on frugivory interactions patterns with direct consequences to the ecosystem functioning (García et al. 2018).

Despite the advances above, it is not clear how the fruit-frugivore interactions change in logged and burned forests. Understanding the potential threat of these disturbances is important as the loss of frugivory interactions directly impact forest maintenance and regeneration (Archibald et al. 2011, Valiente-Banuet et al. 2015). In this context, ecological networks describing the structural and functional organisation of interactions between frugivores and plants over gradients of habitat modification can shed light on the cascading consequences on ecosystem functioning (Pellissier et al. 2018, Guimarães 2020) and resilience (Schleuning et al. 2015). Changes in the interaction patterns between frugivores and plants can be inferred from changes in the network structure (see Tylianakis and Morris 2017). For instance, the loss of species might reduce the number of partners available for establishing interactions, which might increase connectance (i.e., the number of realised interactions regarding those possible ones), a network property related to community stability (Dunne et al. 2002, Tylianakis et al. 2010). Because specialist species and their interactions are more prone to vanish in human-modified scenarios (e.g., Emer et al. 2020, Menezes et al. 2021) while the generalist ones are more likely to persist, one can expect an increase on nestedness, in which a few generalist species connect the whole network by interacting with subsets of more specialist ones (Almeida-Neto et al. 2008). Nested structures in mutualistic networks tend to have higher functional redundancy and niche overlap among its components (Schleuning et al. 2012) and increasing over a gradient of disturbance which mean that the systems has been dominated by generalist interactions performed by generalist species able to thrive in modified landscapes (Sebastián-González et al. 2015).

Loss of certain groups of interactions that perform specific functions, such as large-bodied frugivores important to disperse large-seeded fruits (Emer et al. 2018, 2020) for long-

distances (Jordano et al. 2007, Donoso et al. 2020) declines the network modularity, which refers to groups of species that interact more strongly with each other than with species from other groups (Newman 2006, Olesen et al. 2007). Additionally, loss of specific groups of interactions also reduce the network specialisation, indicating losing diversity of interactions with dominance of generalists ones (Schleuning et al. 2012). Nonetheless, the spatial distribution of interactions across sites can be analysed with a beta-diversity approach (Poisot et al. 2012). By exploring specific components, such as turnover, beta-diversity has been used to gain insights into how human disturbances alter interactions composition and the implication on network structures (Pellissier et al. 2018). For instance, fires may alter the plant–pollinator interactions beta-diversity, mainly modulated by the spatial turnover of species, which may impact the pollination function, essential to the recovery of plant communities after fire events (Burkle et al. 2022).

By combining the network and beta-diversity components we address how selective logging and forest fires affects frugivory interactions. We studied 17 forest sites distributed across four forest classes, namely: undisturbed (control), logged, historically and recently-burned forests. Given that forest fires had strong impact on animal (Peres et al. 2003, Slik and Van Balen 2006, Moura et al. 2013) and plant assemblages (Barlow et al. 2006, Berenguer et al. 2021), in our first prediction, we expect to record a low number of species and interactions, especially in recently-burned forests, in which networks will be compounded by interactions involving few generalist species (Dugger et al. 2019). Secondly, because recently-burned forests are inhabited mostly by generalist species able to cope with environmental changes, we expect that the remaining generalist interactions will lead to changes in network structure toward higher nestedness and connectedness (Emer et al. 2020). In this scenario, due to the loss of fruit-frugivore interactions diversity we expected a decrease on network modularity and specialisation (Menezes et al. 2021). Furthermore, we expect lower values of beta-diversity and

consistently high turnover of species and interactions in recently-burned forests, which means that the composition of interactions will change due to species replacement caused by fires (Brodie et al. 2015, Gallego-Zamorano et al. 2020). Meanwhile, as logged and historically-burned had almost two decades to recover, we expect greater values of beta-diversity and similar interactions composition to undisturbed forests (Mestre et al. 2013, Solar et al. 2015).

3.3 Methods

3.3.1. Study area and sampling design

Our study was conducted in the central-eastern Brazilian Amazon, comprising three municipalities: Belterra, Mojuí dos Campos and Santarém (Figure 3.1). The study areas comprised *terra firme* forests with canopy height of 30-40 m, and occasional emergent species up to 50 m. Fruit production peaks in the wet season, from December to July (Barlow and Peres 2006). The landscape encompasses several land-use types, including pristine and disturbed forests surrounded by agricultural land uses (Gardner et al. 2013). In 2015 and 2016, the region was affected by an extreme drought resulting from an El Niño event, when over 1 million hectares of forests burned (Withey et al. 2018, Figure 3.1).

Data were collected in 17 forest transects distributed among four forest classes following Gardner et al. (2013): (i) undisturbed forests - pristine forest tracts with no logging or fire effects (n = 5), (ii) logged forests - selective logged forests (n = 4), (iii) historically-burned forests - selective logged and fires equal or more than 18 years ago (n = 4), (iv) recently-burned forests - selective logged, while fires occurred 3 years ago, following the 2015-16 El Niño (n = 4) (Figure 3.1, Table S3.1). For all logged forests, selective logging occurred more than 30 years ago (considering the year of sampling). Logging and fires took place ≥ 18 years prior to surveys were estimated by combination of field assessments and a visual inspection of

satellite images between 1988 and 2010 (Gardner et al. 2013). Each transect was 1000 m long and separated by at least 1.5 km from each other.

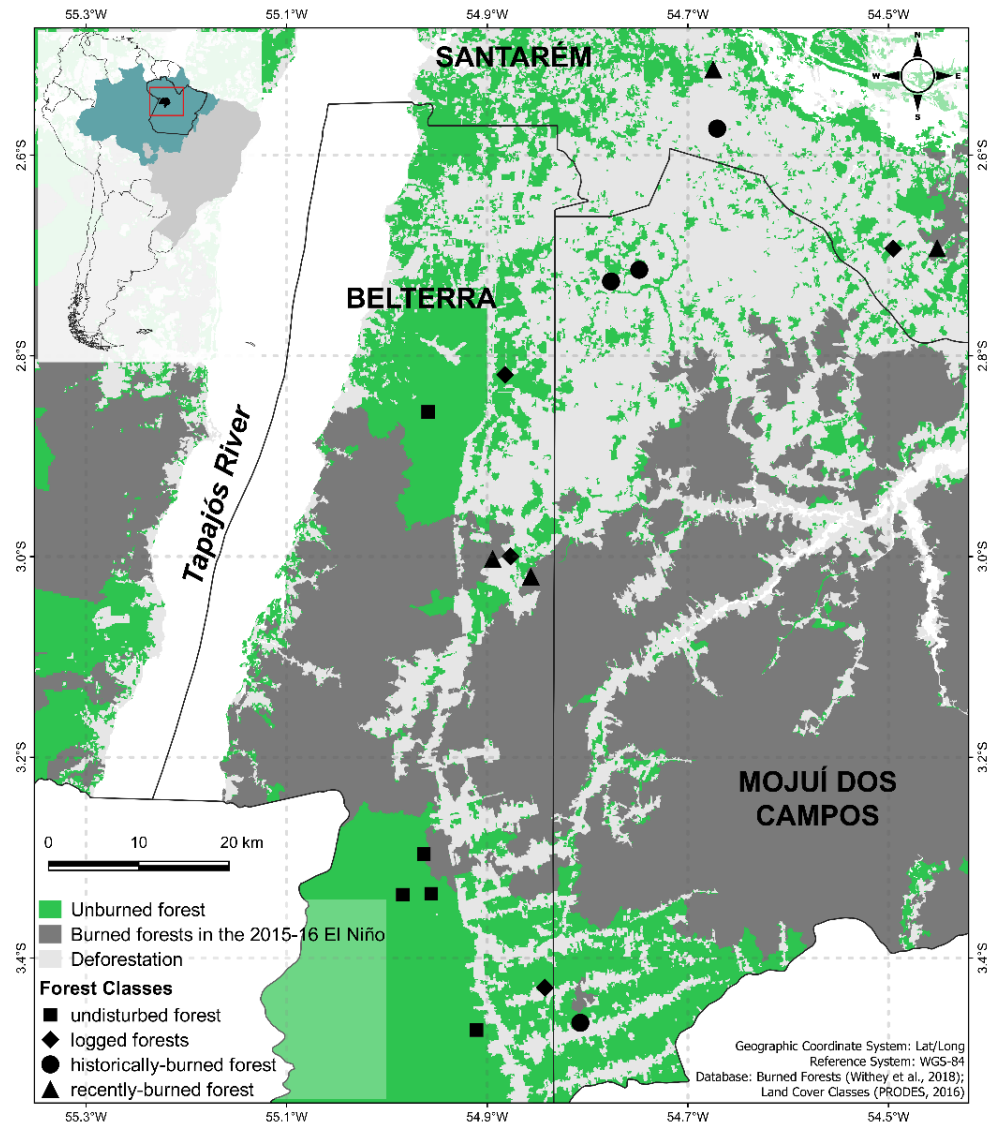


Figure 3.1. Study area. (a) The inset shows the Amazon biome (light green) within Brazil (light grey) and the Santarém region (black). (b) Santarém region. (c) Numbers and points mark the locations of the 17 forest transects sampled in: undisturbed forest (undisturbed); logged forest (selective logged ≥ 30 years before sampling); historically-burned forest (selective logging ≥ 30 years before sampling and burned in the past ≥ 18 years before sampling), and recently-burned forest (selective logging ≥ 30 years before sampling and burned recently (three years before sampling)).

3.3.2. *Fruit-frugivore interactions*

From February 2019 to March 2020, we recorded frugivory interactions involving fleshy-fruited plants and frugivorous birds and non-volant mammals (see Frugivory interactions section in Supporting information). For each interaction, we recorded the plant and frugivore species as well as the number of frugivores of the same species interacting (Pizo and Galetti 2010). Tree species were identified by local parobotanists at the lowest taxonomic level possible.

3.3.3 *Sampling methods*

Because we aimed to maximise the chance of detecting plant-frugivore interactions in our field sites, we used three complementary sampling methods, as follows:

Transects: Frugivory interactions sampled for transect-days = 227, except for 22 transect-days when the observations were made in two transects. Sampling was conducted between 6:00 a.m. and 6:00 p.m., except on rainy days. Observations included plants within 25 m from both sides of the transect. Each transect was sampled at least twice in a month, during 10 months.

Focal: Along each transect, zoochoric plants were chosen based on ripe fruit availability and were observed for a period of 30 to 240-min/day. Focal samplings were taken parallel to each transect - i.e., during transect sampling, if a tree with high ripe fruit densities was seen, we stopped the transects and did focal observation on it. This method increases the chance of detecting interactions between rare species (Pizo and Galetti 2010, Jordano 2016).

Camera trap: Passive camera traps were used to detect frugivory interactions, especially those cryptic or difficult to record, for example involving large terrestrial birds and nocturnal mammals (Rivas-Romero and Soto-Shoender 2015). Three to six camera traps with movement sensors (APEMAN - 16MP with Infrared Night Vision up to 65ft/20m) were used in each transect. We placed cameras in trees with ripe fruit availability and climbing suitability. The

same as for focal samplings, cameras were installed in zoochoric plants when fruits started ripening and removed at the end of the fruiting period, thus sampling effort differed through the transects (see Supplementary material). Cameras were positioned either 30 cm off the ground or about 5–15 m from the ground in the subcanopy, near and facing infructescence or fallen fruits to increase the probability of recording interactions (Zhu et al. 2022). Camera traps were programmed to be active 24-h daily to record 20-second videos with 20-second intervals between recordings. Sampling effort was calculated as the sum of hours in which each camera trap was active. Consecutive videos of the same species were considered independent if more than an hour had passed between recording events (Rivas-Romero and Soto-Shoender 2015, Acevedo-Quintero et al. 2020). When two or more individuals were recorded in a single video, each individual was recorded as a separate event.

3.3.4 Interaction networks

We built a quantitative bipartite network for each transect, in which interaction frequencies (ij) in an adjacency matrix (a) represent the number of pairwise associations (a_{ij}) between an animal (i) and a plant species (j) (Figure 3.2). Then, we estimated the following non-correlated network components ($r < 0.7$):

- (i) number of frugivore species (A);
- (ii) number of plant species (P);
- (iii) network size (S): the total number of species in a network;
- (iv) number of unique pairwise interactions (I): unique combinations of each frugivore and plant species recorded;
- (v) total number of interactions (Nt): the sum of all frugivorous-plant pairwise interactions at each site;

- (vi) Connectance (C): the proportion of realised interactions in relation to the total of possible interactions calculated as $C = N_t / (AP)$, where N_t is the total number of interactions in the network. A represents the number of animal species and P is the number of plant species. High connected networks have connectivity values close to 1;
- (vii) Weighted nestedness ($wNODF$): Estimates the presence of generalist species interacting with a subset of more specialist ones (Ulrich et al. 2009, Almeida-Neto and Ulrich 2011). $wNODF$ is a measure of quantitative nestedness, in which the matrix filling is according to the frequency of interactions; the higher the nestedness, the higher the values towards 1;
- (viii) Modularity: Tested for the occurrence of groups of frugivores and plant species that interact more often among themselves than with species in other groups (or modules, Olesen et al. 2007). More modular networks present values close to 1. To estimate the level of modularity and number of modules in our sample of networks, we used the DIRT_LPA_wb_plu algorithm (Beckett 2016);
- (ix) Specialisation ($H2'$): quantifies the deviation of the observed interactions from those expected given interaction frequencies (measured as species marginal totals); the more exclusive the interactions, the larger is the $H2'$ value, which ranges from 0 for the most generalised networks to 1 for a completely specialised network;

3.3.5 Beta-diversity of interactions

We investigate the effects of fire and logging on the beta diversity of species and interactions (Baselga 2010). We used abundance-based dissimilarity matrices to quantify the pairwise differences on the interaction composition (β_{int}), frugivores (β_{frug}) and plants (β_{plants}) at landscape level (differences among transects without considering forest class) and habitat level (differences within each forest class) (Carstensen et al. 2014, Dehling et al. 2020). We analysed the networks in two steps. First, we measured the species and interaction dissimilarity among

transects in the same forest class to understand how beta-diversity varies within the same type of human disturbance, or with no human interference as the case of the undisturbed forests. Then, to understand the overall species and interactions beta-diversity at the landscape level, we measured the dissimilarity between all pairwise combinations of the 17 frugivory networks.

3.3.6 Analyses

First, we evaluated the sampling effort of interaction networks (Jordano 2016) and estimated the expected interaction number based on the Chao1 estimator (Chao et al. 2014, see Supporting information, Figure S3.1, Table S3.2). Then, we inspected the spatial auto-correlation between transects for frugivores, plants and interactions (Supporting information, Figure S3.2). Further, to test the effects of fire and logging upon network components, we used generalised linear models with Poisson distribution for count data: frugivore species (A), plant species (P), network size (S), number of unique pairwise interactions (I), total number of interactions (Ni), and Gaussian distribution for the other components: connectance, wNODF, H2' specialisation and modularity (Zuur et al. 2009). We used forest classes as the explanatory variable in all models. To control for differences in sampling effort (hours) among forest classes, we calculated the square root of the number of interactions divided by the square root of the network size and included that as a fixed covariate in all models (Schleuning et al. 2012). Connectance and modularity metrics were first logit-transformed to solve the issue of being bounded from zero to one and then log-transformed to solve non-normal distribution (Warton and Hui 2011). GLMs were fitted with the *glm* function in the *lme4* package (Bates et al. 2018). Models with differences in the least-square means (frugivores, size and unique interactions) we tested the pairwise differences among forest classes with *emmeans* function with $\pm$ 95% confidence interval (Lenth et al. 2020). The frugivory interactions in undisturbed forests served as a baseline for comparison to all other models.

To test whether the observed network parameters differ from those expected by chance we contrasted the observed value for each network metric (connectance, wNODF, H2' specialisation and modularity) to those obtained from null models (100 randomizations each) generated with the Patefield and Vaznull algorithms and fitting by z-scores (Dormann et al. 2009). Patefield uses fixed marginal totals while randomising the interactions among species scores (Dormann et al. 2009). In turn, vaznull does not maintain the marginal totals constant but takes into account the interaction frequencies and keeps the same number of qualitative interactions as in the observed matrix - i.e., keeps connectance constant (Vázquez et al. 2007). Both null models constrained network size and were created using the *nullmodel* function in the *bipartite* package (Dormann et al. 2009). Undisturbed forests served as a baseline for comparison to all other models. All analyses were carried out in the R program (R Core Team 2018).

Beta-diversity index was based on Bray–Curtis dissimilarity and partitioned into two components (Baselga 2013). The first component - corresponds to species/interactions turnover, when species or interactions are replaced by others. The second component estimates nestedness and describes the species/interaction loss from one site to the other without any substitution. We quantified beta-diversity in the *betapart* package using *beta.mult.abund* function to compute the overall dissimilarity across all forest classes (Baselga and Orme 2012). Concomitantly, we draw a nonmetric multidimensional scaling (NMDS, two axes) to represent differences in species and interactions composition in landscape and habitat level. We used frequency of interactions and the Bray-Curtis similarity index to perform an ordination of forest classes that was based on their dissimilarities in species and interactions composition. The NMDS ordination was created using the *metaMDS* function in the *vegan* package (Oksanen et al. 2015).

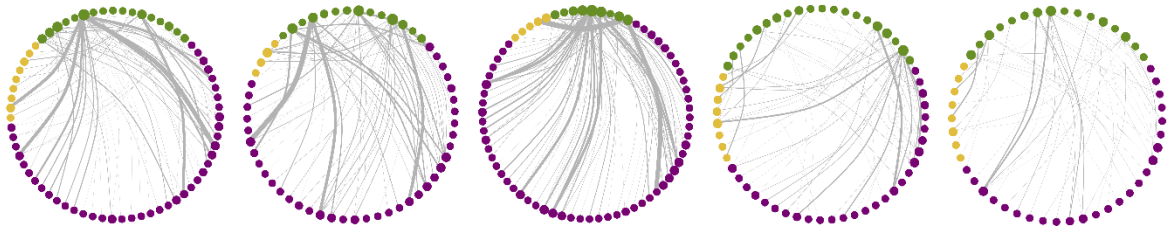
3.4 Results

3.4.1 Overview of fruit-frugivore interactions

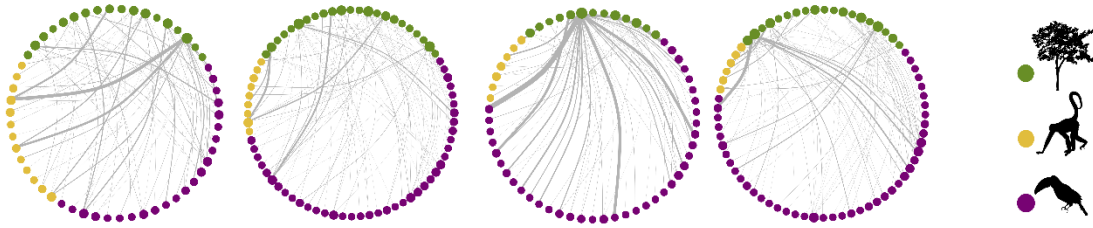
We recorded 4,670 pairwise interactions (991 unique frugivore and plant associations) in all forest classes, 2,600 (55.65%) of which by focal plant observations, while 1,339 (28.7%) and 731 (15.64%) records were made by transects and camera traps, respectively (Table S3.2). According to Chao estimator, the sampling effort led to an average detection of 71.41% (SD = 8.02) of total possible interactions, with the lowest value found for undisturbed forests ($67.63 \pm 5.69\%$) and the highest for logged forests ($74.26 \pm 7.43\%$, Table S3.2). Overall, we recorded 174 frugivore species: 146 birds (n=3,665 interactions) and 28 mammals (n=1,005 interactions, Table S3.3) interacting with 165 plant species (Table S3.4). We could not confirm the identification of 17 frugivores, which were identified only at family level - i.e., 13 birds and 4 mammals (Table S3.3).

Individuals belonging to the Ramphastidae, Thraupidae and Pipridae represented 43% of the total interactions (18.2%, 13.7% and 11%, respectively). *Ceratopipra rubrocapilla* (Red-headed Manakin, 8.9%), *Ramphastos vitellinus* (Channel-billed Toucan, 5.1%), *Dasyprocta leporina* (Red-rumped agouti, 4.3%), *Ramphastos tucanus* (White-throated Toucan, 3.9%) and *Pteroglossus bitorquatus* (Red-necked Aracari, 3.9%) were the most commonly frugivores (larger dark red and yellow nodes, Figure 3.2). Regarding the plants, Melastomataceae, Moraceae and Urticaceae were the most representative families recorded in 51.9% of the interactions (18.3%, 17.8% and 15.8%, respectively). The most commonly fruit eaten were *Coussapoa tessmannii* (Urticaceae, 9.7%), followed by an unidentified *Ficus* species (Moraceae, 8.7%), *Brosimum acutifolium* (Moraceae, 7.1%) and *Miconia pyrifolia* (Melastomataceae, 5.3%) (larger green nodes in Figure 3.2).

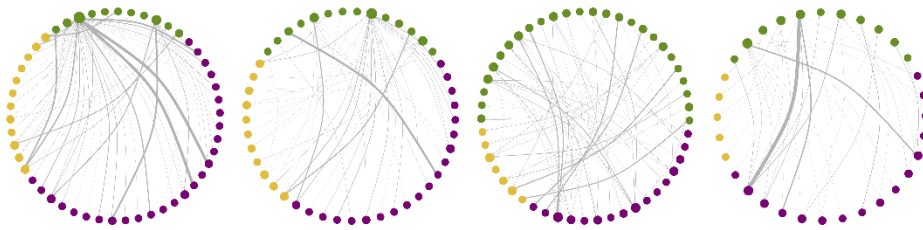
Undisturbed forests



Logged forests



Historically-burned forests



Recently-burned forests

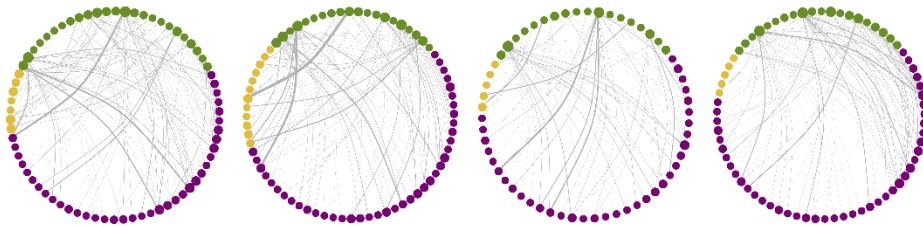


Figure 3.2. The structure of the 17 frugivory networks from undisturbed and human-modified forests in central-eastern Brazilian Amazon. Yellow and purple dots represent mammal and bird species, respectively, while plant species are the green dots. The size of the dot is proportional to the species degree, i.e., their number of pairwise frugivory interactions. Fruit-frugivore interactions are denoted by the grey lines connecting two dots, the width of which represents the frequency of those interactions.

3.4.2 Fire and logging effects on network components

Historically-burned forests had a significantly lower number of frugivores and overall network size in comparison to the other forest classes (Figure 3.3a, 3.3b, Table S3.5, S3.6, S3.7). Similarly, these forests had the lower number of unique pairwise interactions (Figure 3.3e, Table S3.5, S3.8), while the total number of plants and interactions did not change significantly in comparison to the other forest classes (Figure 3.3c, 3.3d, Table S3.5).

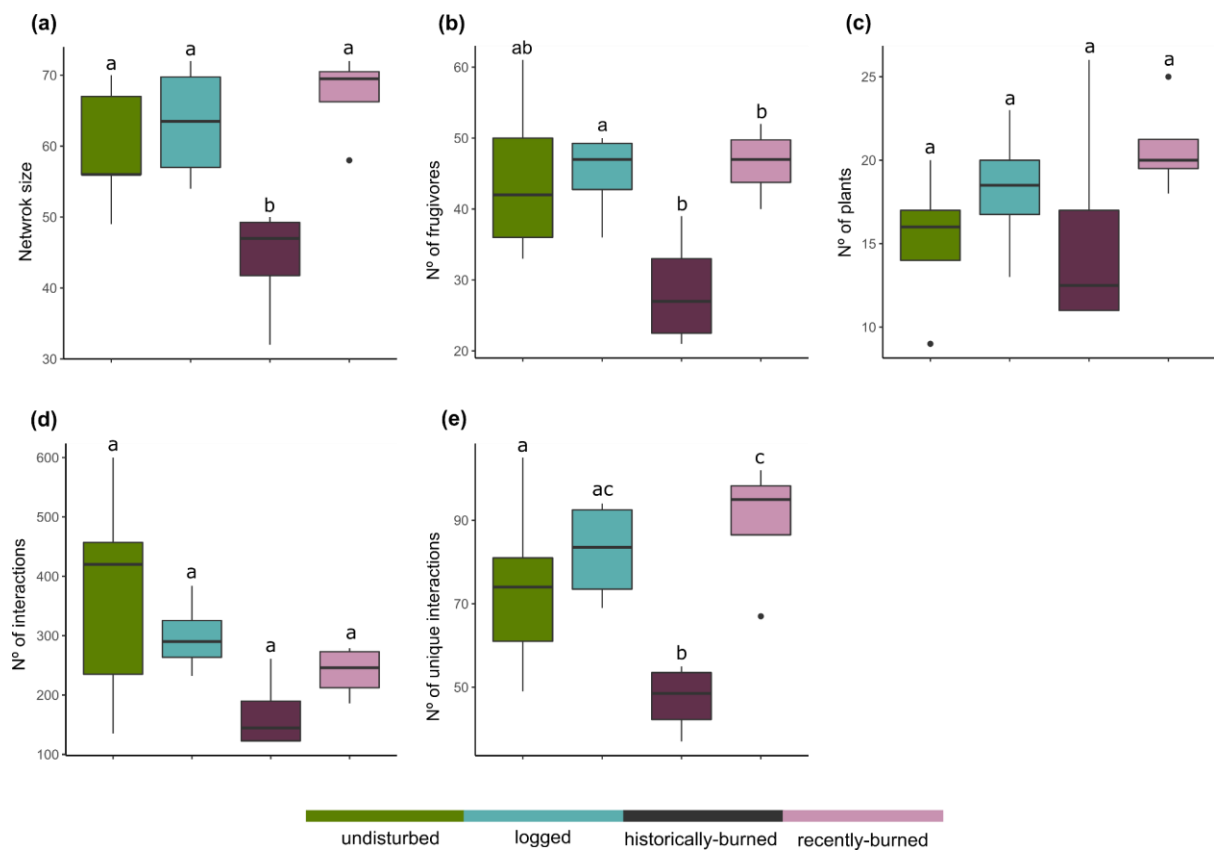


Figure 3.3. Effects of logging and fire on (a) network size (i.e., total number of frugivore and plant species); (b) number of frugivores (birds and mammals); (c) number of plant species; (d) total number of interactions, and (e) number of unique pairwise interactions. Different letters represent statistical differences among forest classes at $p < 0.05$, black dots are potential outliers and lines inside box plots represent median values.

We did not detect any effects of logging and fires in the network structure (Figure S3.4, Table S3.5, S3.9). Based on null models, connectance remained low in all forest classes (Figure S3.4a, Table S3.9). Contrary, observed nested values did not differ from Patefield and Vaznull null models (Figure S3.4b, Table S3.9). Meanwhile, we found a greater specialisation than expected by chance in all networks (Figure S3.4d, Table S3.9). Lastly, all networks were significantly different from null models when tested for modularity, which was consistently high across all forest classes, ranging from 0.48 to 0.72 (Figure S3.4c, Table S3.9). The number of modules was similar among forest classes, ranging between 4 and 15, leading to a compartmentalised structure within each of the 17 frugivory networks. Undisturbed forests had the lowest number of modules (Mean = 8, SD = 3.4), while recently-burned forests had the highest number (Mean = 11.5, SD = 2.6) (Figure S3.5). Although the median of frugivore and plant species per module did not vary significantly among forest classes, values ranged from 3.11 ± 4.3 in historically-burned to 5.52 ± 6.5 in undisturbed forests when considering frugivores, and plants varied from 1.8 ± 1.5 in recently-burned to 2.17 ± 1.5 in historically-burned forests. Most modules were formed by one or two plants and a few frugivore species related to functional aspects, such as taxonomic group (mammals and birds).

3.4.3 Fire and logging effects on beta-diversity

Considering the landscape level beta-diversity, we found high values of dissimilarity in interaction ($\beta_{\text{Int}} = 0.98$), plants ($\beta_{\text{Plants}} = 0.96$) and frugivores ($\beta_{\text{Frug}} = 0.90$, Figure S3.6, Table S3.10). Although the local level dissimilarity was lower than landscape level classes, values were high especially for interactions and plants (Table S3.10), interactions ($\beta_{\text{Int}} = 0.96$), plants species ($\beta_{\text{Plants}} = 0.90$) and frugivorous ($\beta_{\text{Frug}} = 0.75$, Figure S3.6, Table S3.10).

The turnover remains the main driver of changes in beta-diversity in both habitat and landscape level, higher in habitat level, 97.5%, 85.3% and 93.9% for interactions, frugivores

and plants, respectively, while nestedness was low in all forest classes (Table S3.10). These high turnover values translate into high dissimilarity of interactions among forest classes, the differences were especially higher between historically-burned and undisturbed forests (Figure 3.4). In total, 819 out of 991 (82.6%) unique interactions were only recorded in a single forest class, only the interaction between *Virola michelii* and *Ramphastos tucanus* was shared among all forest classes. The distinct composition was also found at the species level. We recorded a distinguished frugivorous composition between disturbed (logged and burned) and undisturbed forest (Figure 3.4). Among 174 frugivores recorded in the studied landscape, 68 species were recorded only in one forest class, while 29 species (21 birds and 8 mammals, or 16.6% of all species) were present in all forest classes. The plant composition was even more distinct (Figure 3.4). Only three plant species (*Laetia procera*, *Schefflera morototoni* and *Virola michelii*) were recorded in all forest classes, while 51 plant species occurred in two or more networks (30.9%). On the other hand, 120 plant species occurred exclusively in a single forest class (72.7%), 41 species were exclusively recorded in recently-burned areas, 30 in logged, 27 in historically-burned forests and 22 in undisturbed forests.

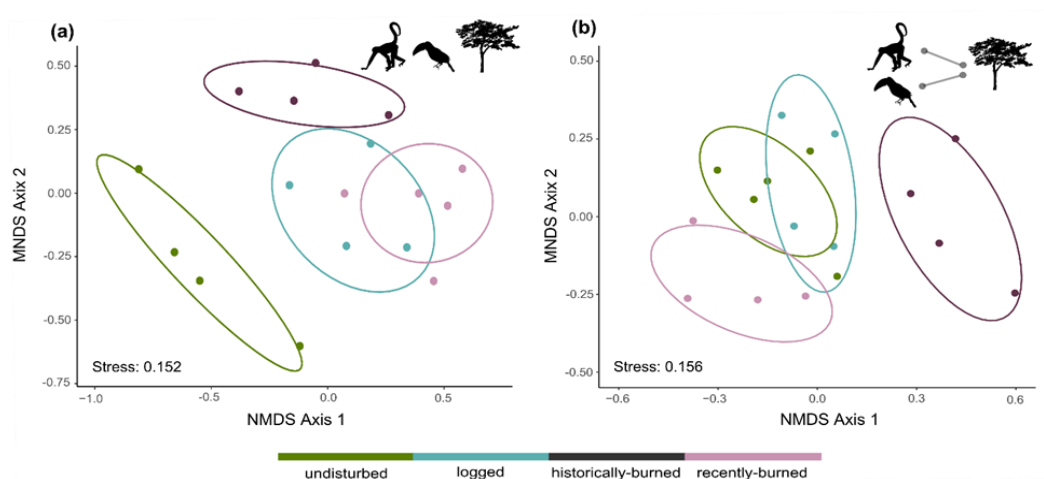


Figure 3.4. NMDS ordination of the 17 sites that were sampled in the Amazon Forest: (a) size (i.e., total number of frugivore and plant species), and (b) number of unique pairwise interactions. Points represent the transects and ellipses of the forest classes.

3.5 Discussion

We showed that fires reduce the number of species and unique fruit-frugivore interactions but not change the structure of frugivory networks in the Amazonian forests. Moreover, we reported high beta-diversity of species and interaction in all forest classes, driven mainly by turnover. In turn, logging and fires, particularly historic fires, changed the species and interaction composition towards a distinct community found in undisturbed forests. Our study provides one of the first pieces of evidence about the pervasive effects of long-term fires on the number and composition of fruit-frugivore interactions. These negative effects are likely to cascade to the provision of ecological services such as the seed-dispersal promoted by animals, with implications for the maintenance of ecosystem functionality and resilience of tropical forests.

3.5.1 Fires and logging effects on frugivory networks

Contrary to our expectations, Amazonian frugivory networks are losing species and unique interactions due to historic, not recent fires. The lack of effects of recent fires in the species and interaction number may still not be detectable once many fruiting trees are still alive right post-fires. Fire-induced plant mortality lasts for as long as eight years after fire events (Silva et al. 2018), which may maintain the resource (i.e., fruits) in a short-term period (Mestre et al. 2013). However, in the long-term fires can substantially reduce output of fruits, affecting animals who rely on plants for food (Barlow and Peres 2006, Butt et al. 2015, Marjakangas et al. 2020). Loss of unique interactions lead to extirpation of irreplaceable sets of traits and evolutionary history which may compromise ecological functions related to forest dynamics maintenance (Emer et al. 2019). As the local extinction of interaction is not random, it is more pervasive for those who may not survive the environmental filters created by human-driven disturbances (Bomfim et al. 2018, Emer et al. 2018). For example, the impoverishment of interaction involving the

dispersion of large-sized species may affect the carbon storage - ultimately influencing biogeochemical cycles (Bello et al. 2015).

Despite the reduction in species and interactions in historically-burned forests, no significant effects were found on network structure, all of our 17 frugivory networks were poorly connected and nested, with high values of modularity and specialisation. Although such structure is expected in pristine neotropical fruit-frugivore networks, this pattern was contrary to our expectations for human-disturbed forests (Schleuning et al. 2014, Dugger et al. 2019). Given the logging and fire impacts, we expected simplified interaction networks centred on a few generalist species resulting in the homogenization of pairwise interactions and further declines in network modularity and specialisation (Emer et al. 2020). The high modularity found in all forest classes may indicate that interactions are organised according to phylogenetic patterns and species and traits preferences (Schleuning et al. 2014). Moreover, the lack of significant changes on network specialisation across forest classes suggests a consistent lower interaction niche overlap among species in terms of sharing interacting partners and/or resources (Schleuning et al. 2012). In turn, higher interaction diversity in tropical forests may lead to higher specialisation due to greater niche partitioning (Valiente-Banuet et al. 2015).

Nonetheless, the lack of evidence of negative effects of logging and fires on frugivore network structure may reflect the overrepresentation of some frugivore clades (e.g., Ramphastidae, Thraupidae and Pipridae) which were abundant at all sites. Previous studies have shown that increases in generalist frugivore species which make strongly-weighted contributions to network structure can counterbalance the loss of specialists (Rumeu et al. 2017, Acevedo-Quintero et al. 2020). Additionally, the persistence of most mid- and large-sized frugivores (e.g., *Dasyprocta leporina*, *Mazama* spp, *Penelope* spp, *Ramphastos* spp) in all forest classes and their high dispersal abilities may have contributed to the resilience of the network structure to logging and fire disturbances. Furthermore, the persistence of some plant

families, such as Melostomataceae, may also maintain the network structure; these habitat generalist species produce small fruits important in the diet of many animal species, especially for Pipridae (Mestre et al. 2013)

3.5.2 Fire and logging effects on beta-diversity

Although the consistently high species beta-diversity is an inherent quality of tropical forest (Solar et al. 2015, Silveira et al. 2016), these results are contrary to those expected to recently-burned forests. As fires promote strong direct impacts, such a high species mortality rate (Barlow and Silveira 2009, Berenguer et al. 2021), we expected low values of species beta-diversity that might result in decreases in the beta-diversity of pairwise interactions (Dehling et al. 2020). However, the increasing forest heterogeneity following human-driven disturbances can contribute to great beta-diversity and high turnover between forests (Arroyo-Rodríguez et al. 2017, 2020). For instance, open forests created by logging and fires can be used by a large pool of occasional visitors from adjacent habitats that contribute to the maintenance of high levels of beta-diversity in human-disturbed forests (Barlow and Peres 2008, Peres et al. 2010, Lees et al. 2013). Additionally, the consistent differences in species and interaction composition among forest classes, especially between burned and unburned forests is reinforced by earlier findings (Mestre et al. 2013) and directly impacting the interactions composition (Dormann and Strauss 2014). The high turnover of interactions between networks is central to the great diversity of frugivory interactions fulfilling the ecosystem process of seed-dispersal and predation and conferring long-term ecosystem resilience (Dehling et al. 2020).

Even though the maintenance of network structure despite the variation in species and interaction number confer resilience to Amazonian forests (Hidasi-Neto et al. 2012), we highlight that the loss of species and interactions observed in historically-burned forests may

lead to important implications to ecosystem functionality. Loss of species implies reductions in niche occupancy as well as the functional redundancy in the networks, which in the longstanding run compromise the network resilience and the maintenance of the ecosystem functionality (Dugger et al. 2019). Meanwhile, the consistent difference in species composition in logged and burned forests and the evident impacts of past fires in interaction composition may indicate divergent paths in regenerating forests compared to pristine forests. Moreover, logging and fires are commonly associated with other disturbance, such as hunting, which can lead to population size reductions or even local extinctions of some larger-bodied frugivores (Brodie et al. 2015, Benítez-López et al. 2017). The negative impact of hunting on the abundance of frugivorous mammals (reduction of 49%, Osuri et al. 2020) and birds (declined by 58%, Benítez-López et al. 2017) significantly disrupts the functions performed by them, such as large seed-dispersal (Bomfim et al. 2018). Therefore, as mid- and large- frugivores are not fully replaced by small species, conservation efforts need to be targeted at the maintenance of the diversity of dispersers.

3.5.3 The limitation of the study

Even though our study employed an extensive sampling effort and used different methods to survey fruit-frugivore interactions, we did not achieve the asymptote of the pairwise fruit-frugivore completeness sampling curves in any of the studied forests. Moreover, we had different sampling completeness among forest classes, which made the ascendant curve even more evident for sites with lower sampling intensity. Sampling the entire interacting community is challenging not only because of rare interactions, especially in species-rich communities such as Amazonian forests (Jordano 2016). Another caveat is the bias in the choice of trees for focal observations. As we did focal sampling in plants with high fruit availability, we may have overestimated the importance of some species of plants and

frugivores in the interactions recorded. Lastly, tree height and forest density may also limit the observation of interactions, especially in undisturbed forests where observation of the canopy is more difficult. That said, sampling of interactions and species identification were consistent among forest classes and performed by highly skilled professionals. Thus, our design permits confidence that these results are robust and representative of changes in fruit-frugivore interactions in the Amazonian *terra firme* rainforest.

3.5.4 Conclusions

Our study provides the first empirical report demonstrating impacts of historic fires on frugivory interactions in Amazonian forests. Overall, our results suggest a degree of resilience in network structure, the loss and change in the composition of species and their interactions following fires seem to be a good predictor of the directions of changes in ecosystem processes. Fires are likely to play a more subtle role in determining the future forest dynamics even after nearly two decades, which may be enhanced given the increase in fire frequency in the Amazon region. Notably, the high species and interaction turnover among forests allows the higher diversity of local interactions and, on a regional scale, has an important conservation implication to maintain the high levels of fruit-frugivore interaction biodiversity.

3.6 Acknowledgments

We thank the Large Scale Biosphere-Atmosphere Program (LBA) for logistical and infrastructure support during field measurements. We are deeply grateful to our field and laboratory assistants: Gilson Oliveira, Joni Oliveira, Josué Oliveira, Josiane Oliveira, Marcos Oliveira and Renilson Freitas, as well as all collaborating private land owners for their support and access to their land. We also thank Lais Lautenschlager Rodrigues and Sara Moreira for the screening camera trap data, also to Carlos Rodrigo Brocardo, Everton Miranda and Rodrigo

Fadini for helping in mammal identification. We are grateful to multiple funding agencies for financial support: Conselho Nacional de Pesquisa (CNPq; grants CNPq-CAPES 441659/2016-0 and 441573/2020-7 [PELD-RAS], MCIC-CNPq 420254/2018-8 [RESFLORA] and CNPq-PrevFogo-IBAMA 441949/2018-5 [SEM-FLAMA]), Instituto Nacional de Ciência e Tecnologia – Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0) and Embrapa (SEG: 02.08.06.005.00), in Brazil; the Darwin Initiative (17-023), The Nature Conservancy, and Natural Environment Research Council (NERC; NE/F01614X/1, NE/G000816/1, NE/K016431/1 and NE/P004512/1), in the UK. E.B. and J.B. were also funded by H2020-MSCA-RISE (691053-ODYSSEA). F.F. and J.B. acknowledge funding provided by BNP Paribas Foundation (Climate and Biodiversity Initiative; BioClimate project). MAP thanks the CNPq for a research grant (304742/2019-8).

3.7 Author contribution

LCR and MAP conceived the original idea of this study. LCR and EB conceived the study design, conducted the sampling and organised the database. LCR and CE conducted the data analyses with input from FF and MAP. LCR wrote the manuscript, with significant contributions of all co-authors. All authors discussed the results and revised the manuscript before submission.

3.8 References

- Acevedo-Quintero, J. F., J. G. Zamora-Abrego, and D. García. 2020. From structure to function in mutualistic interaction networks: Topologically important frugivores have greater potential as seed dispersers. *Journal of Animal Ecology* 89:2181–2191.
- Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and

- measurement. *Oikos* 117:1227–1239.
- Almeida-Neto, M., and W. Ulrich. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software* 26:173–178.
- Archibald, S. a, S. Levin, S. a Archibald, W. a Hoffmann, W. J. Bond, N. Hanan, J. Ratnam, W. Hawthorne, T. Orgle, D. Roy, B. Van Wilgen, R. Scholes, G. Duff, D. Bowman, G. Cook, M. a Batalha, V. R. Pivello, S. T. Meirelles, K. K. Caylor, O. Kolle, J. Lloyd, B. Stocks, J. Levine, H. Van Der Jeugd, W. D. Stock, S. J. Van Rensburg, M. S. Waldram, W. J. Bond, W. D. Stock, and D. Fairbanks. 2011. Global Resilience of Tropical Forest. *Science* 334:232–235.
- Arroyo-Rodríguez, V., L. Fahrig, M. Tabarelli, J. I. Watling, L. Tischendorf, M. Benchimol, E. Cazetta, D. Faria, I. R. Leal, F. P. L. Melo, J. C. Morante-Filho, B. A. Santos, R. Arasa-Gisbert, N. Arce-Peña, M. J. Cervantes-López, S. Cudney-Valenzuela, C. Galán-Acedo, M. San-José, I. C. G. Vieira, J. W. F. Slik, A. J. Nowakowski, and T. Tscharntke. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters* 23:1404–1420.
- Arroyo-Rodríguez, V., F. P. L. Melo, M. Martínez-Ramos, F. Bongers, R. L. Chazdon, J. A. Meave, N. Norden, B. A. Santos, I. R. Leal, and M. Tabarelli. 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews* 92:326–340.
- Asner, G. P., T. K. Rudel, T. M. Aide, R. Defries, and R. Emerson. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23:1386–1395.
- Barlow, J., E. Berenguer, R. Carmenta, and F. França. 2020. Clarifying Amazonia’s burning crisis. *Global Change Biology* 26:319–321.

- Barlow, J., and C. A. Peres. 2004. Ecological responses to El Niño-induced surface fires
Ecological responses to El Nin in central Brazilian Amazonia: management implications
for flammable tropical forests. *Philosophical Transactions of the Royal Society B:
Biological Sciences* 359:367–380.
- Barlow, J., and C. A. Peres. 2006. Effects of single and recurrent wildfires on fruit production
and large vertebrate abundance in a central Amazonian forest. *Biodiversity and
Conservation* 15:985–1012.
- Barlow, J., and C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in an
Amazonian forest. Pages 1787–1794 *Philosophical Transactions of the Royal Society B:
Biological Sciences*.
- Barlow, J., C. A. Peres, L. M. P. Henriques, P. C. Stouffer, and J. M. Wunderle. 2006. The
responses of understorey birds to forest fragmentation, logging and wildfires: An
Amazonian synthesis. *Biological Conservation* 128:182–192.
- Barlow, J., and J. M. Silveira. 2009. The consequences of fire for the fauna of humid tropical
forests. Page *Tropical Fire Ecology*.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity.
Global Ecology and Biogeography 19:134–143.
- Baselga, A. 2013. Separating the two components of abundance-based dissimilarity: Balanced
changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*
4:552–557.
- Baselga, A., and C. D. L. Orme. 2012. Betapart: An R package for the study of beta diversity.
Methods in Ecology and Evolution 3:808–812.
- Beckett, S. J. 2016. Improved community detection in weighted bipartite networks. *Royal
Society Open Science* 3:140536.
- Bello, C., M. Galetti, M. A. Pizo, L. F. S. Magnago, M. F. Rocha, R. A. F. Lima, C. A. Peres,

- O. Ovaskainen, and P. Jordano. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1:1–10.
- Benítez-López, A., R. Alkemade, A. M. Schipper, D. J. Ingram, P. A. Verweij, J. A. J. Eikelboom, and M. A. J. Huijbregts. 2017. The impact of hunting on tropical mammal and bird populations. *Science* 356:180–183.
- Berenguer, E., T. A. Gardner, J. Ferreira, L. E. O. C. Aragão, R. Mac Nally, J. R. Thomson, I. C. G. Vieira, and J. Barlow. 2018. Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology* 106:2190–2203.
- Berenguer, E., G. D. Lennox, J. Ferreira, Y. Malhi, L. E. O. C. Aragão, J. R. Barreto, F. Del Bon Espírito-Santo, A. E. S. Figueiredo, F. França, T. A. Gardner, C. A. Joly, A. F. Palmeira, C. A. Quesada, L. C. Rossi, M. M. M. de Seixas, C. C. Smith, K. Withey, and J. Barlow. 2021. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* 118:1–8.
- Boissier, O., F. Feer, P. Y. Henry, and P. M. Forget. 2020. Modifications of the rain forest frugivore community are associated with reduced seed removal at the community level. *Ecological Applications* 30:1–16.
- Bomfim, J. de A., P. R. Guimarães, C. A. Peres, G. Carvalho, and E. Cazetta. 2018. Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. *Ecography* 41:1–11.
- Brodie, J. F., A. J. Giordano, E. F. Zipkin, H. Bernard, J. Mohd-Azlan, and L. Ambu. 2015. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conservation Biology* 29:110–121.
- Bullock, E. L., C. E. Woodcock, C. Souza, and P. Olofsson. 2020. Satellite-based estimates

- reveal widespread forest degradation in the Amazon. *Global Change Biology* 26:2956–2969.
- Burkle, L. A., R. T. Belote, and J. A. Myers. 2022. Wildfire severity alters drivers of interaction beta-diversity in plant–bee networks. *Ecography* 2022:e05986.
- Butt, N., L. Seabrook, M. Maron, B. S. Law, T. P. Dawson, J. Syktus, and C. A. Mcalpine. 2015. Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. *Global Change Biology* 21:3267–3277.
- Cai, W., S. Borlace, M. Lengaigne, P. Van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. Mcphaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, and F. F. Jin. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111–116.
- Carstensen, D. W., M. Sabatino, K. Trøjelsgaard, and L. P. C. Morellato. 2014. Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLoS ONE* 9.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Dehling, D. M., G. Peralta, I. M. A. Bender, P. G. Blendinger, K. Böhning-Gaese, M. C. Muñoz, E. L. Neuschulz, M. Quitián, F. Saavedra, V. Santillán, M. Schleuning, and D. B. Stouffer. 2020. Similar composition of functional roles in Andean seed-dispersal networks, despite high species and interaction turnover. *Ecology* 101:1–11.
- Dennis, A. J., E. W. Schupp, R. A. Green, and D. A. Wetcott. 2007. *Seed Dispersal: Theory and its Application in a Changing World*.
- Donoso, I., M. C. Sorensen, P. G. Blendinger, W. D. Kissling, E. L. Neuschulz, T. Mueller, and M. Schleuning. 2020. Downsizing of animal communities triggers stronger

- functional than structural decay in seed-dispersal networks. *Nature Communications* 11.
- Dormann, C. F., J. Frund, N. Bluthgen, and B. Gruber. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *The Open Ecology Journal* 2:7–24.
- Dormann, C. F., and R. Strauss. 2014. A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution* 5:90–98.
- Dugger, P. J., P. G. Blendinger, K. Böhning-Gaese, L. Chama, M. Correia, D. M. Dehling, C. Emer, N. Farwig, E. C. Fricke, M. Galetti, D. García, I. Grass, R. Heleno, F. A. F. Jacomassa, S. Moraes, C. Moran, M. C. Muñoz, E. L. Neuschulz, L. Nowak, A. Piratelli, M. A. Pizo, M. Quitián, H. S. Rogers, R. A. Ruggera, F. Saavedra, M. S. Sánchez, R. Sánchez, V. Santillán, D. G. Schabo, F. R. da Silva, S. Timóteo, A. Traveset, M. G. R. Vollstädt, and M. Schleuning. 2019. Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography* 28:248–261.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America* 99:12917–12922.
- Emer, C., M. Galetti, M. A. Pizo, P. R. Guimarães, S. Moraes, A. Piratelli, and P. Jordano. 2018. Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. *Ecology Letters* 21:484–493.
- Emer, C., M. Galetti, M. A. Pizo, P. Jordano, and M. Verdú. 2019. Defaunation precipitates the extinction of evolutionarily distinct interactions in the Anthropocene. *Science Advances* 5:1–9.
- Emer, C., P. Jordano, M. A. Pizo, M. C. Ribeiro, F. R. da Silva, and M. Galetti. 2020. Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. *Biotropica* 52:81–89.
- Fonseca, M. G., L. M. Alves, A. P. D. Aguiar, E. Arai, L. O. Anderson, T. M. Rosan, Y. E.

- Shimabukuro, and L. E. O. e. C. de Aragão. 2019. Effects of climate and land-use change scenarios on fire probability during the 21st century in the Brazilian Amazon. *Global Change Biology* 25:2931–2946.
- Gallego-Zamorano, J., A. Benítez-López, L. Santini, J. P. Hilbers, M. A. J. Huijbregts, and A. M. Schipper. 2020. Combined effects of land use and hunting on distributions of tropical mammals. *Conservation Biology* 34:1271–1280.
- García, D., I. Donoso, and J. Rodríguez-Pérez. 2018. Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function. *Functional Ecology* 32:2742–2752.
- Gardner, T. A., J. Ferreira, J. Barlow, A. C. Lees, LukeParry, I. C. G. Vieira, E. Berenguer, R. Abramovay, A. Aleixo, C. Andretti, LuizE.O.C.Aragão, IvaneiAraújo, W. S. de Ávila, R. D. Bardgett, M. Batistella, R. A. Begotti, T. Beldini, D. E. de Blas, R. F. Braga, D. de L. Braga, J. G. de Brito, P. B. de Camargo, F. C. dos Santos, V. C. de Oliveira, T. M. C. Amanda Cardoso Nunes Cordeiro¹⁵, D. R. de Carvalho, S. A. Castelani, J. C. M. Chaul, C. Cerri, F. De, A. Costa, C. D. F. da Costa, E. Coudel, A. C. Coutinho, D. Cunha, Á. D’Antona, J. Dezincourt, K. Dias-Silva, M. Durigan, and J. C. D. M. Esquerdo. 2013. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:20130307–20130307.
- Gatti, L. V., L. S. Basso, J. B. Miller, M. Gloor, L. Gatti Domingues, H. L. G. Cassol, G. Tejada, L. E. O. C. Aragão, C. Nobre, W. Peters, L. Marani, E. Arai, A. H. Sanches, S. M. Corrêa, L. Anderson, C. Von Randow, C. S. C. Correia, S. P. Crispim, and R. A. L. Neves. 2021. Amazonia as a carbon source linked to deforestation and climate change. *Nature* 595:388–393.
- Guimarães, P. R. 2020. The Structure of Ecological Networks Across Levels of Organization.

- SOM. *Annual Review of Ecology, Evolution, and Systematics* 51:433–460.
- Hawes, J. E., I. C. G. Vieira, L. F. S. Magnago, E. Berenguer, J. Ferreira, L. E. O. C. Aragão, A. Cardoso, A. C. Lees, G. D. Lennox, J. A. Tobias, A. Waldron, and J. Barlow. 2020. A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. *Journal of Ecology* 108:1373–1385.
- Hidasi-Neto, J., J. Barlow, and M. V Cianciaruso. 2012. Bird functional diversity and wildfires in the Amazon: The role of forest structure. *Animal Conservation* 15:407–415.
- Howe, H. F., F. Howe, and J. Smallwood. 1982. Ecology of seed dispersal. *Annual review of ecology and systematics*. Volume 13:201–228.
- Jordano, P. 2016. Sampling networks of ecological interactions. *Functional Ecology* 30:1883–1893.
- Jordano, P., C. Garcia, J. A. Godoy, and J. L. García-Castaño. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America* 104:3278–3282.
- Lees, A. C., N. G. de Moura, C. B. Andretti, B. J. W. Davis, E. V. Lopes, L. Magalli Pinto Henriques, A. Aleixo, J. Barlow, J. Ferreira, and T. A. Gardner. 2013. One hundred and thirty-five years of avifaunal surveys around Santarém, central Brazilian Amazon. *Revista Brasileira de Ornitologia* 21:16–57.
- Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.5. URL: <https://CRAN.R-project.org/package=emmeans>.
- Marjakangas, E. L., N. Abrego, V. Grøtan, R. A. F. de Lima, C. Bello, R. S. Bovendorp, L. Culot, É. Hasui, F. Lima, R. L. Muylaert, B. B. Niebuhr, A. A. Oliveira, L. A. Pereira, P. I. Prado, R. D. Stevens, M. H. Vancine, M. C. Ribeiro, M. Galetti, O. Ovaskainen, E. M. N. Abrego, V. Grøtan, R. A. F. De Lima, C. Bello, R. S. Bovendorp, L. Culot, É. Hasui,

- F. Lima, R. Lara, M. Bernardo, B. B. Niebuhr, A. A. Oliveira, L. Augusto, P. Paulo, R. D. Stevens, M. Humberto, V. Milton, and C. Ribeiro. 2020. Fragmented tropical forests lose mutualistic plant – animal interactions. *Diversity and Distributions* 26:154–168.
- Matricardi, E. A. T., D. L. Skole, O. B. Costa, M. A. Pedlowski, J. H. Samek, and E. P. Miguel. 2020. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science* 369:1378–1382.
- Menezes, Í. P., C. Emer, E. Cazetta, and J. C. Morante-filho. 2021. Deforestation Simplifies Understory Bird Seed-Dispersal Networks in Human-Modified Landscapes. *Frontiers in Ecology and Evolution* 9:640210.
- Mestre, L. A. M., M. A. Cochrane, and J. Barlow. 2013. Long-term Changes in Bird Communities after Wildfires in the Central Brazilian Amazon. *Biotropica* 45:480–488.
- Moura, N. G., A. C. Lees, C. B. Andretti, B. J. W. Davis, R. R. C. Solar, A. Aleixo, J. Barlow, J. Ferreira, and T. A. Gardner. 2013. Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. *Biological Conservation* 167:339–348.
- Newman, M. E. J. 2006. Modularity and community structure in networks. *Proceedings of the National Academy of Sciences of the United States of America* 103:8577–8582.
- Nunes, C. A., E. Berenguer, F. França, J. Ferreira, A. C. Lees, J. Louzada, E. J. Sayer, R. Solar, C. C. Smith, L. E. O. C. Aragão, D. de L. Braga, P. B. de Camargo, C. E. P. Cerri, R. C. de Oliveira, M. Durigan, N. Moura, V. H. F. Oliveira, C. Ribas, F. Vaz-de-Mello, I. Vieira, R. Zanetti, and J. Barlow. 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. *Proceedings of the National Academy of Sciences* 119.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, Oh. R.B., S. G.L., P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *Vegan: Community Ecology Package* R Package. version 2.3-1.

- Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* 104:19891–19896.
- Osuri, A. M., U. Mendiratta, R. Naniwadekar, V. Varma, and S. Naeem. 2020. Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds. *Frontiers in Forests and Global Change* 2:87.
- Pellissier, L., C. Albouy, J. Bascompte, N. Farwig, C. Graham, M. Loreau, M. A. Maglianesi, C. J. Melián, C. Pitteloud, T. Roslin, R. Rohr, S. Saavedra, W. Thuiller, G. Woodward, N. E. Zimmermann, and D. Gravel. 2018. Comparing species interaction networks along environmental gradients. *Biological Reviews* 93:785–800.
- Peres, C. A., J. Barlow, and T. Haugaasen. 2003. Vertebrate responses to surface wildfires in a central Amazonian forest. *ORYX* 37:97–109.
- Peres, C. A., T. A. Gardner, J. Barlow, J. Zuanon, F. Michalski, A. C. Lees, I. C. G. Vieira, F. M. S. Moreira, and K. J. Feeley. 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. *Biological Conservation* 143:2314–2327.
- Pizo, M. A., and M. Galetti. 2010. Métodos e Perspectivas da Frugivoria e Dispersão de Sementes por Aves. *Biologia*:492–504.
- Poisot, T., E. Canard, D. Mouillot, N. Mouquet, and D. Gravel. 2012. The dissimilarity of species interaction networks. *Ecology Letters* 15:1353–1361.
- R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rivas-Romero, J. A., and J. R. Soto-Shoender. 2015. Filling in the Gaps: Evaluating the Use of Camera Traps in the Canopy to Examine Frugivore Visits to *Oreopanax echinops* in the Highlands of Guatemala. *Southwestern Naturalist* 60:366–397.
- Rumeu, B., M. Devoto, A. Traveset, J. M. Olesen, P. Vargas, M. Nogales, and R. Heleno.

2017. Predicting the consequences of disperser extinction: richness matters the most when abundance is low. *Functional Ecology* 31:1910–1920.
- Schleuning, M., J. Fründ, and D. García. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: An extension of trait-based concepts to plant-animal interactions. *Ecography* 38:380–392.
- Schleuning, M., J. Fründ, A. M. Klein, S. Abrahamczyk, R. Alarcón, M. Albrecht, G. K. S. Andersson, S. Bazarian, K. Böhning-Gaese, R. Bommarco, B. Dalsgaard, D. M. Dehling, A. Gotlieb, M. Hagen, T. Hickler, A. Holzschuh, C. N. Kaiser-Bunbury, H. Kreft, R. J. Morris, B. Sandel, W. J. Sutherland, J. C. Svenning, T. Tscharntke, S. Watts, C. N. Weiner, M. Werner, N. M. Williams, C. Winqvist, C. F. Dormann, and N. Blüthgen. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* 22:1925–1931.
- Schleuning, M., L. Ingmann, R. Strauß, S. A. Fritz, B. Dalsgaard, D. Matthias Dehling, M. Plein, F. Saavedra, B. Sandel, J. C. Svenning, K. Böhning-Gaese, and C. F. Dormann. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters* 17:454–463.
- Sebastián-González, E., B. Dalsgaard, B. Sandel, and P. R. Guimarães. 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global Ecology and Biogeography* 24:293–303.
- Silva, C. V. J., L. E. O. C. Aragão, J. Barlow, F. Espirito-Santo, P. J. Young, L. O. Anderson, E. Berenguer, I. Brasil, I. F. Brown, B. Castro, R. Farias, J. Ferreira, F. França, P. M. L. A. Graça, L. Kirsten, A. P. Lopes, C. Salimon, M. A. Scaranello, M. Seixas, F. C. Souza, and H. A. M. Xaud. 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20180043.

- Silveira, J. M., J. Louzada, J. Barlow, R. Andrade, L. Mestre, R. Solar, S. Lacau, and M. A. Cochrane. 2016. A Multi-Taxa Assessment of Biodiversity Change After Single and Recurrent Wildfires in a Brazilian Amazon Forest. *Biotropica* 48:170–180.
- Slik, J. W. F., and S. Van Balen. 2006. Bird community changes in response to single and repeated fires in a lowland tropical rainforest of eastern Borneo. *Biodiversity and Conservation* 15:4425–4451.
- Solar, R. R. de C., J. Barlow, J. Ferreira, E. Berenguer, A. C. Lees, J. R. Thomson, J. Louzada, M. Maués, N. G. Moura, V. H. F. Oliveira, J. C. M. Chaul, J. H. Schoereder, I. C. G. Vieira, R. Mac Nally, and T. A. Gardner. 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters* 18:1108–1118.
- Tylianakis, J. M., E. Laliberté, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biological Conservation* 143:2270–2279.
- Tylianakis, J. M., and R. J. Morris. 2017. Ecological Networks Across Environmental Gradients. *Annual Review of Ecology, Evolution, and Systematics* 48:25–48.
- Ulrich, W., M. Almeida-Neto, and N. J. Gotelli. 2009. A consumer's guide to nestedness analysis. *Oikos* 118:3–17.
- Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, D. García, J. M. Gómez, P. Jordano, R. Medel, L. Navarro, J. R. Obeso, R. Oviedo, N. Ramírez, P. J. Rey, A. Traveset, M. Verdú, and R. Zamora. 2015. Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology* 29:299–307.
- Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–1127.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: The analysis of proportions in ecology. *Ecology* 92:3–10.

Withey, K., E. Berenguer, A. F. Palmeira, F. D. B. Espírito-Santo, G. D. Lennox, C. V. J. Silva, L. E. O. C. Aragão, J. Ferreira, F. França, Y. Malhi, L. C. Rossi, and J. Barlow. 2018. Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20170312.

Zhu, C., W. Li, T. Gregory, D. Wang, P. Ren, D. Zeng, Y. Kang, P. Ding, and X. Si. 2022. Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. *Remote Sensing in Ecology and Conservation* 8:92–104.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*.

3.9 Supporting information

Table S3.1 Number of studies plots in different forest disturbance classes

Forest class	Forest description	N° transects
undisturbed forest	pristine forest with no logging and fire effects	5
logged forest	selective logging occurred ≥ 30 years prior sampling	4
historically-burned forest	≥ 30 years selective logged and ≥ 18 years burned forests prior sampling	4
recently -burned forests	≥ 30 years selective logged and 3 years burned forests prior sampling	4

3.9.1 Frugivory interactions

We considered frugivory interactions the following feeding behaviours: seed was swallowed, pulp consumption (when the frugivore pecked the fruit to obtain pulp pieces but did not swallow the seed), seeds carried away (when the frugivore took the seeds away from the plant without swallowing it) and predated seeds (when the frugivore damaged the seeds) (see Jordano and Schupp 2000).

3.9.2 Sampling completeness

Each cell represents the frequencies of frugivory interactions between frugivore animal and plant species (interaction richness) on the columns and the time period on the rows (sampling effort). Then, the interaction accumulation curves were compounded by summing all the time periods sequentially with increasing sampling effort (hours) and the total number of interactions recorded in each transect (Jordano 2016, Figure S3.1). We additionally calculated sampling completeness for each network, as the ratio between the number of observed interaction links and expected interaction link number based on the Chao 1 estimator, using interactions with 100 randomizations (Chao et al. 2014). The curves were generated using the function *specaccum* and the interaction species richness estimator Chao1 was calculated with *estimateR* function in the *vegan* package (Oksanen et al. 2015). The sampling unit in our analyses is one monitoring day. Logistical constraints did not allow us to monitor more trees or to standardise sampling effort across survey periods and individual trees. Because we used different methods and had more than one camera working simultaneously, one monitoring hour represents one camera hour (i.e., one camera monitoring for one hour).

We sampled frugivory interactions for 31,484 hours considering all methodologies (Table S3.2). As we were dependent on fruit production to install the cameras, the sampling effort was not equally distributed among transects, averaging $1,852 \pm 273.55$ h (range 1,056 - 2,280 h, Figure S3.1). From direct observations (transect census and focal plants) we accumulated $1,556 \pm 91.5$ h per transect. Regarding camera traps, we installed a total of 88 camera traps, adding up to 1,345 sampling days and $29,928 \pm 1,760$ h of sampling per transect. The Chao estimator showed a detection of $67.63 \pm 5.43\%$ in undisturbed forests, $74.26 \pm 9.16\%$ in logged forests, 72.19 ± 4.45 and 14.76 ± 13.1 recently-burned and historically-burned forests, respectively (see Table S3.1).

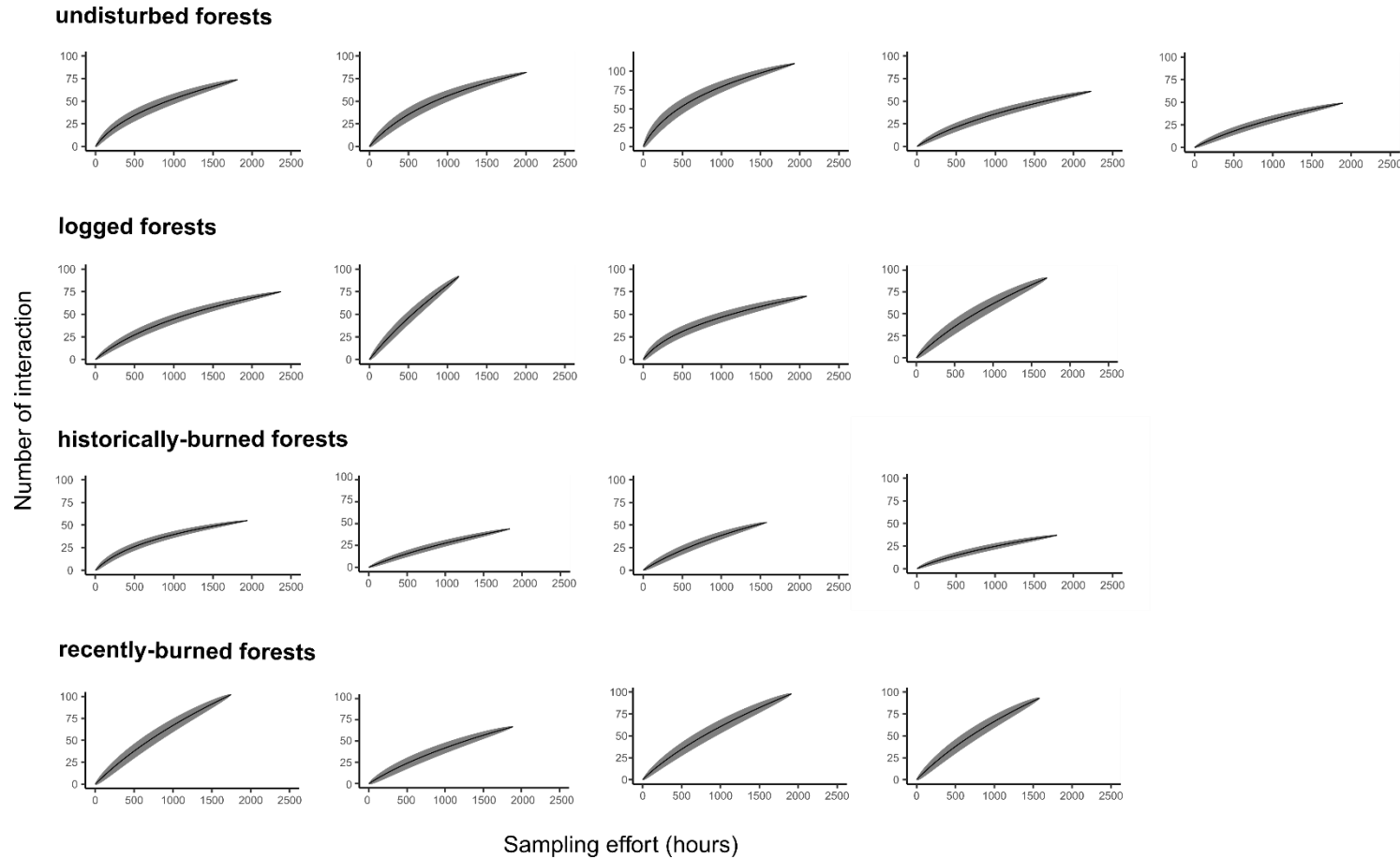


Figure S3.1 Accumulation curves of interaction number with increasing sampling effort (hours) in 17 transects distributed in four forest classes. Interactions number (dark lines) with the standard error (grey lines). Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned).

Table S3.2 Description of the fruit-frugivore interaction in the Brazilian Amazon Forests. Seventeen transects sampled along distinct forest in the Amazon Forests: Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned). Samplings were based on hours. See methods in the main text for details of each network component.

Forest classes	Total sampling (h)	Transect/ Focal samplings (h)	Trap sampling (h)	N° Animal species (A)	N° Plants species (P)	N° Size (S)	Unique pairwise interactions (I)	Total pairwise interactions (Ni)	Chao1 (%)
undisturbed	1818	90	1728	50	17	67	74	420	61.16
undisturbed	2010	90	1920	42	14	56	81	457	63.78
undisturbed	1938	90	1848	61	9	70	105	600	75
undisturbed	2226	90	2136	36	20	56	61	235	69.32
undisturbed	1893	93	1800	33	16	49	49	135	69.77
logged	2373	93	2280	36	17	53	74	305	76.55
logged	1148	92	1056	49	23	72	92	232	58.47

logged	2090	98	1992	45	13	58	69	384	78.05
logged	1704	96	1608	50	19	69	94	274	69.56
historically-burned	1941	93	1848	39	11	50	55	261	82.37
historically-burned	1841	89	1752	31	14	45	44	123	60.38
historically-burned	1578	90	1488	23	26	49	53	166	88.25
historically-burned	1794	90	1704	21	11	32	37	122	66.07
recently-burned	1745	89	1656	45	25	70	102	271	68.44
recently-burned	1914	90	1824	52	20	72	96	278	77.48
recently-burned	1890	90	1800	40	18	58	67	186	72.67
recently- burned	1581	93	1488	49	20	69	93	221	69.38

Table S3.3 Frugivorous species recorded eating fruits. The numbers represent the frequencies of interaction involving the species.

Frugivores species	Class	undisturbed	logged	historically-burned	recently-burned
<i>Tinamus tao</i>	Bird	3	1		
<i>Tinamus guttatus</i>	Bird		1		
<i>Crypturellus soui</i>	Bird				1
<i>Penelope supercilialis</i>	Bird	26	10	1	6
<i>Penelope pileata</i>	Bird	11	12	21	10
<i>Aburria kujubi</i>	Bird	9			9
<i>Ortalis motmot</i>	Bird		2	1	
<i>Pauxi tuberosa</i>	Bird	2	3		1
<i>Patagioenas plumbea</i>	Bird	5	17		
<i>Patagioenas subvinacea</i>	Bird	6	6		2
<i>Geotrygon montana</i>	Bird	4	4	5	1
<i>Columbina talpacoti</i>	Bird				1
<i>Psophia dextralis</i>	Bird	96	10		
<i>Trogon melanurus</i>	Bird	8	14		
<i>Trogon viridis</i>	Bird	12	8	2	5
<i>Trogon ramonianus</i>	Bird	6	1	1	
<i>Trogon curucui</i>	Bird	1	7		
<i>Trogon rufus</i>	Bird			4	
<i>Trogon collaris</i>	Bird				1
<i>Baryphthengus martii</i>	Bird		1		
<i>Momotus momota</i>	Bird			19	
<i>Ramphastos tucanus</i>	Bird	51	37	8	34
<i>Ramphastos vitellinus</i>	Bird	86	50	7	31
<i>Selenidera gouldii</i>	Bird	5			1
<i>Pteroglossus inscriptus</i>	Bird	7	15	1	19
<i>Pteroglossus aracari</i>	Bird	24	19	25	30
<i>Pteroglossus bitorquatus</i>	Bird	44	23	1	16
<i>Pteroglossus sp1</i>	Bird	1			
<i>Melanerpes cruentatus</i>	Bird		1		11
<i>Campephilus rubricollis</i>	Bird	2	4		
<i>Celeus flavus</i>	Bird	8	1		
<i>Celeus elegans</i>	Bird	1	3		
<i>Celeus undatus</i>	Bird	2	6		2
<i>Brotogeris chrysoptera</i>	Bird	2	22	1	1
<i>Pyrilia vulturina</i>	Bird		1		
<i>Pionus fuscus</i>	Bird		2		3
<i>Pionus menstruus</i>	Bird	3	4		6
<i>Amazona amazonica</i>	Bird			1	2
<i>Amazona farinosa</i>	Bird	4	3		10
<i>Amazona sp1</i>	Bird	1			

<i>Amazona</i> sp2	Bird	1			
<i>Forpus passerinus</i>	Bird				1
<i>Pionites leucogaster</i>	Bird	2			
<i>Deroptyus accipitrinus</i>	Bird	2			1
<i>Pyrrhura amazonum</i>	Bird	1		1	3
<i>Ara macao</i>	Bird				1
<i>Ara severus</i>	Bird			1	1
<i>Ara chloropterus</i>	Bird		1		
Psitacidae sp1	Bird	1			
<i>Hylexetastes uniformis</i>	Bird		5		
<i>Tyranneutes stolzmanni</i>	Bird	9	6	1	1
<i>Chiroxiphia pareola</i>	Bird			29	1
<i>Lepidothrix iris</i>	Bird	29	14		
<i>Ceratopipra rubrocapilla</i>	Bird	121	85	78	16
<i>Phoenicircus carnifex</i>	Bird	2			
<i>Querula purpurata</i>	Bird	5	3	1	5
<i>Lipaugus vociferans</i>	Bird	72	25	5	13
<i>Cotinga cayana</i>	Bird	29	16		5
<i>Cotinga cotinga</i>	Bird	3			
<i>Gymnoderus foetidus</i>	Bird				1
<i>Xipholena lamellipennis</i>	Bird	35	21		
<i>Schiffornis turdina</i>	Bird	8	2		1
<i>Laniocera hypopyrra</i>	Bird	8	1		1
<i>Iodopleura isabellae</i>	Bird	10		1	1
<i>Tityra cayana</i>	Bird				4
<i>Tityra semifasciata</i>	Bird	17	4		17
<i>Tityra</i> sp1	Bird		1		
<i>Pachyramphus rufus</i>	Bird				1
<i>Pachyramphus castaneus</i>	Bird				1
<i>Pachyramphus polychopterus</i>	Bird				1
<i>Pachyramphus marginatus</i>	Bird	2		2	
<i>Pachyramphus minor</i>	Bird	7	2		
<i>Piprites chloris</i>	Bird	1			
<i>Mionectes oleagineus</i>	Bird			2	2
<i>Mionectes macconnelli</i>	Bird	16	1		
<i>Tolmomyias poliocephalus sclateri</i>	Bird		1		13
<i>Tolmomyias flaviventris</i>	Bird				1
<i>Myiornis ecaudatus</i>	Bird	2			
<i>Lophotriccus galeatus</i>	Bird				5
<i>Zimmerius acer</i>	Bird	1	1		
<i>Ornithion inerme</i>	Bird	1		4	1
<i>Elaenia</i> sp1	Bird			3	
<i>Myiopagis gaimardii</i>	Bird	1			2
<i>Tyrannulus elatus</i>	Bird	2		1	1
<i>Attila spadiceus</i>	Bird		1	8	1
<i>Legatus leucophaeus</i>	Bird	1	1	1	2
<i>Ramphotrigon ruficauda</i>	Bird				2

<i>Myiarchus tuberculifer</i>	Bird				4
<i>Myiarchus</i> sp1	Bird		1	2	
<i>Pitangus sulphuratus</i>	Bird		1	23	5
<i>Myiodynastes maculatus</i>	Bird		2	1	2
<i>Megarynchus pitangua</i>	Bird			6	2
<i>Myiozetetes cayanensis</i>	Bird		1	8	
<i>Myiozetetes luteiventris</i>	Bird				1
<i>Tyrannus melancholicus</i>	Bird		3	14	
<i>Empidonomus varius</i>	Bird		1	1	1
<i>Conopias trivirgatus</i>	Bird	2			
<i>Sublegatus</i> sp1	Bird		1		
Tyrannidae sp1	Bird				1
Tyrannidae sp2	Bird				1
<i>Lathrotriccus euleri</i>	Bird		1		
<i>Vireo chivi</i>	Bird			2	8
<i>Turdus fumigatus</i>	Bird			7	3
<i>Turdus albicollis</i>	Bird	11			
<i>Euphonia chlorotica</i>	Bird		1		
<i>Euphonia minuta</i>	Bird	1			
<i>Euphonia violacea</i>	Bird		3		9
<i>Euphonia rufiventris</i>	Bird	4	7		
<i>Euphonia</i> sp1	Bird				2
<i>Psarocolius decumanus</i>	Bird			1	5
<i>Psarocolius viridis</i>	Bird	10	5		3
<i>Cacicus cela</i>	Bird		2		29
<i>Cacicus haemorrhous</i>	Bird	1			1
<i>Icterus cayanensis</i>	Bird	1			
<i>Lamprospiza melanoleuca</i>	Bird	30	4		10
<i>Cyanoloxia rothschildii</i>	Bird				2
<i>Parkerthraustes humeralis</i>	Bird		4		
<i>Chlorophanes spiza</i>	Bird	6	1		
<i>Hemithraupis guira</i>	Bird	10	8		
<i>Cyanerpes caeruleus</i>	Bird	15	1		
<i>Cyanerpes cyaneus</i>	Bird	12	1	1	
<i>Dacnis cayana</i>	Bird	23	20	12	16
<i>Dacnis lineata</i>	Bird	10			1
<i>Saltator maximus</i>	Bird		1		
<i>Saltator coerulescens</i>	Bird			1	
<i>Saltator grossus</i>	Bird				1
<i>Coereba flaveola</i>	Bird				1
<i>Loriotus luctuosus</i>	Bird	3	1	12	8
<i>Loriotus cristatus</i>	Bird	26	10	3	11
<i>Maschalethraupis surinamus</i>	Bird	20	2		
<i>Lanio versicolor</i>	Bird	2			
<i>Ramphocelus carbo</i>	Bird	1	1	1	6
<i>Ixothraupis punctata</i>	Bird	23	23	2	
<i>Thraupis episcopus</i>	Bird		8	3	17
<i>Thraupis palmarum</i>	Bird	4	10	16	22

<i>Stilpnia nigrocincta</i>	Bird				3
<i>Tangara mexicana</i>	Bird	2	9	2	14
<i>Tangara velia</i>	Bird	3			2
Thraupidae sp1	Bird	7			
Thraupidae sp2	Bird	1			
Sp1	Bird	1			
Sp2	Bird				2
Sp3	Bird	1			
Sp4	Bird	1			
Sp5	Bird	1			
Sp6	Bird	1			
<i>Caluromys philander</i>	Mammal		4		1
<i>Didelphis marsupialis</i>	Mammal	3	6	7	5
Didelphidae sp	Mammal				1
<i>Philander opossum</i>	Mammal		1		
<i>Marmosa demerarae</i>	Mammal		2	1	
<i>Metachirus nudicaudatus</i>	Mammal		5	3	
<i>Marmosops</i> sp	Mammal			3	
rat	Mammal	1	1	5	1
<i>Alouatta belzebul</i>	Mammal	3	7	7	6
<i>Ateles marginatus</i>	Mammal	21	4		1
<i>Mico argentatus</i>	Mammal	2	10	9	33
<i>Saimiri sciureus</i>	Mammal	13	5	17	7
<i>Sapajus apella</i>	Mammal	5	26	6	17
<i>Chiropotes albinasus</i>	Mammal	3	5		
<i>Callicebus moloch</i>	Mammal	2		4	3
<i>Dasyprocta leporina</i>	Mammal	96	59	14	12
<i>Makalata didelphoides</i>	Mammal			2	
<i>Proechimys</i> sp	Mammal	2	8	21	14
<i>Guerlinguetus aestuans</i>	Mammal	2	1		20
<i>Sciurus</i> sp	Mammal		5		
<i>Cerdocyon thous</i>	Mammal			1	
<i>Eira barbara</i>	Mammal	1			
<i>Nasua nasua</i>	Mammal		14	4	5
<i>Mazama americana</i>	Mammal	1		1	1
<i>Mazama nemorivaga</i>	Mammal	7			
<i>Dicotyles tajacu</i>	Mammal	1	3		
<i>Tapirus terrestris</i>	Mammal	1			
<i>Cuniculus paca</i>	Mammal	9	13		5

Table S3.4 Plant morphotypes involved in frugivory interaction. The numbers represent the frequencies of interaction involving the species.

Family	Species	undisturbed	logged	historically-burned	recently-burned
Achariaceae	<i>Lindackeria latifolia</i>			12	
Achariaceae	<i>Lindackeria paraensis</i>			2	
Anacardiaceae	<i>Spondias mombin</i>			14	
Anacardiaceae	<i>Tapirira guianensis</i>		1	1	
Annonaceae	<i>Annona exsucca</i>			2	3
Annonaceae	<i>Bocageopsis multiflora</i>	9			7
Annonaceae	<i>Guatteria schomburgkiana</i>		5		
Annonaceae	<i>Guatteria poeppigiana</i>		3	11	3
Annonaceae	<i>Guatteria</i> sp1				1
Annonaceae	<i>Xylopi aromatic</i>			2	
Annonaceae	<i>Xylopi nitida</i>		15		14
Apocynaceae	<i>Geissospermum sericeum</i>				2
Araceae	<i>Anthurium clavigerum</i>	5			
Araceae	<i>Heteropsis</i> sp1	1			
Araliaceae	<i>Schefflera morototoni</i>	11	38	38	3
Arecaceae	<i>Acrocomia aculeata</i>			1	
Arecaceae	<i>Astrocaryum tucuma</i>			1	
Arecaceae	<i>Astrocaryum aculeatum</i>				28
Arecaceae	<i>Astrocaryum gynacanthum</i>	1			
Arecaceae	<i>Attalea maripa</i>			6	
Arecaceae	<i>Attalea speciosa</i>		2	2	
Arecaceae	<i>Oenocarpus distichus</i>		3		
Boraginaceae	<i>Cordia bicolor</i>		1		2
Boraginaceae	<i>Tournefortia bicolor</i>				2
Burseraceae	<i>Burseraceae</i> sp1		4		
Burseraceae	<i>Crepidospermum rhoifolium</i>				5
Burseraceae	<i>Protium tenuifolium</i>	7			1
Burseraceae	<i>Trattinnickia burserifolia</i>	12	6		
Cannabaceae	<i>Trema micrantha</i>				141
Chrysobalanaceae	<i>Licania kunthiana</i>	1			
Combretaceae	<i>Buchenavia grandis</i>				23
Combretaceae	<i>Buchenavia congesta</i>	5	5		
Connaraceae	<i>Rourea ligulata</i>	34			68
Cucurbitaceae	<i>Gurania</i> sp1		41		
Dilleniaceae	<i>Dilleniaceae</i> sp1				6
Dilleniaceae	<i>Doliocarpus brevipedicellatus</i>		3		
Ebenaceae	<i>Diospyros capreifolia</i>	6	2	57	

Ebenaceae	<i>Diospyros carbonaria</i>	3		4	
Euphorbiaceae	<i>Glycydendron amazonicum</i>			1	
Fabaceae	<i>Amphiodon effusus</i>	12			4
Fabaceae	<i>Copaifera reticulata</i>			4	
Fabaceae	<i>Dalbergia</i> sp1	65			3
Fabaceae	<i>Dialium guianensis</i>		1		
Fabaceae	<i>Dipteryx odorata</i>				2
Fabaceae	<i>Enterolobium schomburgkii</i>	2			2
Fabaceae	<i>Hymenaea courbaril</i>		2		
Fabaceae	<i>Hymenaea parvifolia</i>			8	
Fabaceae	<i>Inga capitata</i>		2	1	
Fabaceae	<i>Inga rubiginosa</i>			2	2
Fabaceae	<i>Inga</i> sp1			11	
	<i>Stryphnodendron</i>				
Fabaceae	<i>pulcherrimum</i>	1			
Gnetaceae	<i>Gnetum</i> sp1				2
Goupiaceae	<i>Goupia_galbra</i>	1			
Humiriaceae	<i>Endopleurauchi</i>	4	27		62
Humiriaceae	<i>Sacoglottis guianensis</i>	53	31		
Icacinaceae	<i>Dendrobangia boliviana</i>		2		
Lauraceae	<i>Licania</i> sp1				12
Lauraceae	<i>Mezilaurus crassiramea</i>			6	
Lauraceae	<i>Mezilaurus decurrens</i>		13		
Lauraceae	<i>Nectandra</i> sp1	1			
Lauraceae	<i>Ocotea glomerata</i>	36		15	
Lauraceae	<i>Ocotea longifolia</i>			18	13
Lauraceae	<i>Ocotea</i> sp1	3			
Lauraceae	<i>Ocotea</i> sp2			3	
Lauraceae	<i>Ocotea</i> sp3		2		
Lauraceae	<i>Ocotea</i> sp4			21	
Lauraceae	<i>Sextonia rubra</i>		95		
Lecythidaceae	<i>Bertholletia excelsa</i>	3			
Leguminosae	<i>Apuleia leiocarpa</i>				1
Loranthaceae	<i>Psittacanthus</i> sp1			2	
Malpighiaceae	<i>Byrsonima crispa</i>	23		9	
Malpighiaceae	<i>Byrsonima densa</i>	2			
Malpighiaceae	<i>Mezia</i> sp1	1			
Melastomataceae	<i>Bellucia grossularioides</i>			2	
Melastomataceae	<i>Melastomataceae</i> sp1			3	
Melastomataceae	<i>Miconia affinis</i>		9	23	
Melastomataceae	<i>Miconia chrysophylla</i>	5	6		
Melastomataceae	<i>Miconia dispar</i>		3		
Melastomataceae	<i>Miconia egensis</i>		18	6	
Melastomataceae	<i>Miconia eriodonta</i>			12	

Melastomataceae	<i>Miconia manauara</i>	46	14		66
Melastomataceae	<i>Miconia minutiflora</i>		15		3
Melastomataceae	<i>Miconia poeppigii</i>		2		
Melastomataceae	<i>Miconia prasina</i>	28	1		74
Melastomataceae	<i>Miconia pyrifolia</i>	25			
Melastomataceae	<i>Miconia ruficalyx</i>		22		
Melastomataceae	<i>Miconia</i> sp1				2
Melastomataceae	<i>Miconia</i> sp2	114	11	83	
Melastomataceae	<i>Mouriria brevipes</i>		12		
Meliaceae	<i>Guarea grandifolia</i>				1
Meliaceae	<i>Trichilia micrantha</i>				47
Mistletoe	<i>Mistletoe</i> sp1			8	
Moraceae	<i>Brosimum acutifolium</i>	217	115		
Moraceae	<i>Brosimum guianense</i>				7
Moraceae	<i>Ficus citrifolia</i>				29
Moraceae	<i>Ficus</i> sp1	97	292		21
Moraceae	<i>Ficus</i> sp2				4
Moraceae	<i>Ficus</i> sp3		1		
Moraceae	<i>Ficus obtusifolia</i>		17		
Moraceae	<i>Ficus</i> sp5				2
Moraceae	<i>Maquira sclerophylla</i>	4	2		5
Myristicaceae	<i>Iryanthera</i> sp1				9
Myristicaceae	<i>Virola calophylla</i>				1
Myristicaceae	<i>Virola crebrinervia</i>				2
Myristicaceae	<i>Virola michelii</i>	49	7	1	51
Myristicaceae	<i>Virola</i> sp1		5		
Myrtaceae	<i>Eugenia patrisii</i>			1	
Myrtaceae	<i>Myrcia</i> sp1			2	
Myrtaceae	<i>Myrcia splendens</i>			3	48
Myrtaceae	<i>Myrciaria floribunda</i>		8		
Myrtaceae	<i>Myrtaceae</i> sp1				3
Myrtaceae	<i>Myrtaceae</i> sp2	3			
Myrtaceae	<i>Myrtaceae</i> sp3		1		
NA	liana sp1			11	
NA	liana sp5			4	
NA	liana sp6				1
NA	liana sp7	1			
NA	Sp15				1
NA	Sp1				3
NA	Sp2				1
NA	Sp3				1
NA	Sp4				1
NA	Sp5				1
NA	Sp6				2

Poaceae	<i>Lasiacis ligulata</i>				5
Polygonaceae	<i>Coccoloba ascendens</i>		4		
Putranjivaceae	<i>Drypetes variabilis</i>		3		
Rubiaceae	<i>Chimarrhis turbinata</i>		3		
Rubiaceae	<i>Coussarea albescens</i>	1			
Rubiaceae	<i>Coussarea</i> sp1				4
Salicaceae	<i>Casearia arborea</i>			37	
Salicaceae	<i>Laetia procera</i>	1	23	2	69
Sapotaceae	<i>Chrysophyllum lucentifolium</i>				1
Sapotaceae	<i>Manilkara bidentata</i>	5			3
Sapotaceae	<i>Manilkara paraensis</i>	17		3	2
Sapotaceae	<i>Pouteria cladantha</i>		3		
Sapotaceae	<i>Pouteria decorticans</i>	3			
Sapotaceae	<i>Pouteria elegans</i>				4
Sapotaceae	<i>Pouteria engleri</i>				5
Sapotaceae	<i>Pouteria macrophylla</i>		15		
Sapotaceae	<i>Pouteria procera</i>				4
Sapotaceae	<i>Pouteria</i> sp1		1		
Sapotaceae	<i>Pradosia granulosa</i>			7	
Sapotaceae	<i>Pradosia surinamensis</i>	1			
Sapotaceae	<i>Sapotaceae</i> sp1	1			
Sapotaceae	<i>Sapotaceae</i> sp2	1			
Simaroubaceae	<i>Simaba guianensis</i>		4		
Simaroubaceae	<i>Simarouba amara</i>				2
Siparunaceae	<i>Siparuna guianensis</i>		1	4	
Siparunaceae	<i>Siparuna</i> sp1				1
Solanaceae	<i>Solanum salviifolium</i>				2
Urticaceae	<i>Cecropia distachya</i>	1	4		11
Urticaceae	<i>Cecropia obtusa</i>	3			
Urticaceae	<i>Cecropia palmata</i>			6	11
Urticaceae	<i>Cecropia sciadophylla</i>	127	83		
Urticaceae	<i>Coussapoa angustifolia</i>		19		
Urticaceae	<i>Coussapoa tessmannii</i>	49	45		
Urticaceae	<i>Pourouma guianensis</i>		11		9
Urticaceae	<i>Pourouma mollis</i>		1		
Violaceae	<i>Coussarea paniculata</i>	1	2		
Violaceae	<i>Payparola</i> sp1	11			
Violaceae	<i>Rinorea guianensis</i>	1			2
Vitaceae	<i>Cissus paraensis</i>			2	
Vitaceae	<i>Cissus verticillata</i>				14
Vochysiaceae	<i>Erisma uncinatum</i>	4			

3.9.3 Spatial auto-correlation

As we expected a greater similarity in species composition on the forests that are closer to each other, we tested the spatial auto-correlation for frugivores, plants and interactions. We used UTM (Universal Transverse Mercator) coordinate and the abundance of frugivores, plants and interactions of each forest transect to build the dissimilarity matrix based on Bray-Curtis index. Then, based on Pearson correlation coefficient, we performed a Mantel test with 1,000 permutations run using *mantel* function on *vegan* Package (Oksanen et al. 2015). However, we did not detect spatial autocorrelation in frugivores ($r = -0.079$, $p = 0.76$), plants ($r = -0.056$, $p = 0.7$) and interactions ($r = 0.02$, $p = 0.4$) (Figure S3.2).

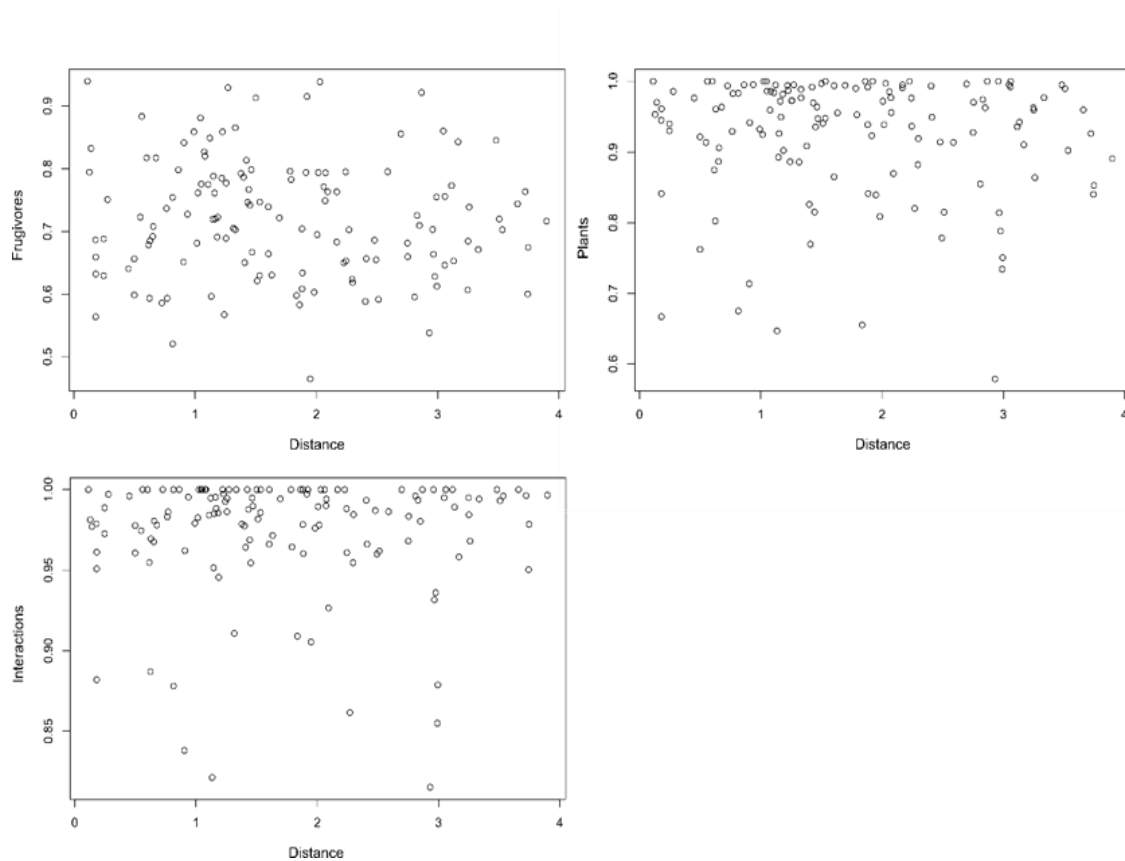


Figure S3.2 Spatial autocorrelation on frugivores, plants and interactions species sampled across 17 forest transects.

3.9.3 Distance measures

As the control area (undisturbed) can influence the species distribution acting as a source for species colonisation of the surrounding areas (Tscharntke et al. 2012), we measure the effects of forest control (undisturbed forests) on species and interactions occurrence. We used the shortest path (kilometres) between each transect to the nearest forest control and the abundance of frugivores, plants and interactions of each forest transect to build the dissimilarity matrix based on Bray-Curtis index. Then, Pearson-based on Mantel tests with 1,000 permutations run using *mantel* function on *vegan* Package (Oksanen et al. 2015). We detect a weak correlation among forest control distance in frugivores ($r = 0.142$, $P = 0.142$), plants ($r = 0.189$, $P = 0.041$) and interactions ($r = 0.157$, $P = 0.051$) (Figure S3.3) occurrence. Thus, we did not include distance on our models.

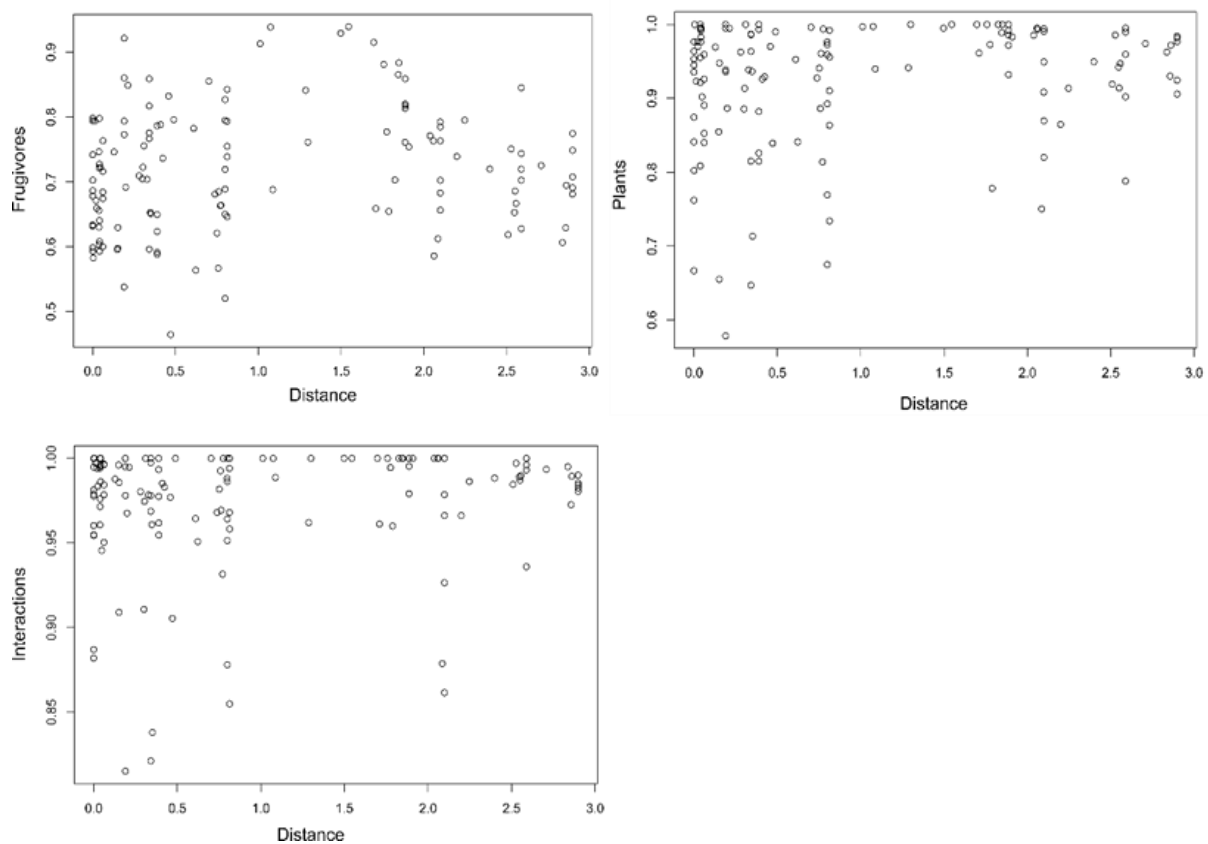


Figure S3.3 Distance from control forests (undisturbed forest) correlation on frugivores, plants and interactions composition.

Table S3.5 Results from Generalised Linear Models testing the effects of human-driven forest disturbances on frugivory networks in the Amazon Forest. Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned).

Network metric	Model		Estimate	Std. Error	t-value	P-value
Number of frugivores species (A)	forest	logged	0.08	0.10	0.75	0.45
	class +	historically-burned	-0.31	0.13	-2.36	0.02
		recently-burned	0.20	0.12	1.65	0.10
	sampling		0.28	0.12	2.36	0.02
Number of plants species (P)	forest	logged	0.11	0.17	0.68	0.50
	class +	historically-burned	-0.14	0.19	-0.75	0.46
		recently-burned	0.14	0.18	0.76	0.45
	sampling		-0.36	0.19	-1.97	0.05
Network size	forest	logged	0.08	0.09	0.92	0.36
	class +	historically-burned	-0.26	0.11	-2.42	0.02
		recently-burned	0.17	0.10	1.73	0.08
	sampling		0.10	0.10	0.99	0.32
Number of unique interactions (I)	forest	logged	0.17	0.08	2.15	0.03
	class +	historically-burned	-0.32	0.10	-3.19	0.00
		recently-burned	0.34	0.09	3.72	0.00
	sampling		0.26	0.09	2.91	0.00
Number of links (Ni)	forest	logged	-9.71	32.91	-0.30	0.77
	class +	historically-burned	-70.13	36.10	-1.94	0.08
		recently-burned	16.12	37.03	0.44	0.67
	sampling		279.49	35.62	7.85	0.00
Connectance	forest	logged	0.11	0.09	1.19	0.26
	class +	historically-burned	0.21	0.10	2.12	0.06
		recently-burned	0.09	0.10	0.90	0.39
	sampling		0.28	0.10	2.73	0.02
Patefield	forest	logged	0.00	0.00	-0.88	0.40
	class +	historically-burned	0.00	0.00	1.00	0.34
		recently-burned	0.00	0.00	0.91	0.38
	sampling		0.00	0.00	2.03	0.07

Vaznull	forest class +	logged	0.00	0.00	-1.15	0.27
		historically-burned	0.00	0.00	-0.58	0.57
		recently-burned	-0.01	0.00	-1.97	0.07
	sampling		0.00	0.00	-0.23	0.82
Nestedness	forest class +	logged	-0.41	2.61	-0.16	0.88
		historically-burned	4.70	2.86	1.64	0.13
		recently-burned	3.39	2.94	1.15	0.27
	sampling		12.19	2.83	4.31	0.00
Patefield	forest class +	logged	-1.11	1.61	-0.69	0.50
		historically-burned	0.06	1.76	0.03	0.97
		recently-burned	-0.74	1.81	-0.41	0.69
	sampling		1.61	1.74	0.92	0.37
Vaznull	forest class +	logged	-0.83	1.28	-0.65	0.53
		historically-burned	0.71	1.40	0.51	0.62
		recently-burned	-0.07	1.44	-0.05	0.96
	sampling		2.83	1.38	2.05	0.06
H2' Specialization	forest class +	logged	-0.02	0.06	-0.37	0.72
		historically-burned	-0.01	0.06	-0.22	0.83
		recently-burned	-0.09	0.06	-1.36	0.20
	sampling		-0.03	0.06	-0.55	0.59
Patefield	forest class +	logged	4.38	8.74	0.50	0.63
		historically-burned	6.62	9.58	0.69	0.50
		recently-burned	2.55	9.83	0.26	0.80
	sampling		10.33	9.46	1.09	0.30
Vaznull	forest class +	logged	1.40	2.77	0.50	0.62
		historically-burned	2.03	3.04	0.67	0.52
		recently-burned	0.72	3.11	0.23	0.82
	sampling		3.20	3.00	1.07	0.31
Modularity	forest class +	logged	-0.18	0.25	-0.72	0.49
		historically-burned	-0.04	0.27	-0.14	0.89
		recently-burned	-0.18	0.28	-0.66	0.52
	sampling		-0.53	0.27	-1.97	0.07
Patefield	forest class +	logged	-3.76	6.16	-0.61	0.55
		historically-burned	-1.62	6.76	-0.24	0.81
		recently-burned	-5.15	6.93	-0.74	0.47
	sampling		-14.21	6.67	-2.13	0.05
Vaznull	forest class +	logged	-1.74	2.40	-0.73	0.48
		historically-burned	-1.08	2.63	-0.41	0.69
		recently-burned	-2.03	2.70	-0.75	0.47
	sampling		-5.57	2.60	-2.15	0.05

Table S3.6 The effect of fire and logging on the number of frugivorous species in the Amazonian forests, assessed using generalised linear mixed-effects models with *emmeans* test for post-hoc pairwise comparisons.

Forest class	Estimate	P-value
undisturbed - logged	-0.07	0.87
undisturbed - historically-burned	0.3	0.08
undisturbed - recently-burned	-0.19	0.34
logged - historically-burned	-0.38	<0.01
logged - recently-burned	-0.12	<0.01
recently-burned - historically-burned	-0.5	<0.01

Table S3.7 The effect of fire and logging on the network size (frugivores and plants) in the Amazonian forests, assessed using generalised linear mixed-effects models with *emmeans* test for post-hoc pairwise comparisons.

Forest class	Estimate	P-value
undisturbed - logged	-0.05	0.89
undisturbed - historically-burned	0.3	< 0.01
undisturbed - recently-burned	-0.12	0.47
logged - historically-burned	-0.36	< 0.01
logged - recently-burned	-0.06	0.89
recently-burned - historically-burned	-0.42	< 0.01

Table S3.8 The effect of fire and logging on the number of unique frugivory interactions in the Amazonian forests, assessed using generalised linear mixed-effects models with *emmeans* test for post-hoc pairwise comparisons.

Forest class	Estimate	P-value
undisturbed - logged	-0.17	0.13
undisturbed - historically-burned	0.32	< 0.01
undisturbed - recently-burned	-0.33	< 0.01
logged - historically-burned	-0.49	< 0.01
logged - recently-burned	-0.65	0.17
recently-burned - historically-burned	-0.16	< 0.01

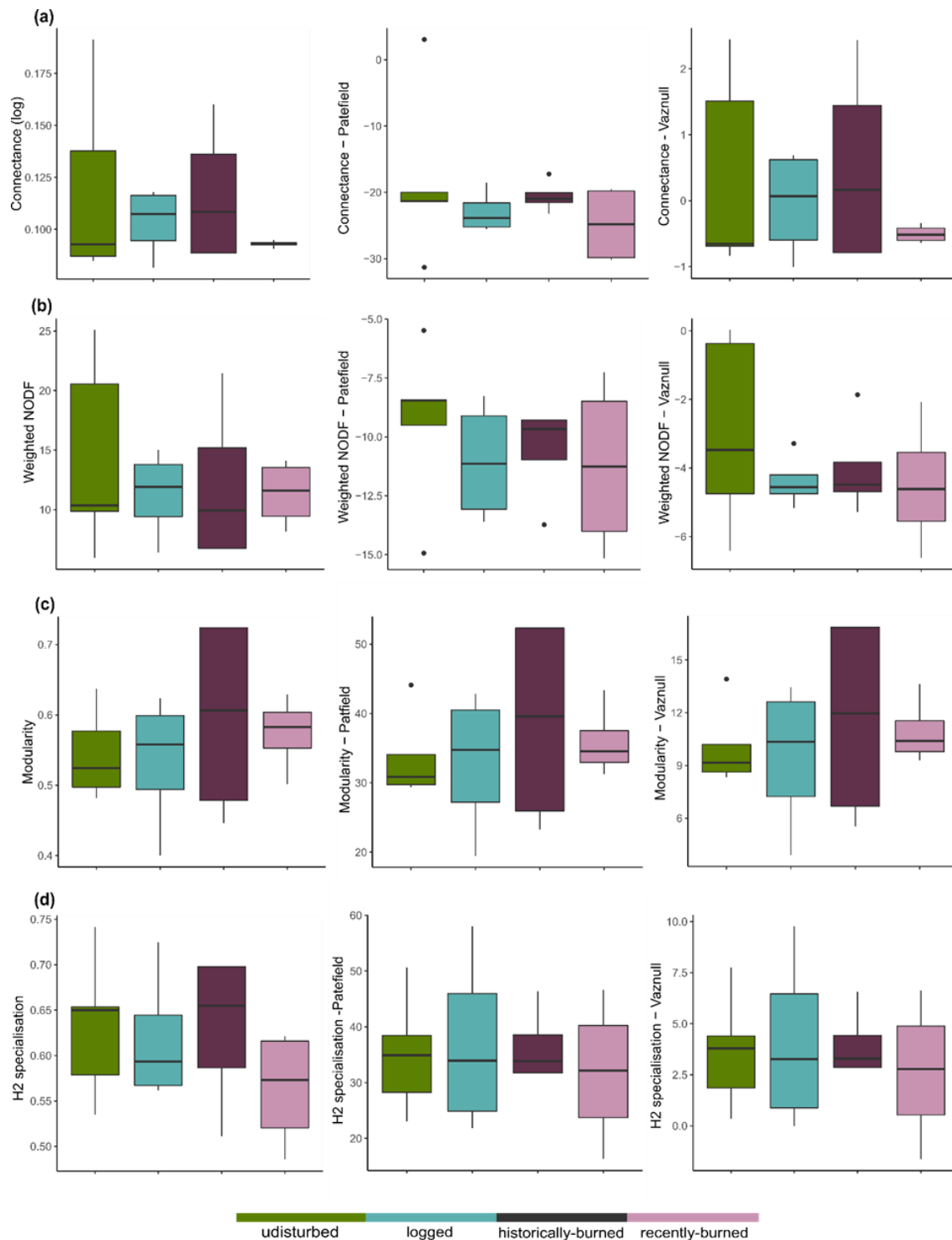


Figure S3.4 The effect of selective logging and forest fires on the structure of frugivory networks: (a) connectivity; (b) Weighted-NODF; (c) Specialisation H2'; and (d) modularity, in the Amazonian forests. The first column shows the results of each metric from the observed values, second and third columns are the z-score obtained using Patefield and Vaznull null

models, respectively (see Methods for details of each model). Black dots are potential outliers and lines inside boxplots represent median values. Forest classes correspond: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned).

Table S3.9 Network metrics and null models for connectance, wNODF, modularity and specialisation (see methods in the main text for details of each network component), of 17 transects sampled along distinct forest classes in the Amazonian forests: undisturbed forest; logged ≥ 30 years prior sampling (logged); logged ≥ 30 years and burned ≥ 18 years prior sampling (historically-burned); and logged ≥ 30 years prior sampling and burned 3 years before the study (recently-burned). First is the observed value in each network, second and third are the z-score of Patefield and Vaznull null models, respectively.

Connectance				Nestedness			H2 specialization			Modularity		
Forest class	Observed	Patefield	Vaznull	Observed	Patefield	Vaznull	Observed	Patefield	Vaznull	Observed	Patefield	Vaznull
undisturbed	0.09	-20.08	-0.84	9.87	-8.61	-3.38	0.74	31.71	3.78	0.50	30.86	9.16
undisturbed	0.14	-21.36	1.51	25.09	-7.11	-0.34	0.54	40.65	4.29	0.52	29.74	8.33
undisturbed	0.19	2.75	2.45	20.56	-5.63	0.25	0.58	20.94	0.39	0.48	29.37	8.62
undisturbed	0.09	-31.31	-0.69	10.36	-12.83	-6.59	0.65	53.67	7.62	0.58	34.08	10.20
undisturbed	0.09	-18.82	-0.66	5.96	-9.70	-4.71	0.65	25.66	1.87	0.64	44.10	13.91
logged	0.12	-25.49	0.60	15.02	-11.02	-4.61	0.57	44.38	5.24	0.53	29.80	8.35

logged	0.08	-21.27	-1.01	6.39	-9.58	-4.56	0.56	19.81	0.03	0.62	42.83	13.46
logged	0.12	-25.08	0.69	13.39	-11.65	-5.30	0.73	61.49	9.62	0.40	19.47	3.90
logged	0.10	-17.48	-0.46	10.44	-8.45	-3.19	0.62	23.53	1.20	0.59	39.72	12.34
historically-burned	0.13	-23.15	1.11	21.46	-8.52	-1.88	0.61	49.07	6.44	0.45	23.28	5.54
historically-burned	0.09	-19.74	-0.79	6.76	-9.48	-4.44	0.70	28.82	2.87	0.72	52.32	16.86
historically-burned	0.09	-19.74	-0.79	6.76	-9.48	-4.44	0.70	28.82	2.87	0.72	52.32	16.86
historically-burned	0.16	-17.16	2.44	13.11	-11.77	-5.42	0.51	37.99	3.60	0.49	26.83	7.07
recently-burned	0.09	-30.20	-0.44	9.87	-13.02	-6.79	0.53	40.30	4.20	0.60	35.59	10.85
recently-burned	0.09	-29.75	-0.34	13.34	-11.68	-5.32	0.61	49.33	6.51	0.57	33.49	9.94
recently-burned	0.09	-18.72	-0.64	8.16	-9.09	-3.96	0.62	23.76	1.28	0.63	43.33	13.64
recently-burned	0.10	-18.36	-0.59	14.13	-7.42	-1.94	0.49	14.80	-1.54	0.50	31.26	9.30

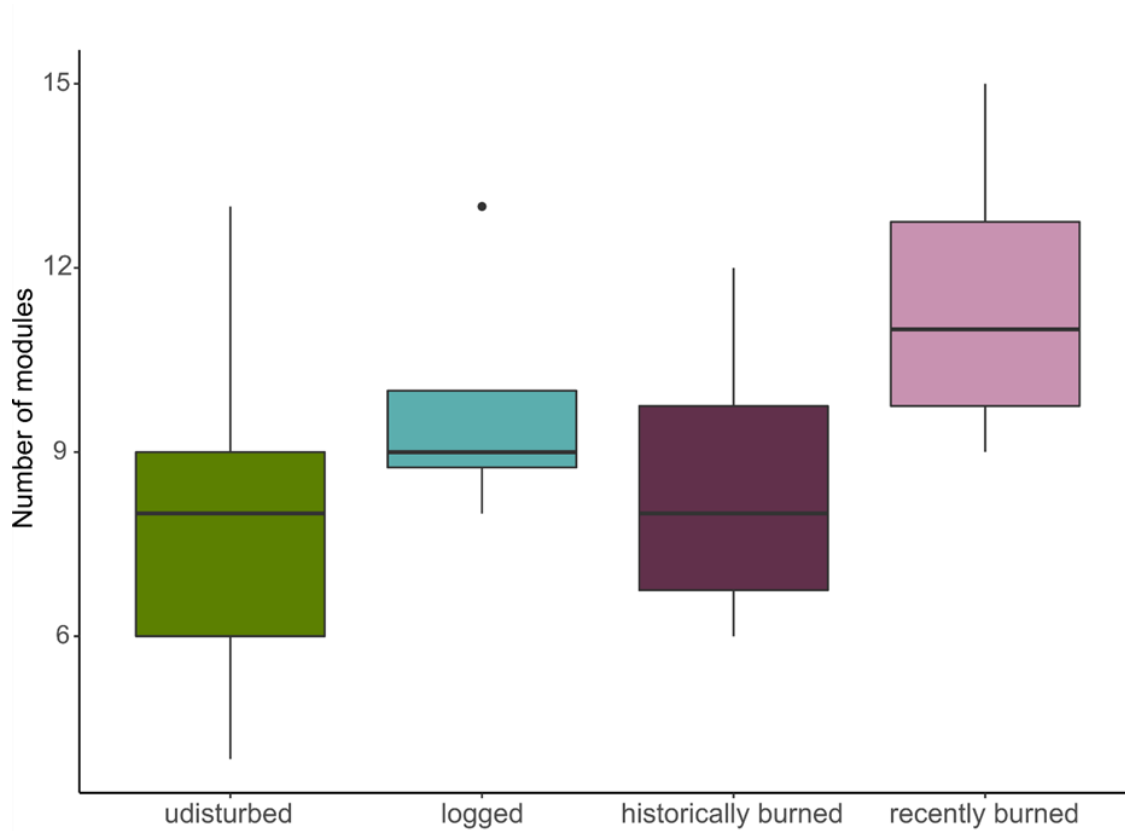


Figure S3.5 Differences on the number of modules among forest classes. Black dots are potential outliers and lines inside boxplots represent median values.

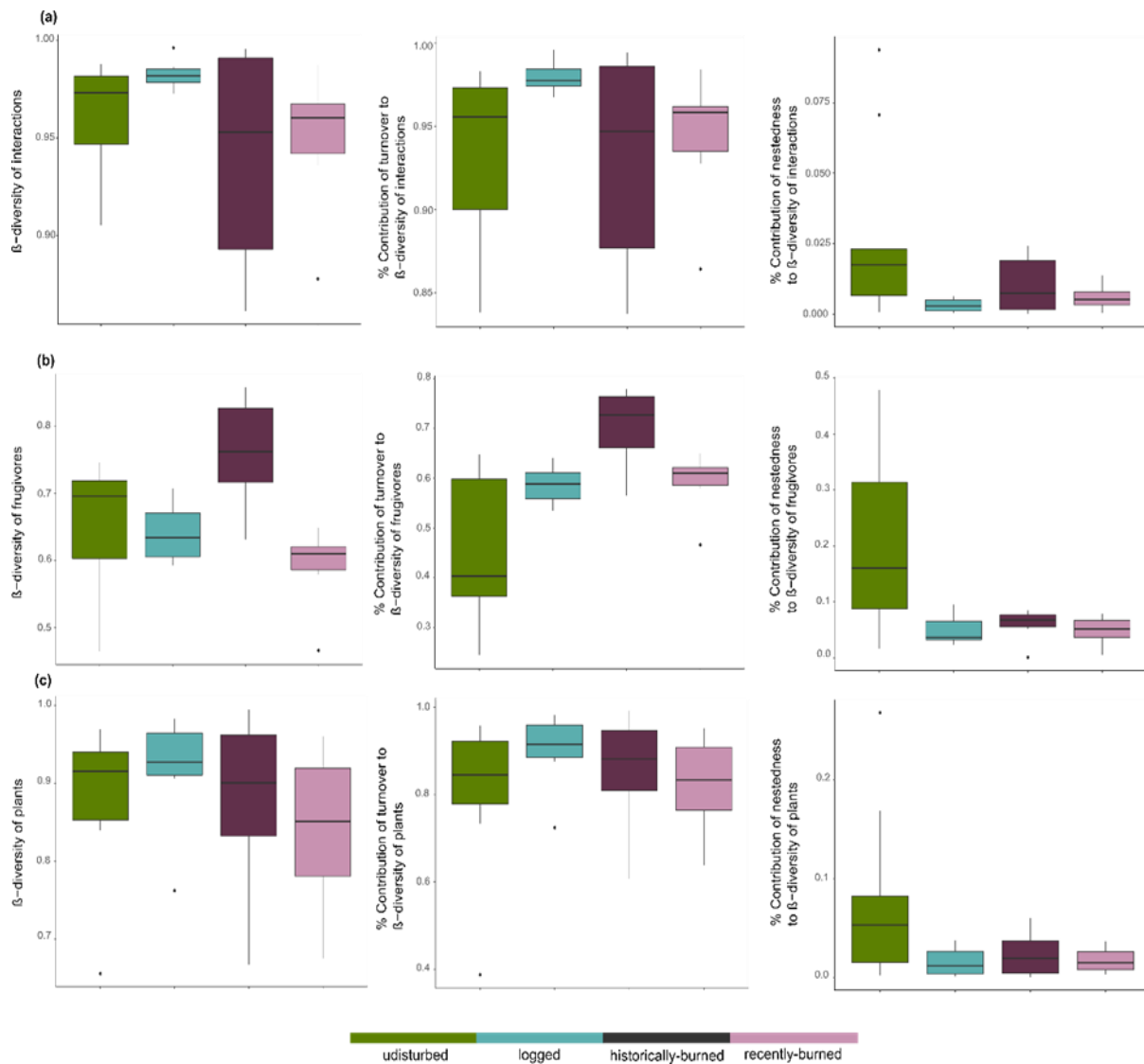


Figure S3.6 The effect of selective logging and forest fires on the beta-diversity based on occurrence data of: (a) interactions; (b) frugivores; and (c) plant species. The first column boxplot is the total of beta-diversity, second and third is the percentage contribution of the turnover and nestedness component to the total beta-diversity observed among forest classes. Black dots are potential outliers and lines inside boxplots represent median values.

Table S3.10 Beta diversity of frugivores, plants and interactions of 17 ecological networks among distinct forest classes sampled in the Amazon Forests. Beta-diversity was estimated for the whole landscape (total) and within each forest class. β -total corresponds to the sum of species and interactions dissimilarity. β -turnover implies the replacement of some species and interactions by others and β -nestedness considers that a subset of species and interactions of sites with smaller numbers of species are subsets of the biotas at richer sites.

Components	Level	β total	β turnover	β nestedness
Frugivores	landscape	0.90	0.85	0.05
	undisturbed	0.75	0.61	0.14
	logged	0.72	0.67	0.05
	historically-burned	0.81	0.75	0.06
	recently-burned	0.73	0.68	0.04
Plants	landscape	0.96	0.94	0.02
	undisturbed	0.91	0.86	0.04
	logged	0.93	0.92	0.01
	historically-burned	0.91	0.88	0.03
	recently-burned	0.87	0.85	0.02
Interactions	landscape	0.98	0.98	0.01
	undisturbed	0.96	0.94	0.02
	logged	0.98	0.98	<0.01
	historically-burned	0.96	0.94	0.01
	recently-burned	0.95	0.95	0.01

3.9.3 References

- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Jordano, P. 2016. Sampling networks of ecological interactions. *Functional Ecology* 30:1883–1893.
- Jordano, P., and E. W. Schupp. 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591–615.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, Oh. R.B., S. G.L., P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *Vegan: Community Ecology Package* R Package. version 2.3-1.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012, August 1. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87:661-685.

CHAPTER THREE

Predation on artificial caterpillars following understory fires in human-modified Amazonian forests



Predation on artificial caterpillars following understorey fires in human-modified Amazonian forests

Liana Chesini Rossi^{1,2}  | Erika Berenguer^{3,4}  | Alexander Charles Lees^{2,5}  |
 Jos Barlow^{4,6}  | Joice Ferreira^{7,8}  | Filipe M. França⁹  | Paulo Tavares⁸  |
 Marco Aurélio Pizo¹ 

¹Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

²Division of Biology and Conservation Ecology, Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

³Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

⁴Lancaster Environment Centre, Lancaster University, Lancaster, UK

⁵Cornell Lab of Ornithology, Cornell University, Ithaca, USA

⁶Setor de Ecologia e Conservação, Universidade Federal de Lavras, Lavras, MG, Brazil

⁷Embrapa Amazônia Oriental, Belém, PA, Brazil

⁸Programa de Pós-Graduação em Ecologia (PPGECO) e Programa de Pós-Graduação em Ciências Ambientais (PPGCA), Universidade Federal do Pará, Belém, PA, Brazil

⁹School of Biological Sciences, University of Bristol, Bristol, UK

Correspondence

Liana Chesini Rossi, Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), CEP 13506-900, Rio Claro, SP, Brazil.
 Email: lianachesini@unesp.br

Funding information

Fondation BNP Paribas; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: CNPq-CAPES 441659/2016-0, CNPq-PrevFogo-IBAMA 441949/2018-5, CNPq 574008/200 and MCIC-CNPq 420254/2018-8; H2020-MSCA-RISE, Grant/Award Number: 691053-ODYSSEA; Empresa Brasileira de Pesquisa Agropecuária, Grant/Award Number: 02.08.06.005.00; Darwin Initiative, Grant/Award Number: 17-023; The Nature Conservancy and Natural Environment Research Council (NERC), Grant/Award Number: NE/F01614X/1, NE/G000816/1, NE/K016431/1 and NE/P004512/1

Associate Editor: Tomás A. Carlo

Handling Editor: Sofia Gripenberg

Abstract

Tropical forests are facing several impacts from anthropogenic disturbances, climate change, and extreme climate events, with potentially severe consequences for ecological functions, such as predation on folivorous invertebrates. Folivory has a major influence on tropical forests by affecting plant fitness and overall seedling performance. However, we do not know whether the predation of folivorous arthropods by birds, mammals, reptiles, and other arthropods is affected by anthropogenic disturbances such as selective logging and forest fires. We investigated the impacts of both pre-El Niño human disturbances and the 2015–2016 El Niño understorey fires on the predation of 4500 artificial caterpillars across 30 Amazonian forest plots. Plots were distributed in four pre-El Niño forest classes: undisturbed, logged, logged-and-burned, and secondary forests, of which 14 burned in 2015–16. We found a higher predation incidence in forests that burned during the El Niño in comparison with unburned ones. Moreover, logged-and-burned forests that burned again in 2015–16 were found to have significantly higher predation incidence by vertebrates than other forest classes. However, overall predation incidence in pre-El Niño forest disturbance classes was similar to undisturbed forests. Arthropods were the dominant predators of artificial caterpillars, accounting for 91.5% of total predation attempts. Our results highlight the resilience of predation incidence in human-modified forests, although the mechanisms underpinning this resilience remain unclear.

Abstract in Portuguese is available with online material.

KEYWORDS

Amazon, arthropods, dummy caterpillar, El Niño, forest degradation, forest fires, forest regeneration, herbivory control

1 | INTRODUCTION

Degraded primary forests, including those affected by human-driven disturbances, such as selective logging and understorey fires, are rapidly becoming ubiquitous in the tropics (Lewis et al., 2015). Between 1995 and 2017, more Amazonian forests were degraded by human activities than deforested (337,427 km² of degradation vs. 308,311 km² of deforestation; Matricardi et al., 2020). Amazonia is also undergoing rapid changes in regional climate—in the past 40 years, the average temperature has increased by 1.5°C (Gloor et al., 2015) and the dry season has become longer and drier (Fu et al., 2013). Degraded forests have more open canopies and combined with rising temperatures and changing rainfall regimes this leaves forests more likely to sustain understorey fires (Holdsworth & Christopher, 1997). During the 2015–16 El Niño, over one million hectares of forests burned in the lower Tapajós region in eastern Brazilian Amazon, even affecting previously undisturbed forests (Withey et al., 2018).

The impacts of human disturbance on species richness and composition in Amazonian forests have been intensively studied. Selective logging, for example, disproportionately affects terrestrial insectivorous passerine birds (Hamer et al., 2015; Moura et al., 2016), while understorey fires negatively impact the abundance of predatory ants (Paolucci et al., 2016). Understorey fires can also lead to severe structural changes to forests resulting from high tree mortality (Berenguer et al., 2021; Silva et al., 2018), leading to shifts in vertebrate (Barlow & Peres, 2004; Moura et al., 2013), invertebrate (França et al., 2020; Silveira et al., 2016), and plant communities (Berenguer, Malhi, et al., 2018). Although such drastic modifications in community composition caused by anthropogenic disturbance would likely affect several ecosystem functions, there is little information about anthropogenic impacts on ecological processes, especially on herbivory control—that is, predation incidence on folivorous arthropods (Murray et al., 2020; Schwab et al., 2021).

Due to their hyper abundance (average of 18,439 species/ha in tropical forests; Basset et al., 2012) and diversity in the use of resources, arthropods can influence several ecosystem processes. For example, folivorous arthropods can create intense pressure on plant communities (Barreto et al., 2021), causing reductions in leaf area (Morrison & Lindell, 2012) and negative impacts on plant fitness and biomass (Dirzo, 1984; Van Bael et al., 2003). Top-down control by predatory species such as vertebrates, other arthropods, and parasitoids may help regulate the abundance of folivorous arthropods (Hairston et al., 1960; Mäntylä et al., 2011). In tropical forests, other arthropods (Lemessa et al., 2015; Zvereva et al., 2020) and birds (Mäntylä et al., 2011; Van Bael et al., 2003) are the most important predators of folivorous arthropods, exerting significant herbivory control (Vidal & Murphy, 2018). However, the relative importance of predator groups, such as arthropods and birds, is not static—that is, it can be altered by changes in forest condition (Dodonov et al., 2016). Previous studies

investigating the impact of forest quality on predation incidence on folivorous arthropods found a lower predation incidence with increasing forest disturbance (Boesing et al., 2017; Schwab et al., 2021). However, most studies have focused on disturbances that occurred several years prior to sampling (Boesing et al., 2017; Edwards et al., 2012) and, to the best of our knowledge, no studies have investigated the impact of recent understorey fires on the predation of folivorous arthropods.

Artificial caterpillars are a frequently-used tool to evaluate the impact of forest disturbance on predation incidence (Meyer et al., 2015; Murray et al., 2020; Roels et al., 2018; Roslin et al., 2017; Schwab et al., 2021; Seifert et al., 2015). Even though the predation on artificial caterpillars is often lower in comparison with natural prey (Lövei & Ferrante, 2017; Nagy et al., 2020), the technique is still a robust way of comparing predation incidence between habitat types (Roels et al., 2018; Schwab et al., 2021; Tvardikova & Novotny, 2012). Furthermore, this methodology allows the identification of predators by assessing the types of marks left on the “predated” artificial caterpillars (Low et al., 2014), which is key to comparing the role of different predator groups on the control of folivorous arthropods (Ferrante et al., 2021; Lemessa et al., 2015; Roslin et al., 2017; Sam et al., 2015). For example, in primary rainforests in Costa Rica, arthropods accounted for 86% of all predation incidences on artificial caterpillars, whilst birds accounted for just 11% (Seifert et al., 2015).

Here, we aim to explore how predation incidence on folivorous arthropods varies in human-modified Amazonian rainforests. Using 4,500 artificial caterpillars, as a proxy of folivorous arthropods, we assessed the predation incidence within four pre-El Niño human-modified forest classes: undisturbed, logged, logged-and-burned, and secondary forests. During the 2015–2016 El Niño, almost half of these forests were affected by understorey fires. We examined whether there were differences in the total predation incidence and in predation incidence by different predator groups (a) among pre-El Niño forest disturbance classes without recent fires, and (b) between forests affected by understorey fires during the recent El Niño (EN) and those that remained unaffected. Based on the negative impacts of human-driven disturbances on predator communities—which has been suggested to reduce the top-down control of folivorous arthropods (Murray et al., 2020)—we expected predation incidence to be lower in pre-EN disturbed forests when compared with undisturbed ones, and for it to be even lower in EN-fire-affected forests.

2 | METHODS

2.1 | Study area

Our study area is located in the municipalities of Belterra, Mojuí dos Campos, and Santarém in eastern Amazonia (Figure 1). The landscape encompasses around 1 million hectares of undisturbed

and disturbed primary and secondary forests immersed in an agriculture matrix comprising both large and small private landholdings (Gardner et al., 2013). In 2015 and 2016, the region experienced an abnormally long dry season associated with a strong El Niño event, which resulted in multiple understorey fires (see Aragão et al., 2018; Withey et al., 2018). Prior to the El Niño, we installed 30 study plots (250 × 10 m, 0.25 ha), distributed into undisturbed, selective logged forests (hereafter called “logged”), logged-and-burned, and secondary forests (hereafter called “pre-EN forest disturbance classes,” Table S1). Logging took place ≥18 years prior to sampling, an estimate derived from a combination of field assessments and a visual inspection of satellite images between 1988 and 2010 (Gardner et al., 2013). Plots were located in *terra firme* forests separated by at least 1.5 km from each other. Between November 2015 and January 2016, that is, during the El Niño, 14 plots burned (hereafter “EN-fire-affected plots”), while 16 remained unburned (Figure 1; Table S1).

2.2 | Data collection

Predation experiments were conducted between April 10, and June 15, 2019, corresponding to the middle-end of the wet season. All artificial caterpillars were green, made from odorless non-toxic colored plasticine (Lewis Newplast™) mixing an equal portion of dark and light green to create medium green colored caterpillars (Low et al., 2014; Roslin et al., 2017). Artificial caterpillars (hereafter

“caterpillars”) were crafted to mimic cryptic Lepidoptera larvae in color, shape (i.e., looping position), and size (i.e., 2.5 × 30 mm), thus resembling one of the most globally abundant folivorous groups (Zvereva et al., 2019). Caterpillars were sufficiently malleable to record predation marks. We fixed the caterpillars to the vegetation by passing a wire longitudinally through them (Figure 2a). When placing caterpillars in the field, we removed all handling marks to avoid misidentifying them with predator's marks.

We established five 20 × 5 m sub-plots within each of the 30 forest plots. We placed 30 caterpillars in each sub-plot, totaling 150 caterpillars per plot, and 4,500 caterpillars across the experiment. All caterpillars were installed on understorey vegetation branches, between 1.0 and 4.5 m from the ground, separated by at least 1 m from each other. Although predation incidence is often reported as being higher in the canopy (Loiselle & Farji-Brener, 2002), we only evaluated predation in the understorey due to the difficulties of placing caterpillars in the tall canopy (i.e., 30–50 m). All branches were chosen to prevent the caterpillars from being obscured by vegetation. The position of the caterpillars was marked with a tag on another branch of the same plant. This approach facilitated recovery while limiting the risk to obstruct or influence predator behavior. After 14 days of field exposure, a single observer (LCR) recovered all caterpillars and assessed whether they had been predated, attributing predation marks to different predator groups.

The identification of predation marks on recovered caterpillars was based on the beak, mandibular tooth or radula marks guided by images available in the literature (Low et al., 2014; Tvardikova

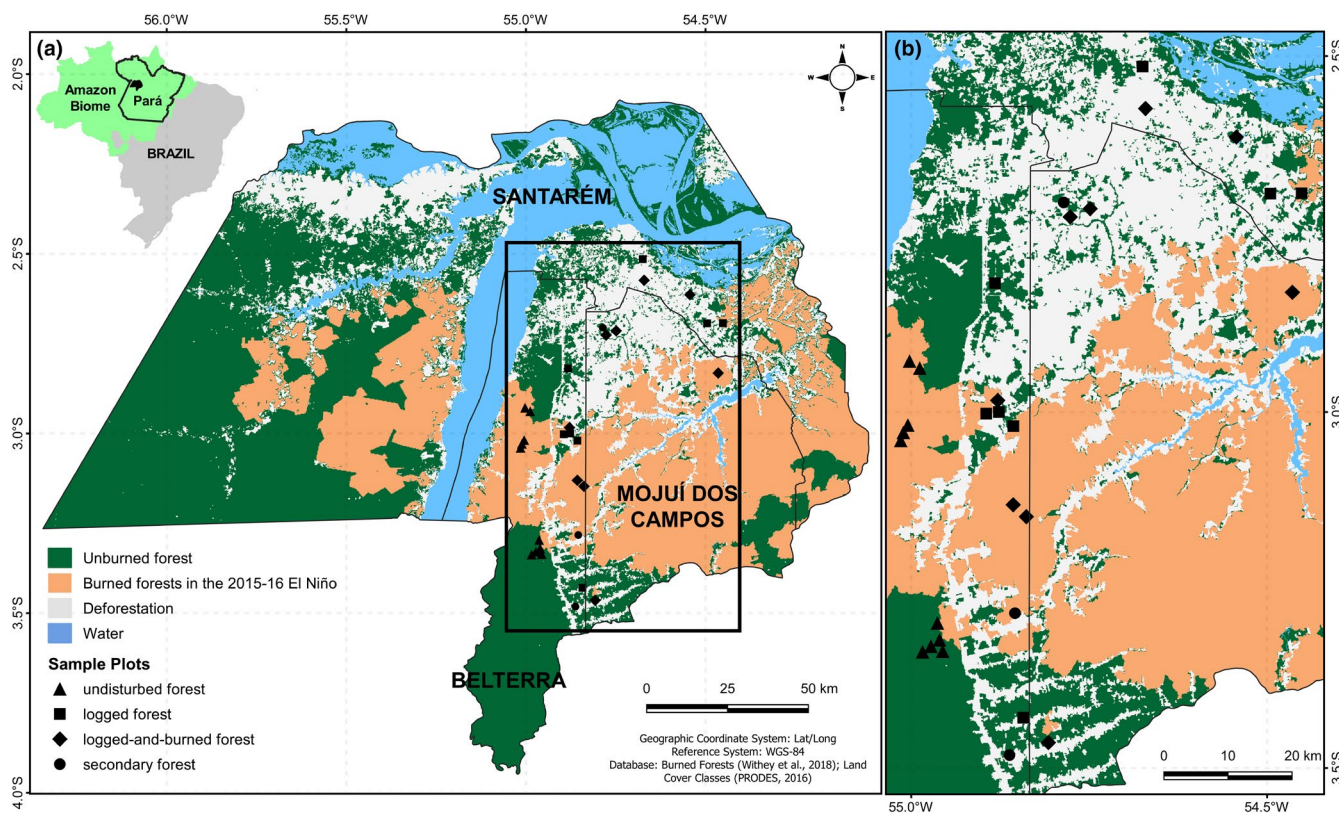


FIGURE 1 (a) Our study region in relation to the Brazilian Amazon. (b) The location of our study plots

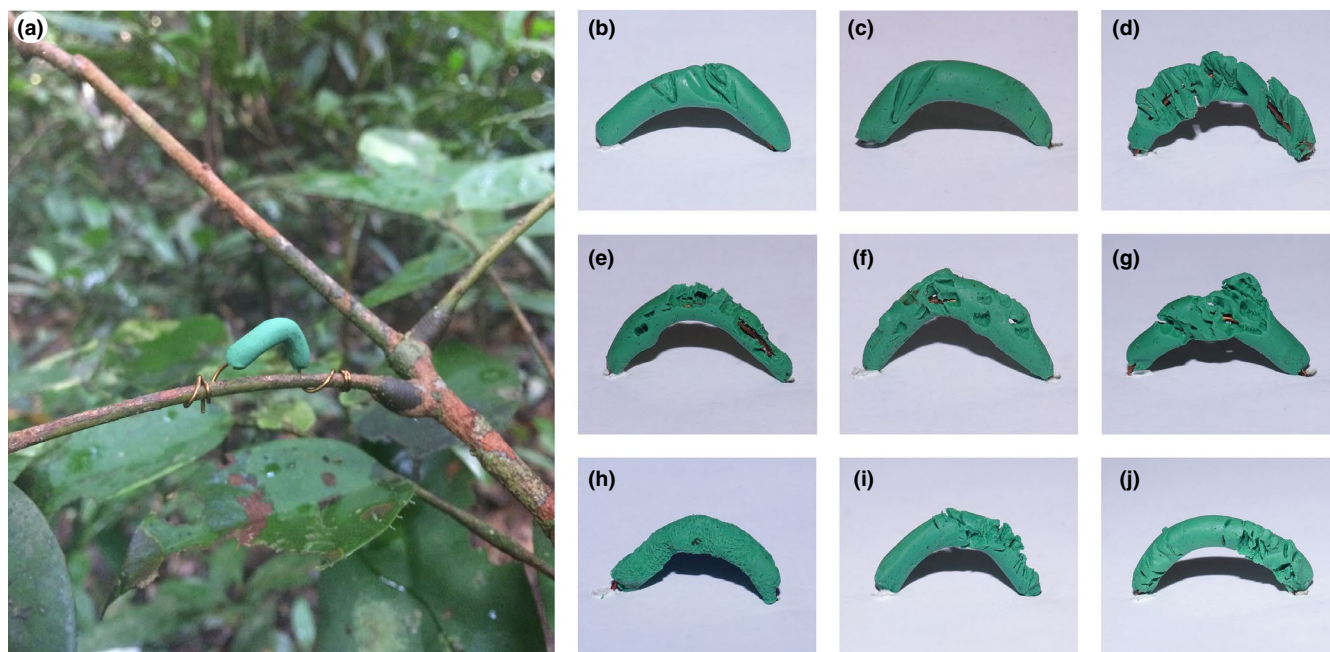


FIGURE 2 Examples of artificial caterpillars used in our experiment. (a) Caterpillar placed on a twig. Caterpillars with (b–d) bird, (e–g) mammal, and (h–j) arthropod predation marks

& Novotny, 2012) and an online identification guide (available at <https://tvardikova.weebly.com/downloads.html>). We also complemented our arthropod bite mark assessment through direct observations—that is, when we saw real attacks on caterpillars (Figure S2). All predation marks were attributed to one of four predator groups: arthropods, birds, reptiles, and mammals (Roels et al., 2018). Arthropod predators include ants, wasps, beetles, and isopods (Howe et al., 2009), while mammalian predators include marsupials and rodents (Low et al., 2014). Multiple marks made by the same type of predator on a single caterpillar were categorized as a single predation event. Of the 4,500 installed caterpillars, 28 were unrecovered because they were either crushed by a falling tree or lost due to the disappearance of the flag.

2.3 | Data analysis

We analyzed two response variables: (a) total predation incidence, measured as presence/absence of predation marks on caterpillars and (b) predation incidence by different predator groups, separated into two categories: arthropods and vertebrates (i.e., birds, mammals, and reptiles).

2.3.1 | Predation incidence across pre-EN forest disturbance classes and EN-fire-affected plots

In our first model (Model 1), we assessed the effects of pre-EN forest disturbance on total predation incidence, removing plots that burned during the 2015–16 El Niño ($n = 16$). Our second model

(Model 2) explored the impact of the El Niño understorey fires on total predation incidence including all forest plots ($n = 30$).

2.3.2 | Effects of different predator groups across pre-EN forest disturbance classes and EN-fire-affected plots

In this set of analyses, we evaluated the differences in predation incidence caused by arthropod (Model 3) and vertebrate predators (Model 4). These two response variables were analyzed across the pre-EN forest disturbance classes but did not include plots that burned in 2015–16 ($n = 16$). Our last two models assessed the impact of the 2015–16 El Niño understorey fires on the same response variables, thus leading to a model including arthropods (Model 5) and another including only the vertebrate predators (Model 6). Models 5 and 6 included all sampled plots ($n = 30$). Given that we were testing the difference in predation incidence between arthropods and vertebrates, Models 3–6 only included caterpillars with predation marks.

To test the effect of pre-EN forest disturbance classes and El Niño understorey fires on predation incidence, we used generalized linear mixed-effects models with a binomial response with logit link function and response variable as presence/absence data. All models had forest class as a fixed effect and plot as a random effect, and were built with the “glmer” function of the “lme4” package (Bates et al., 2018). We tested the significance and selected the optimum models running likelihood ratio tests in the “ordinal” package with the “drop1” function using the Chi-square distribution. Models 2 and 6 had differences in the least-square

means of predation in each forest class (including pre-EN forest disturbed classes and EN-fire-affected plots) tested with “em-means” with $\pm 95\%$ confidence interval (Lenth et al., 2020). The predation incidence in undisturbed forests served as a baseline for comparison to all other models. All analyses were performed in R 3.5.1 (R Core Team, 2018).

3 | RESULTS

We recovered 99.4% of the caterpillars ($n = 4,472$) of which 2,858 (64.9%) exhibited predation marks after 14 days exposed. We were unable to identify the predator group for only one caterpillar—although we suspect it was a bird (Figure S1), which was subsequently removed from all analyses. Predation marks were mainly made by arthropods ($n = 2,615$, 91.5%; Figure 2h–j), followed by birds ($n = 247$, 8.6%; Figure 2b–d), mammals ($n = 158$, 5.5%; Figure 2e–g), and reptiles ($n = 2$, 0.06%). Only 7% ($n = 200$) of the attacked caterpillars had marks belonging to more than one predator group. The percentages were measured based on the total number of caterpillars that exhibited predation marks ($n = 2,858$), not on the total number of marks; therefore, the total number of marks does not represent 100%.

3.1 | Effects of pre-EN forest disturbance classes and El Niño understorey fires on total predation incidence

Among the plots that did not burn in 2015–16, there were no significant differences in predation incidence between pre-EN forest disturbance classes (Figure 3; Table S2). When including EN-fire-affected plots, we found that predation incidence was significantly higher in pre-EN undisturbed forests that experienced fires in 2015–16 (Figure 3; Table S2; Table S3).

3.2 | Effects of pre-EN forest disturbance classes and El Niño understorey fires on the predation by different groups

Predation incidence by arthropods was higher than by vertebrates in all forest classes, irrespective of fire occurrence in 2015–16 (Figure 4). Predation incidence by arthropods was not affected by either the pre-EN forest disturbance classes or El Niño-associated fires (Figure 4a; Table S2). We also found no difference in predation incidence by vertebrates across the different pre-EN forest disturbance classes (Figure 4b; Table S2). When analyzing the effects of the recent El Niño fires, we found that logged-and-burned forests that burned again in 2015–16 presented significantly higher predation incidence by vertebrates than both undisturbed and logged-and-burned forests that were not affected by fires in 2015–16 (Figure 4b; Table S2; Table S4).

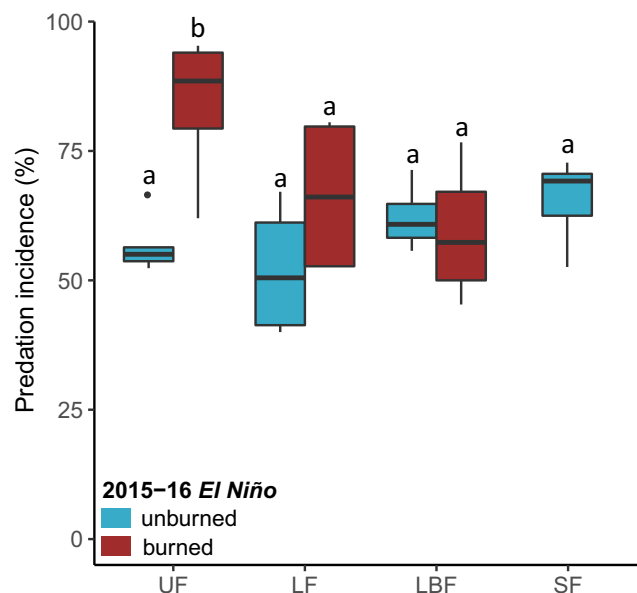


FIGURE 3 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015–16 El Niño (red) and those that remained unaffected (blue). Different letters indicate significant differences among forest classes following pairwise comparisons (Table S3). Pre-EN forest disturbance classes: UF—undisturbed forests, LF—logged forests, LBF—logged-and-burned forests, and SF—secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles)

4 | DISCUSSION

We found no differences in predation incidence among pre-EN forest disturbance classes. Although we demonstrate that predation incidence on artificial caterpillars may increase in the aftermath of Amazonian understorey fires, this evidence is not strong—for example, most EN-fire-affected forests exhibited similar predation incidence to those of unburned forests. The range of predation incidence was more variable within pre-EN disturbed forests in comparison with pre-EN undisturbed ones, and in EN-fire-affected forests when compared with unburned ones. Our results also suggest that predation incidence on artificial caterpillars in undisturbed and human-modified Amazonian forests is predominantly driven by arthropods.

4.1 | Predation incidence across pre-EN forest disturbance classes

We expected predation incidence to be strongly impacted by pre-EN forest disturbance, being lower in disturbed forests when compared with undisturbed ones, given that human-driven disturbances can

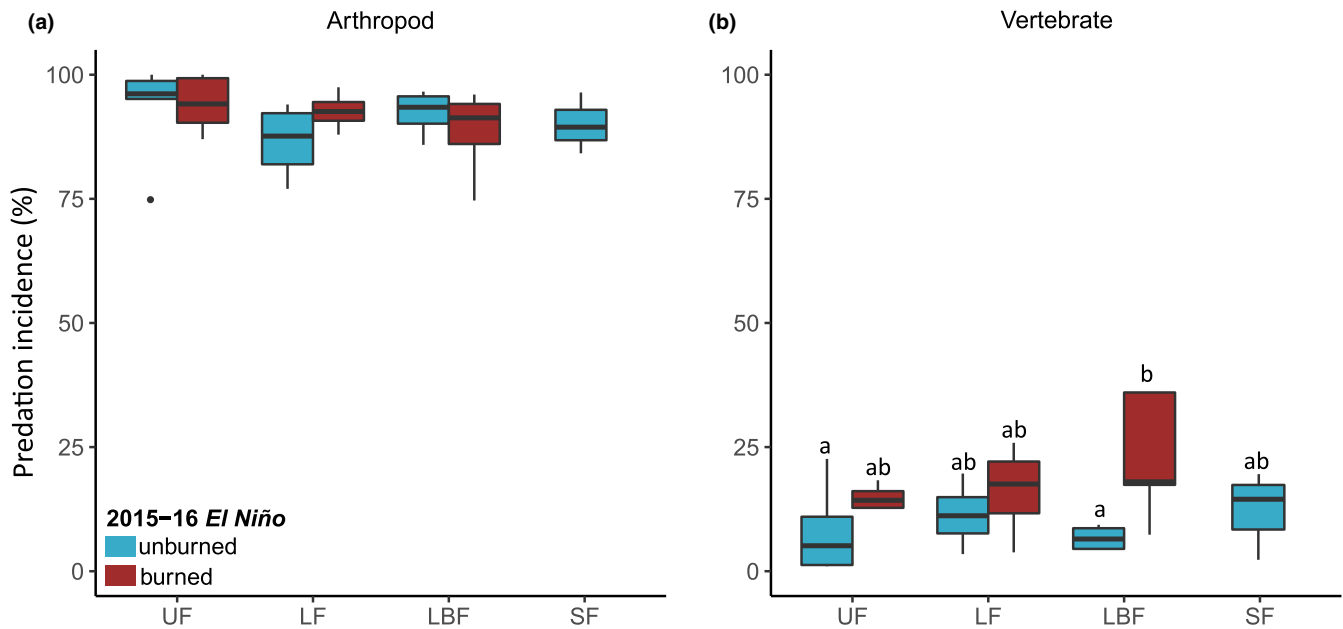


FIGURE 4 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015–16 El Niño (red) and those that remained unaffected (blue). Predation incidence was divided into two groups: (a) caused by arthropods, (b) caused by vertebrates (birds, mammals, and reptiles). Different letters indicate significant differences among forest classes following pairwise comparisons (Table S4). Pre-EN forest disturbance classes: UF—undisturbed forests, LF—logged forests, LBF—logged-and-burned forests, and SF—secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles)

negatively impact predator communities (Moura et al., 2013; Symes et al., 2018). Surprisingly, our results showed no effect of pre-EN forest disturbance on predation. However, it is important to recognize that our study plots are distributed within a large forested matrix, which can act as a source for species colonization (Tscharrntke et al., 2012). As such, in more fragmented landscapes, with small and isolated fragments, where forest faunas are more impoverished, predation incidence on folivorous arthropods may be less resistant to anthropogenic impacts (Fáveri et al., 2008; Lees & Peres, 2006).

4.2 | Predation incidence in EN-fire-affected forests

Given that forest fires drive shifts in the community composition of predatory arthropods and vertebrates by altering habitat availability (Barlow et al., 2006; Kelly et al., 2020; Paolucci et al., 2016; Silveira et al., 2016), we expected a lower predation incidence in EN-fire-affected forests. However, predation incidence remained similar between most EN-fire-affected and unaffected sites, only becoming significantly higher in previously undisturbed forests that burned in 2015–16. We cannot pinpoint the exact mechanism behind these findings. However, one possibility is that the increased density of vegetation in the understorey of recently burned forests, as a result of light gaps created by tree mortality, enhances environmental complexity, thus helping some arboreal predators, specially arthropods to find their prey and consequently increasing predation

incidence (Jimenez-Soto et al., 2019; Yang et al., 2018). Another possibility for the higher predation incidence in previously undisturbed forests that burned in 2015–16 is the dominance of pioneer plant species with lower amounts of secondary compounds (Barton & Koricheva, 2010; Boege & Marquis, 2006; Silva et al., 2018) in the understorey of recently burned forests may provide a local and ephemeral increase in resources for folivorous arthropods enabling the increase in populations number with a cascade effect on the increase of predator populations and predation incidence. Pioneer species would have been common in pre-EN disturbed forests, but not in undisturbed ones (Berenguer, Gardner, et al., 2018), thus providing new resources in these forests.

4.3 | The role of different predator groups

Studies across the globe, including tropical forests, have found a high incidence of arthropod predation on artificial caterpillars (Fáveri et al., 2008; Loiselle & Farji-Brener, 2002; Roslin et al., 2017; Witwicka et al., 2019; Zvereva et al., 2020). Arthropod predation can account for up to 98% of the total predation attempts on artificial caterpillars in undisturbed rainforests after 48 h of exposure (Seifert et al., 2016), a figure similar to ours (91% on average, after 14 days). This high predation incidence by arthropods is expected due to their high diversity and abundance in tropical regions (Novotny et al., 2006; Sam et al., 2015). Our results show that the predation incidence exerted by arthropods can be maintained at high levels even after forest

disturbance. However, we do not know whether this finding is due to resilience to disturbance of the arthropod predator community or due to high functional redundancy in the system (e.g., Nunes et al., 2021). In other words, even if some species of arthropod predators disappear after fires, others that perform the same function (i.e., predation of folivorous arthropods) may maintain predation incidence comparable with unburned forests (Perez-Alvarez et al., 2021).

Among vertebrates, predation incidence upon artificial caterpillars varies widely. In the case of birds, from 1% to 52% in tropical forests (Molleman et al., 2016; Sam et al., 2015). After 14 days of exposure, our results of 8.6% are within the lower end of this range. Mammals predated 5.5% of the caterpillars, a figure slightly higher than that previously reported—that is, <1% to 4% (Schwab et al., 2021; Seifert et al., 2015). Predation of caterpillars by reptiles is generally rare (Murray et al., 2020; Schwab et al., 2021), with some studies not registering any (Roels et al., 2018; Roslin et al., 2017; Zvereva et al., 2020). We found only two caterpillars predated by reptiles, out of the 2,858 which presented predation marks.

4.4 | Caveats

Artificial caterpillars are an effective method to infer predation incidence across habitats and among predator groups (Howe et al., 2009; Lövei & Ferrante, 2017; Roslin et al., 2017; Schwab et al., 2021). Through the standardization of this methodology, it is possible to compare predation incidence and predator composition among areas (Lövei & Ferrante, 2017). However, we highlight that our results should be carefully interpreted as these caterpillars are a simple visual approximation of real prey (Howe et al., 2009; Murray et al., 2020). Important factors such as posture and mobility (Lövei & Ferrante, 2017; Suzuki & Sakurai, 2015), olfaction (Hughes et al., 2010; Mäntylä et al., 2011; Sam et al., 2015), color (Ghim & Hodos, 2006), leaf damage (Sam et al., 2015), and plant chemical responses are not manifested in artificial models (Amo et al., 2013; Heil & Kost, 2006; Pearse et al., 2020). Furthermore, the color and shape of our caterpillars are likely biased towards soliciting interactions from generalist predators (Boesing et al., 2017). Therefore, the study design may fail to record specialized interactions (Zvereva et al., 2019, 2020). Moreover, natural prey abundance can also be an important driver of predation incidence—for example, higher prey abundances lead to predator satiation, which may affect the attack incidence on artificial caterpillars. Finally, given that we sampled EN-fire-affected forests three years after they burnt, we may have failed to detect any immediate post-fire changes in predation incidence—for example, three years might be enough time for predation to be re-established in pre-EN-forest classes.

5 | CONCLUSION

Our experimental study highlights that artificial caterpillar predation is (a) of a comparable magnitude in undisturbed, logged,

logged-and-burned, and secondary Amazonian forests; (b) not largely impacted by recent understorey fires; and (c) mainly performed by arthropods. Understanding the control of folivorous arthropods in human-disturbed forests represents an important step for predicting the future of tropical forests, as herbivory control directly affects forest regeneration.

ACKNOWLEDGMENTS

We thank the Large Scale Biosphere-Atmosphere Program (LBA) for logistical and infrastructure support during field measurements. We are deeply grateful to our field and laboratory assistants: Gilson Oliveira, Jaiane Silva, Joni Oliveira, Josué Oliveira, Josiane Oliveira, Marcos Oliveira, Renilson Freitas, and Yan G. Ramos, as well the all collaborating private land owners for their support and access to their land. We also thank to Elena Zvereva, João Carlos Pena, Lucas Paolucci, Mikhail Kozlov, and Rafael Souza (Urucum) for their support in identifying the marks of attacks on caterpillars, and Pavel Dodonov for assistance during the analysis. We thank the reviewers for their careful reading of our manuscript and their important contributions. We are grateful to multiple funding agencies for financial support: Conselho Nacional de Pesquisa (CNPq; grants CNPq-CAPES 441659/2016-0 [PELD-RAS], MCIC-CNPq 420254/2018-8 [RESFLORA] and CNPq-PrevFogo-IBAMA 441949/2018-5 [SEM-FLAMA]), Instituto Nacional de Ciência e Tecnologia—Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0) and Embrapa (SEG: 02.08.06.005.00), in Brazil; the Darwin Initiative (17-023), The Nature Conservancy, and Natural Environment Research Council (NERC; NE/F01614X/1, NE/G000816/1, NE/K016431/1, and NE/P004512/1), in the UK. E.B. and J.B. were also funded by H2020-MSCA-RISE (691053-ODYSSEA). F.F. acknowledges funding provided by Climate and Biodiversity Initiative of BNP Paribas Foundation (project Bioclimate). This paper is number #91 in the Rede Amazônia Sustentável publication series.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

LCR, EB, and ACL conceived the original idea of this study. LCR and EB conceived the study design, conducted the experiment, and organized the database. LCR and EB conducted the data analyses with input from JB and FF. LCR wrote the manuscript, with significant contributions of all co-authors. All authors discussed the results and revised the manuscript before submission.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ns1rn8pvt> (Rossi et al., 2022).

ORCID

Liana Chesini Rossi  <https://orcid.org/0000-0002-9937-3979>

Erika Berenguer  <https://orcid.org/0000-0001-8157-8792>

Alexander Charles Lees  <https://orcid.org/0000-0001-7603-9081>

Jos Barlow  <https://orcid.org/0000-0003-4992-2594>

Joice Ferreira  <https://orcid.org/0000-0002-4008-2341>

Filipe M. França  <https://orcid.org/0000-0003-3827-1917>

Paulo Tavares  <https://orcid.org/0000-0003-2617-1548>

Marco Aurélio Pizo  <https://orcid.org/0000-0002-3103-0371>

REFERENCES

- Amo, L., Jansen, J. J., van Dam, N. M., Dicke, M., & Visser, M. E. (2013). Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecology Letters*, 16(11), 1348–1355. <https://doi.org/10.1111/ele.12177>
- Aragão, L. E. O. C., Anderson, L. O., Fonseca, M. G., Rosan, T. M., Vedovato, L. B., Wagner, F. H., Silva, C. V. J., Silva Junior, C. H. L., Arai, E., Aguiar, A. P., Barlow, J., Berenguer, E., Deeter, M. N., Domingues, L. G., Gatti, L., Gloor, M., Malhi, Y., Marengo, J. A., Miller, J. B., ... Saatchi, S. (2018). 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, 9(1), 1–12. <https://doi.org/10.1038/s41467-017-02771-y>
- Barlow, J., & Peres, C. (2004). Avifaunal responses to single and recurrent wildfires in Amazonian forests. *Ecological Applications*, 14(5), 1358–1373. <https://doi.org/10.1890/03-5077>
- Barlow, J., Peres, C. A., Henriques, L. M. P., Stouffer, P. C., & Wunderle, J. M. (2006). The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biological Conservation*, 128(2), 182–192. <https://doi.org/10.1016/j.biocon.2005.09.028>
- Barreto, J. R., Berenguer, E., Ferreira, J., Joly, C. A., Malhi, Y., Maria, M., & Barlow, J. (2021). Assessing invertebrate herbivory in human-modified tropical forest canopies. *Ecology and Evolution*, 11(9), 4012–4022. <https://doi.org/10.1002/ece3.7295>
- Barton, K. E., & Koricheva, J. (2010). The ontogeny of plant defense and herbivory: Characterizing general patterns using meta-analysis. *American Naturalist*, 175(4), 481–493. <https://doi.org/10.1086/650722>
- Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A. K., Winchester, N. N., Roubik, D. W., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., ... Lponce, M. (2012). Arthropod diversity in a tropical forest. *Science*, 338(6113), 1481–1484. <https://doi.org/10.1126/science.1226727>
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., & Fox, J. (2018). *Package "lme4": Linear Mixed-Effect Models using "Eigen" and S4 (version 1.1-19)*. pp. 122. Repository: CRAN.
- Berenguer, E., Gardner, T. A., Ferreira, J., Aragão, L. E. O. C., Mac Nally, R., Thomson, J. R., Vieira, I. C. G., & Barlow, J. (2018). Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology*, 106(6), 2190–2203. <https://doi.org/10.1111/1365-2745.12991>
- Berenguer, E., Lennox, G. D., Ferreira, J., Malhi, Y., Aragão, L. E. O. C., Barreto, J. R., Del Bon Espírito-Santo, F., Figueiredo, A. E. S., França, F., Gardner, T. A., Joly, C. A., Palmeira, A. F., Quesada, C. A., Rossi, L. C., de Seixas, M. M. M., Smith, C. C., Withey, K., & Barlow, J. (2021). Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America*, 118(30), e2019377118. <https://doi.org/10.1073/pnas.2019377118>
- Berenguer, E., Malhi, Y., Brando, P., Cardoso Nunes Cordeiro, A., Ferreira, J., França, F., Chesini Rossi, L., Maria Moraes de Seixas, M., & Barlow, J. (2018). Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1760), <https://doi.org/10.1098/rstb.2017.0308>
- Boege, K., & Marquis, R. J. (2006). Plant quality and predation risk mediated by plant ontogeny: Consequences for herbivores and plants. *Oikos*, 115(3), 559–572. <https://doi.org/10.1111/j.2006.0030-1299.15076.x>
- Boesing, A. L., Nichols, E., & Metzger, J. P. (2017). Effects of landscape structure on avian-mediated insect pest control services: A review. *Landscape Ecology*, 32(5), 931–944. <https://doi.org/10.1007/s10980-017-0503-1>
- Dirzo, R. (1984). Herbivory, a phytocentric overview. In R. Dirzo & J. Sarukhan (Eds.), *Perspectives in plant population biology* (pp. 141–165). Sinauer.
- Dodonov, P., Morante-Filho, J. C., Mariano-Neto, E., Cazetta, E., Andrade, E. R. D., Rocha-Santos, L., Inforzato, I., Gomes, F. S., & Faria, D. (2016). Forest loss increases insect herbivory levels in human-altered landscapes. *Acta Oecologica*, 77, 136–143. <https://doi.org/10.1016/j.actao.2016.10.003>
- Edwards, D. P., Woodcock, P., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., & Wilcove, D. S. (2012). Reduced-impact logging and biodiversity conservation: A case study from Borneo. *Ecological Applications*, 22(2), 561–571. <https://doi.org/10.1890/11-1362.1>
- Fáveri, S. B., Vasconcelos, H. L., & Dirzo, R. (2008). Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *Journal of Tropical Ecology*, 24(1), 57–64. <https://doi.org/10.1017/S0266467407004592>
- Ferrante, M., Möller, D., Möller, G., Menares, E., Lubin, Y., & Segoli, M. (2021). Invertebrate and vertebrate predation rates in a hyper-arid ecosystem following an oil spill. *Ecology and Evolution*, 11(17), 12153–12160. <https://doi.org/10.1002/ece3.7978>
- França, F. M., Ferreira, J., Vaz-de-Mello, F. Z., Maia, L. F., Berenguer, E., Ferraz Palmeira, A., Fadini, R., Louzada, J., Braga, R., Hugo Oliveira, V., & Barlow, J. (2020). El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes. *Biotropica*, 52(2), 252–262. <https://doi.org/10.1111/btp.12756>
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R., & Myneni, R. B. (2013). Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America*, 110(45), 18110–18115. <https://doi.org/10.1073/pnas.1302584110>
- Gardner, T. A., Ferreira, J., Barlow, J., Lees, A. C., Parry, L., Vieira, I. C. G., Berenguer, E., Abramovay, R., Aleixo, A., Andretti, C., Aragão, L. E. O. C., Araújo, I., de Ávila, W. S., Bardgett, R. D., Batistella, M., Begotti, R. A., Beldini, T., de Blas, D. E., Braga, R. F., ... Zuanon, J. (2013). A social and ecological assessment of tropical land uses at multiple scales: The Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1619), 20120166. <https://doi.org/10.1098/rstb.2012.0166>
- Ghim, M. M., & Hodós, W. (2006). Spatial contrast sensitivity of birds. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 192(5), 523–534. <https://doi.org/10.1007/s00359-005-0090-5>
- Gloor, M., Barichivich, J., Ziv, G., Brienens, R., Schöngart, J., & Peylin, P. (2015). Recent Amazon climate as background for possible ongoing Special Section. *Global Biogeochemical Cycles*, 29(9), 1384–1399. <https://doi.org/10.1002/2014GB005080>
- Hairton, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 87(879), 421–425. <https://doi.org/10.1086/282146>
- Hamer, K. C., Newton, R. J., Edwards, F. A., Benedick, S., Bottrell, S. H., & Edwards, D. P. (2015). Impacts of selective logging on insectivorous

- birds in Borneo: The importance of trophic position, body size and foraging height. *Biological Conservation*, 188, 82–88. <https://doi.org/10.1016/j.biocon.2014.09.026>
- Heil, M., & Kost, C. (2006). Priming of indirect defences. *Ecology Letters*, 9(7), 813–817. <https://doi.org/10.1111/j.1461-0248.2006.00932.x>
- Holdsworth, A. R., & Christopher, U. (1997). Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Applications*, 7(2), 713–725. <https://doi.org/10.2307/2269533>
- Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis Et Applicata*, 131(3), 325–329. <https://doi.org/10.1111/j.1570-7458.2009.00860.x>
- Hughes, N. K., Price, C. J., & Banks, P. B. (2010). Predators are attracted to the olfactory signals of prey. *PLoS One*, 5(9), 1–4. <https://doi.org/10.1371/journal.pone.0013114>
- Jimenez-Soto, E., Morris, J. R., Letourneau, D. K., & Philpott, S. M. (2019). Vegetation connectivity increases ant activity and potential for ant-provided biocontrol services in a tropical agroforest. *Biotropica*, 51(1), 50–61. <https://doi.org/10.1111/btp.12616>
- Kelly, L. T., Giljohann, K. M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A. F., Buckland, S. T., Canelles, Q., Clarke, M. F., Fortin, M.-J., Hermoso, V., Herrando, S., Keane, R. E., Lake, F. K., McCarthy, M. A., Morán-Ordóñez, A., Parr, C. L., Pausas, J. G., ... Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science*, 370(6519), eabb0355. <https://doi.org/10.1126/science.abb0355>
- Lees, A. C., & Peres, C. A. (2006). Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biological Conservation*, 133(2), 198–211. <https://doi.org/10.1016/j.biocon.2006.06.005>
- Lemessa, D., Hambäck, P. A., & Hylander, K. (2015). Arthropod but not bird predation in Ethiopian homesteads is higher in tree-poor than in tree-rich landscapes. *PLoS One*, 10(5), 1–12. <https://doi.org/10.1371/journal.pone.0126639>
- Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2020). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.4.5. <https://CRAN.R-project.org/package=emmeans>
- Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, 349(6250), 827–832. <https://doi.org/10.1126/science.aaa9932>
- Loiselle, B. A., & Farji-Brener, A. G. (2002). What's up? An experimental comparison of predation levels between canopy and understory in a tropical wet forest. *Biotropica*, 34(2), 327. [https://doi.org/10.1646/0006-3606\(2002\)034\[0327:wsuac\]2.0.co;2](https://doi.org/10.1646/0006-3606(2002)034[0327:wsuac]2.0.co;2)
- Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. *Insect Science*, 24(4), 528–542. <https://doi.org/10.1111/1744-7917.12405>
- Low, P. A., Sam, K., McArthur, C., Posa, M. R. C., & Hochuli, D. F. (2014). Determining predator identity from attack marks left in model caterpillars: Guidelines for best practice. *Entomologia Experimentalis Et Applicata*, 152(2), 120–126. <https://doi.org/10.1111/eea.12207>
- Mäntylä, E., Klemola, T., & Laaksonen, T. (2011). Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia*, 165(1), 143–151. <https://doi.org/10.1007/s00442-010-1774-2>
- Matricardi, E. A. T., Skole, D. L., Costa, O. B., Pedlowski, M. A., Samek, J. H., & Miguel, E. P. (2020). Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*, 369(6509), 1378–1382. <https://doi.org/10.1126/SCIENCE.ABB3021>
- Meyer, S. T., Koch, C., & Weisser, W. W. (2015). Towards a standardized Rapid Ecosystem Function Assessment (REFA). *Trends in Ecology and Evolution*, 30(7), 390–397. <https://doi.org/10.1016/j.tree.2015.04.006>
- Molleman, F., Remmel, T., & Sam, K. (2016). Phenology of predation on insects in a tropical forest: Temporal variation in attack rate on dummy caterpillars. *Biotropica*, 48(2), 229–236. <https://doi.org/10.1111/btp.12268>
- Morrison, E. B., & Lindell, C. A. (2012). Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. *Ecological Applications*, 22(5), 1526–1534. <https://doi.org/10.1890/11-1118.1>
- Moura, N. G., Lees, A. C., Aleixo, A., Barlow, J., Berenguer, E., Ferreira, J., Mac Nally, R., Thomson, J. R., & Gardner, T. A. (2016). Idiosyncratic responses of Amazonian birds to primary forest disturbance. *Oecologia*, 180(3), 903–916. <https://doi.org/10.1007/s00442-015-3495-z>
- Moura, N. G., Lees, A. C., Andretti, C. B., Davis, B. J. W., Solar, R. R. C., Aleixo, A., Barlow, J., Ferreira, J., & Gardner, T. A. (2013). Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. *Biological Conservation*, 167, 339–348. <https://doi.org/10.1016/j.biocon.2013.08.023>
- Murray, K., Soh, M. C. K., Puan, C. L., Abu Hashim, A. K. B., Abdul Patah, P. B., & Peh, K.-H. (2020). Predation on multiple prey types across a disturbance gradient in tropical montane forests of Peninsular Malaysia. *Frontiers in Forests and Global Change*, 3, 1–11. <https://doi.org/10.3389/ffgc.2020.00080>
- Nagy, R. K., Schellhorn, N. A., & Zalucki, M. P. (2020). Fresh, frozen or fake: A comparison of predation rates measured by various types of sentinel prey. *Journal of Applied Entomology*, 144(5), 407–416. <https://doi.org/10.1111/jen.12745>
- Novotny, V., Drozd, P., Miller, S. E., Kulfan, M., Janda, M., Basset, Y., & Weiblen, G. D. (2006). Why are there so many species of herbivorous insects in tropical rainforests? *Science*, 313(5790), 1115–1118. <https://doi.org/10.1126/science.1129237>
- Nunes, C. A., Barlow, J., França, F., Berenguer, E., Solar, R. R. C., Louzada, J., Leitão, R. P., Maia, L. F., Oliveira, V. H. F., Braga, R. F., Vaz-de-Mello, F. Z., & Sayer, E. J. (2021). Functional redundancy of Amazonian dung beetles confers community-level resistance to primary forest disturbance. *Biotropica*, 53(6), 1510–1521. <https://doi.org/10.1111/btp.12998>
- Paolucci, L. N., Maia, M. L. B., Solar, R. R. C., Campos, R. I., Schoederer, J. H., & Andersen, A. N. (2016). Fire in the Amazon: impact of experimental fuel addition on responses of ants and their interactions with myrmecochorous seeds. *Oecologia*, 182(2), 335–346. <https://doi.org/10.1007/s00442-016-3638-x>
- Pearse, I. S., LoPresti, E., Schaeffer, R. N., Wetzell, W. C., Mooney, K. A., Ali, J. G., Ode, P. J., Eubanks, M. D., Bronstein, J. L., & Weber, M. G. (2020). Generalising indirect defence and resistance of plants. *Ecology Letters*, 23(7), 1137–1152. <https://doi.org/10.1111/ele.13512>
- Perez-Alvarez, R., Grab, H., Polyakov, A., & Poveda, K. (2021). Landscape composition mediates the relationship between predator body size and pest control. *Ecological Applications*, 31(6), 1–14. <https://doi.org/10.1002/eap.2365>
- R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org>
- Roels, S. M., Porter, J. L., & Lindell, C. A. (2018). Predation pressure by birds and arthropods on herbivorous insects affected by tropical forest restoration strategy. *Restoration Ecology*, 26(6), 1203–1211. <https://doi.org/10.1111/rec.12693>
- Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C., Cameron, E. K., Dáttilo, W., Donoso, D. A., Drozd, P., Gray, C. L., Hik, D. S., Hill, S. J., Hopkins, T., Huang, S., ... Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356(6339), 742–744. <https://doi.org/10.1126/science.aaj1631>
- Rossi, L. C., Berenguer, E., Lees, A. C., Barlow, J., Ferreira, J., França, F. M., Tavares, P., & Pizo, M. A. (2022). Data from: Predation on artificial caterpillars following understory fires in human-modified Amazonian forests. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.ns1rn8pvt>
- Sam, K., Koane, B., & Novotny, V. (2015). Herbivore damage increases avian and ant predation of caterpillars on trees along a complete

- elevational forest gradient in Papua New Guinea. *Ecography*, 38(3), 293–300. <https://doi.org/10.1111/ecog.00979>
- Schwab, D., Wurz, A., Grass, I., Rakotomalala, A. A. N. A., Osen, K., Soazafy, M. R., Martin, D. A., & Tscharnke, T. (2021). Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes. *Journal of Applied Ecology*, 58(2), 360–371. <https://doi.org/10.1111/1365-2664.13766>
- Seifert, C. L., Lehner, L., Adams, M. O., & Fiedler, K. (2015). Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica. *Journal of Tropical Ecology*, 31(3), 281–284. <https://doi.org/10.1017/S0266467415000012>
- Seifert, C. L., Schulze, C. H., Dreschke, T. C. T., Frötscher, H., & Fiedler, K. (2016). Day vs. night predation on artificial caterpillars in primary rainforest habitats – An experimental approach. *Entomologia Experimentalis Et Applicata*, 158(1), 54–59. <https://doi.org/10.1111/eea.12379>
- Silva, C. V. J., Aragão, L. E. O. C., Barlow, J., Espirito-Santo, F., Young, P. J., Anderson, L. O., Berenguer, E., Brasil, I., Foster Brown, I., Castro, B., Farias, R., Ferreira, J., França, F., Graça, P. M. L. A., Kirsten, L., Lopes, A. P., Salimon, C., Scaranello, M. A., Seixas, M., ... Xaud, H. A. M. (2018). Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1760), 20180043. <https://doi.org/10.1098/rstb.2018.0043>
- Silveira, J. M., Louzada, J., Barlow, J., Andrade, R., Mestre, L., Solar, R., Lacau, S., & Cochrane, M. A. (2016). A multi-taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon forest. *Biotropica*, 48(2), 170–180. <https://doi.org/10.1111/btp.12267>
- Suzuki, T. N., & Sakurai, R. (2015). Bent posture improves the protective value of bird dropping masquerading by caterpillars. *Animal Behaviour*, 105, 79–84. <https://doi.org/10.1016/j.anbehav.2015.04.009>
- Symes, W. S., Edwards, D. P., Miettinen, J., Rheindt, F. E., & Carrasco, L. R. (2018). Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nature Communications*, 9(1), 4052. <https://doi.org/10.1038/s41467-018-06579-2>
- Tscharnke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – Eight hypotheses. *Biological Reviews*, 87(3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tvardikova, K. (n.d.). Guide to “bite marks”. <https://tvardikova.weebly.com/downloads.html>
- Tvardikova, K., & Novotny, V. (2012). Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. *Journal of Tropical Ecology*, 28(4), 331–341. <https://doi.org/10.1017/S0266467412000235>
- Van Bael, S. A., Brawn, J. D., & Robinson, S. K. (2003). Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences of the United States of America*, 100(14), 8304–8307. <https://doi.org/10.1073/pnas.1431621100>
- Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters*, 21(1), 138–150. <https://doi.org/10.1111/ele.12874>
- Withey, K., Berenguer, E., Palmeira, A. F., Espirito-Santo, F. D. B., Lennox, G. D., Silva, C. V. J., Aragão, L. E. O. C., Ferreira, J., França, F., Malhi, Y., Rossi, L. C., & Barlow, J. (2018). Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1760), 20170312. <https://doi.org/10.1098/rstb.2017.0312>
- Witwicka, A., Frydryszak, D., Anto, A., & Czarnoleski, M. (2019). Effects of habitat, leaf damage and leaf rolling on the predation risk of caterpillars in the tropical rain forest of Borneo. *Journal of Tropical Ecology*, 35, 251–253. <https://doi.org/10.1017/S0266467419000191>
- Yang, B., Li, B., He, Y., Zhang, L., Bruelheide, H., & Schuldt, A. (2018). Tree diversity has contrasting effects on predation rates by birds and arthropods on three broadleaved, subtropical tree species. *Ecological Research*, 33(1), 205–212. <https://doi.org/10.1007/s11284-017-1531-7>
- Zvereva, E. L., Castagneyrol, B., Cornelissen, T., Forsman, A., Hernández-Agüero, J. A., Klemola, T., Paolucci, L., Polo, V., Salinas, N., Theron, K. J., Xu, G., Zverev, V., & Kozlov, M. V. (2019). Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey. *Ecology and Evolution*, 9(24), 14273–14285. <https://doi.org/10.1002/ece3.5862>
- Zvereva, E. L., Paolucci, L. N., & Kozlov, M. V. (2020). Top - down factors contribute to differences in insect herbivory between saplings and mature trees in boreal and tropical forests. *Oecologia*, 193, 167–176. <https://doi.org/10.1007/s00442-020-04659-z>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Rossi, L. C., Berenguer, E., Lees, A. C., Barlow, J., Ferreira, J., França, F. M., Tavares, P., & Pizo, M. A. (2022). Predation on artificial caterpillars following understorey fires in human-modified Amazonian forests. *Biotropica*, 00, 1–10. <https://doi.org/10.1111/btp.13097>

4.10 Supporting information

TABLE S4.1 Number of studies plots in different forest disturbance classes (pre-EN forest disturbance class), and of those affected by understorey fires during the 2015-16 El Niño (EN-fire-affected plots).

Pre-EN forest disturbance class	EN-unburned plots	EN-fire-affected plots
undisturbed forest	5	5
logged forest	4	4
logged-and-burned forest	4	5
secondary forest	3	0

TABLE S4.2 Results of Models 1-6 (See Methods).

Models	χ^2- value	<i>P</i> - value
Model 1: total predation incidence ~ pre-EN forest disturbance classes	4.98	0.17
Model 2: total predation incidence ~ EN-fire-affected forests	10.78	<0.01
Model 3: arthropods ~ pre-EN forest disturbance classes	3.31	0.35
Model 4: vertebrates ~ pre-EN forest disturbance classes	2.47	0.48
Model 5: arthropods ~ EN-fire-affected forests	0.14	0.69
Model 6: vertebrates ~ EN-fire-affected forests	9.64	<0.01

TABLE S4.3 The effect of El Niño 2015-16 understory fires on total predation incidence artificial caterpillars along forest disturbance classes in Amazonian Forest, assessed using generalized linear mixed-effects models with *emmeans* test for post-hoc pairwise comparisons. Predation incidence in undisturbed forest served as baseline for comparisons. Pre-EN forest disturbance classes: UF – undisturbed forest; LF – logged forest; LBF – logged-and-burned forest; SF – Secondary forest. Forest that where affected understory fires during the 2015-16 El Niño are named EN-fire-affected. Significant results are highlighted in bold.

Forest classes	Estimate	<i>P</i> - value
UF - EN-fire-affected UF	-1.56	<0.01
UF - EN-fire-affected LF	-0.46	0.90
UF - EN-fire-affected LBF	-0.12	1.00
LF - EN-fire-affected UF	-1.76	<0.01
LF - EN-fire-affected LF	-0.65	0.65
LF - EN-fire-affected LBF	-0.31	0.98
LBF - EN-fire-affected UF	-1.34	<0.05
LBF - EN-fire-affected LF	-0.23	0.99
LBF - EN-fire-affected LBF	0.11	1.00
SF - EN-fire-affected UF	-1.20	0.04
SF - EN-fire-affected LF	-0.09	1.00
SF - EN-fire-affected LBF	2.24	0.99

EN-fire-affected UF - EN-fire-affected LBF	1.45	<0.01
EN-fire-affected UF - EN-fire-affected LF	1.11	0.03
EN-fire-affected LBF - EN-fire-affected LF	-0.34	0.94

TABLE S4.4 The effect of the El Niño 2015-16 fires on the incidence of vertebrates (i.e., birds, mammals and reptiles) predation on artificial caterpillars. Comparations were made using generalized linear mixed-effects models with *emmeans* tests for post-hoc pairwise comparisons. The incidence of predation in undisturbed forest served as baseline for comparison. Pre-EN forest disturbance classes: UF – undisturbed forest; LF – logged forest; LBF – logged-and-burned forest; SF – Secondary Forest. Forests that were affected by understorey fires during the 2015-16 El Niño are named EN-fire-affected. Significant results are highlighted in bold.

Forest class	Estimate	<i>P</i> - value
UF - EN-fire-affected UF	-0.92	0.43
UF - EN-fire-affected LF	-0.95	0.43
UF - EN-fire-affected LBF	-1.38	<0.03
LF - EN-fire-affected UF	-0.42	0.98
LF - EN-fire-affected LF	-0.46	0.98
LF - EN-fire-affected LBF	-0.89	0.51
LBF - EN-fire-affected UF	-0.93	0.47
LBF - EN-fire-affected LF	-0.97	0.33
LBF - EN-fire-affected LBF	-1.4	0.05
SF - EN-fire-affected UF	-0.17	1.00
SF - EN-fire-affected LF	-0.2	0.99
SF - EN-fire-affected LBF	-0.64	0.89

EN-fire-affected UF - EN-fire-affected LF	0.04	1.00
EN-fire-affected UF - EN-fire-affected LBF	0.47	0.84
EN-fire-affected LBF - EN-fire-affected LF	0.43	0.91

FIGURE S4.1 Caterpillar recovered with unidentified marks – although we suspect it was a bird

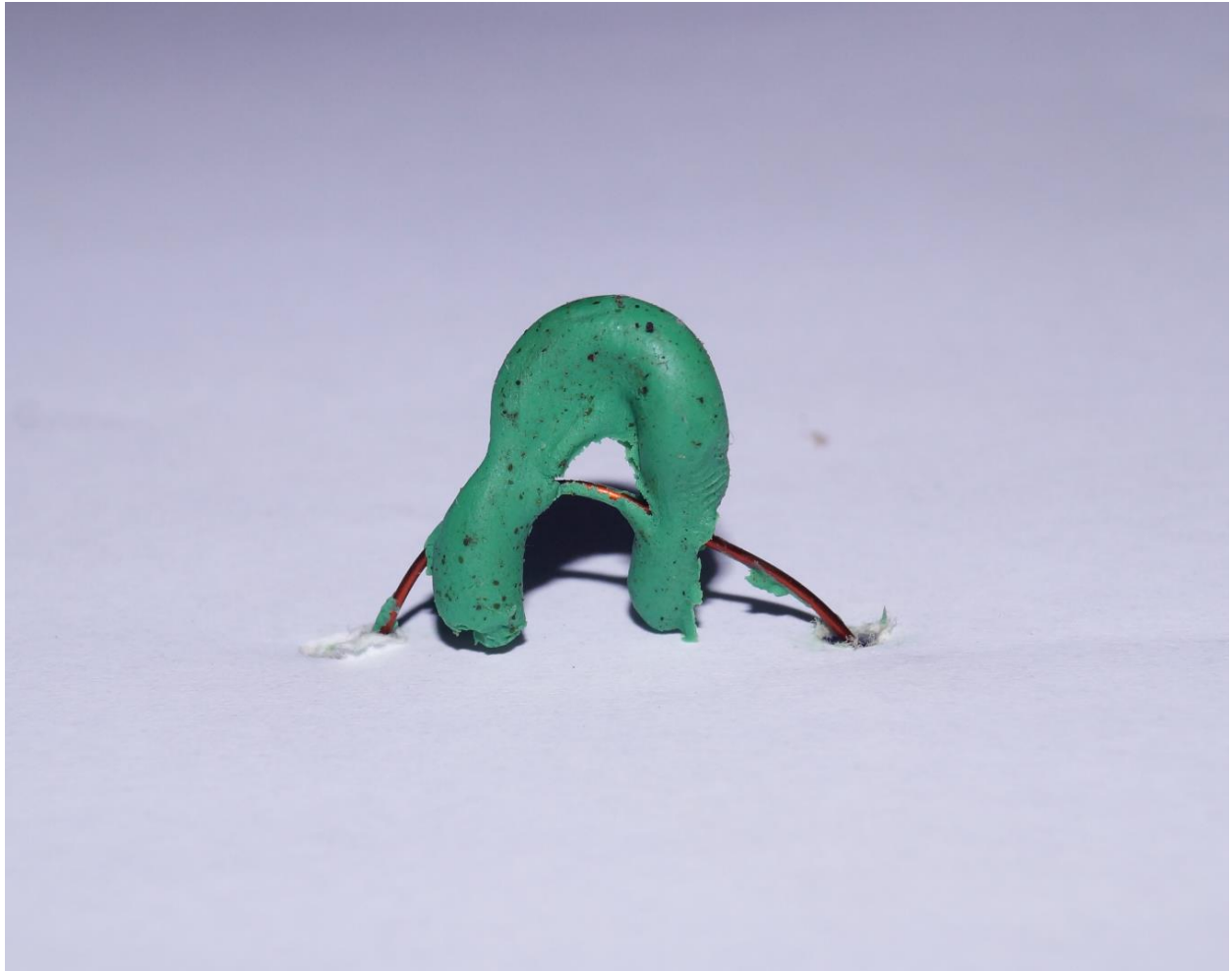


FIGURE S4.2 Ant predation during the installation process



5. CONCLUDING REMARKS



5. CONCLUDING REMARKS

5.1 Key findings

This thesis explored the effects of multiple human-driven forest disturbances on ecological functions, providing significant advancement in our understanding of processes important for Amazonian forests resilience and conservation. These key findings are outlined below:

5.1.1 Responses of Amazonian frugivores to disturbance in human-modified tropical forests (Chapter 1)

In Chapter 1 we uncovered the impacts of forest fires on richness, composition, and functional diversity of frugivorous birds and mammals in variably-degraded Amazonian forests. Although the overall richness was not affected by human-driven disturbances, forest burned more than 18 years prior to the study had a lower number of obligate and large-bodied frugivores as well as lower functional diversity. In the long-term, fires can thus lead to changes in frugivore communities, limiting the occurrence of specialist and large body frugivores, while exerting negative effects on functional diversity with consequences for ecological functions almost 20 years after fire events.

5.1.2 Fruit-frugivore interactions in burned and logged Amazonian forests (Chapter 2)

In Chapter 2 I provided the first empirical study showing the impacts of long-term fires (≥ 18 years before the study) on frugivory interactions in Amazonian forests. Overall, these results suggest a degree of resilience in the network structure in logged and burned forest, historically-burned forests (i.e., forests burned ≥ 18 years and logged) had a lower number of species and unique interactions than undisturbed forests. These results also showed high beta-diversity for

species and interaction in all forest classes, even in burned ones. This greater beta-diversity was explained by the high species and interaction turnover among forests demonstrating higher diversity of fruit-frugivore interaction. Notably, the distinct species and interaction composition in historically-burned forests are likely to play a more subtle role in determining the future of forest dynamics, even nearly two decades after fire events. Studies aimed at understanding the impacts of historic fires on frugivory interactions in Amazonian forests are fundamental given the increase in fire frequency in the Amazon region.

5.1.3 Predation on folivorous arthropods following forest degradation (Chapter 3)

In this Chapter, my co-authors and I used an experimental approach to show the effects of forest disturbance on the control of folivorous arthropods by vertebrates and arthropods. In addition, although we recorded high predation incidence in forests burned during the 2005-16 El Niño, folivore control was not greatly impacted by recent understorey fires. We found that the predation incidence on folivorous arthropods was similar in undisturbed, logged, burned and secondary forests. We also found that arthropod predators, especially ants, were the most common predator. These findings represent an important step for predicting the future of tropical forests, as herbivory control directly affects forest regeneration and hence resilience.

5.2 The future of the forest

Forest degradation rates in the Brazilian Amazon have remained high in recent decades, especially in the last few years, such that currently the extent of degraded forests is greater than that of the deforested forest area (MATRICARDI *et al.*, 2020; SILVA JUNIOR *et al.*, 2021). Fires are one of the major threats to the Amazonian forests, affecting biological communities and ecological process (BARLOW; PERES, 2004; HAWES; PERES, 2014; PIVELLO *et al.*,

2021; SLIK; VAN BALEN, 2006). Here we have shown the pervasive effects of forest fires on ecological communities. Based on our results, long-term fires can lead to changes in frugivore composition, as well as limiting the occurrence of specialist and large-bodied frugivores, while exerting a strong effect by reducing the functional diversity even more than 15 years after fire events. Nonetheless, fires had negative effects on frugivory interactions, reducing diversity and changing the fruit-frugivore interaction composition. Altogether, these findings indicate that neither interaction networks nor the folivores arthropods control were strongly affected by recent fire and selective logging, fires lead to long-term loss diversity of species and interactions which may lead to loss of important ecological function. Indeed, our results showed the loss of large body frugivores in forests burned in the past which may negatively affect dispersal of large seeds with important implications for forest resilience. Thus, with forest fires likely to become more ubiquitous, they are likely to play a more subtle role in determining future forest dynamics.

5.3 Future research priorities

This thesis has contributed in increasing our knowledge about how ecological functions, such as the control of folivorous arthropods and frugivory interactions potentially leading to seed dispersal, are affected by different human-driven forest disturbances, providing further insight into the maintenance of ecosystem processes in tropical forests. Human impacts on tropical forests are expected to continue to grow worldwide (ASNER *et al.*, 2009; BERENGUER *et al.*, 2021; JUNIOR *et al.*, 2020; PIVELLO *et al.*, 2021; SILVA JUNIOR *et al.*, 2021), and exacerbated by increasingly severe climate change predictions (GATTI *et al.*, 2021). As such my mains suggestion for future research directions are:

5.3.1 Long-term monitoring of biodiversity in disturbed forests

The results obtained in this thesis help fill a gap in the knowledge about the long-term responses of ecological function to human-driven forest disturbances. Long-term studies providing a broad understanding about impacts of forest fires and selective logging on tropical forests (MAGURRAN *et al.*, 2010). Research is greatly needed to assess how long forest fires effects will persist impacting frugivore communities and their interaction networks and whether these effects may become apparent on the structure of frugivory networks as well as on ecosystem functions, such as folivore control. Nevertheless, further research is needed to understand how ecological function will be shaped by re-occurring fires.

5.3.2 Usage of different survey methods for sampling

High quality biological surveys are essential to improve the knowledge base which is crucial to set conservation priorities and assessing management actions. Recently, the use of new technologies, such as camera traps and automatic recorders has expanded, improving survey efficiency, allowing a broader taxonomic spectrum to be surveyed, as well as providing insights on the magnitude of human impacts on biodiversity (METCALF *et al.*, 2022; RIVAS-ROMERO; SOTO-SHOENDER, 2015). Passive acoustic recorders and camera trap methods can increase the detection of frugivorous animals, while enhancing our understanding about ecological processes, such as frugivory interactions (ZHU *et al.*, 2021). For instance, camera traps provide a broad temporal sample of species and interaction detections, while detecting cryptic and nocturnal animals, rarely recorded by traditional survey methods (ZHU *et al.*, 2022).

5.3.3 Studies exploring the fruit-frugivore interactions

Animal-plant interactions, such as seed dispersal networks provide essential ecosystem services, fundamental to forest regeneration (CARLO; MORALES, 2015; ROGERS *et al.*,

2021). Despite the importance of frugivory interactions in the maintenance and resilience of tropical forests, our knowledge about these interactions and their responses to human-driven disturbances in the Amazonian forests is limited. This gap in the knowledge is especially alarming in the face of pervasive effects of forest fires which tend to worsen due to climate change (BALDIVIEZO; PASSOS; DE AZEVEDO, 2019; OLIVEIRA *et al.*, 2022). Therefore, there is a growing need for baseline data to understand the frugivory interactions in tropical forests, as well as to better understand further the consequences of human-driven disturbance on seed dispersal process.

5.3.4 Exploring the responses of functional diversity to human-driven disturbances with a phylogenetic perspective

Knowledge of ecological functions is fundamental; higher functional diversity increases the provisioning of ecosystem function via a variety of mechanisms (CARDINALE *et al.*, 2012; HOOPER *et al.*, 2012). Including a phylogenetic approach to functional diversity indexes can provide further insights into understanding how phylogenetic composition affects ecosystem functions along with taking into account the idiosyncratic responses of each community (SRIVASTAVA *et al.*, 2012). For instance, phylogenetic allows us to describe the more affected groups as well as the evolutionary history extinctions due to human-driven disturbances. Furthermore, high phylogenetic diversity is associated with high values of ecosystem functions, which may infer resilience to environmental changes (PRESCOTT *et al.*, 2016; SRIVASTAVA *et al.*, 2012).

5.4 References

ASNER, Gregory P.; RUDEL, Thomas K.; AIDE, T. Mitchell; DEFRIES, Ruth; EMERSON,

- Ruth. A contemporary assessment of change in humid tropical forests. **Conservation Biology**, vol. 23, no. 6, p. 1386–1395, 2009. <https://doi.org/10.1111/j.1523-1739.2009.01333.x>.
- BALDIVIEZO, Cristian Daniel Veliz; PASSOS, Marcela Fortes De Oliveira; DE AZEVEDO, Cristiano Schetini. Knowledge gaps regarding frugivorous ecological networks between birds and plants in Brazil. **Papeis Avulsos de Zoologia**, vol. 59, p. 0–4, 2019. <https://doi.org/10.11606/1807-0205/2019.59.54>.
- BARLOW, Jos; PERES, Carlos. Avifaunal Responses to Single and Recurrent Wildfires in Amazonian Forests. **Ecological Applications**, vol. 14, no. 5, p. 1358–1373, 2004. .
- BERENGUER, Erika; LENNOX, Gareth D.; FERREIRA, Joice; MALHI, Yadvinder; ARAGÃO, Luiz E.O.C.; BARRETO, Julia Rodrigues; DEL BON ESPÍRITO-SANTO, Fernando; FIGUEIREDO, Axa Emanuelle S.; FRANÇA, Filipe; GARDNER, Toby Alan; JOLY, Carlos A.; PALMEIRA, Alessandro F.; QUESADA, Carlos Alberto; ROSSI, Liana Chesini; DE SEIXAS, Marina Maria Moraes; SMITH, Charlotte C.; WITHEY, Kieran; BARLOW, Jos. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. **Proceedings of the National Academy of Sciences of the United States of America**, vol. 118, no. 30, 2021. <https://doi.org/10.1073/pnas.2019377118>.
- CARDINALE, Bradley J.; DUFFY, J. Emmett; GONZALEZ, Andrew; HOOPER, David U.; PERRINGS, Charles; VENAIL, Patrick; NARWANI, Anita; MACE, Georgina M.; TILMAN, David; WARDLE, David A.; KINZIG, Ann P.; DAILY, Gretchen C.; LOREAU, Michel; GRACE, James B.; LARIGAUDERIE, Anne; SRIVASTAVA, Diane S.; NAEEM, Shahid. Biodiversity loss and its impact on humanity. **Nature**, vol. 486, no. 7401, p. 59–67, 2012. DOI 10.1038/nature11148. Available at: <http://dx.doi.org/10.1038/nature11148>.
- CARLO, Tomás A.; MORALES, Juan M. Generalist birds promote tropical forest

- regeneration and increase plant diversity via rare- biased seed dispersal. **Ecology**, vol. 97, no. 7, p. 1–5, 2015. <https://doi.org/10.1890/15-2147.1>.
- GATTI, Luciana V.; BASSO, Luana S.; MILLER, John B.; GLOOR, Manuel; GATTI DOMINGUES, Lucas; CASSOL, Henrique L.G.; TEJADA, Graciela; ARAGÃO, Luiz E.O.C.; NOBRE, Carlos; PETERS, Wouter; MARANI, Luciano; ARAI, Egidio; SANCHES, Alber H.; CORRÊA, Sergio M.; ANDERSON, Liana; VON RANDOW, Celso; CORREIA, Caio S.C.; CRISPIM, Stephane P.; NEVES, Raiane A.L. Amazonia as a carbon source linked to deforestation and climate change. **Nature**, vol. 595, no. 7867, p. 388–393, 14 Jul. 2021. DOI 10.1038/s41586-021-03629-6. Available at: <https://www.nature.com/articles/s41586-021-03629-6>. Accessed on: 7 Feb. 2022.
- HAWES, Joseph E.; PERES, Carlos A. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. **Journal of Tropical Ecology**, vol. 48, no. 4, p. 465–475, 2014. <https://doi.org/10.1111/btp.12315>.
- HOOVER, David U; ADAIR, E Carol; CARDINALE, Bradley J; BYRNES, Jarrett E K; HUNGATE, Bruce A; MATULICH, Kristin L; GONZALEZ, Andrew; DUFFY, J Emmett; GAMFELDT, Lars; CONNOR, Mary I O. Aglobal synthesis reveals biodiversity loss as amajor driver of ecosystem change. **Nature**, vol. 486, no. 7401, p. 105–108, 2012. DOI 10.1038/nature11118. Available at: <http://dx.doi.org/10.1038/nature11118>.
- JUNIOR, Celso H. L. Silva; HEINRICH, Viola H. A.; FREIRE, Ana T. G.; BROGGIO, Igor S.; ROSAN, Thais M.; DOBLAS, Juan; ANDERSON, Liana O.; ROUSSEAU, Guillaume X.; SHIMABUKURO, Yosio E.; SILVA, Carlos A.; HOUSE, Joanna I.; ARAGÃO, Luiz E. O. C. Benchmark maps of 33 years of secondary forest age for Brazil. **scientific Data**, vol. 7, no. 269, p. 1–9, 2020. <https://doi.org/10.1038/s41597-020-00600-4>.
- MAGURRAN, Anne E.; BAILLIE, Stephen R.; BUCKLAND, Stephen T.; DICK, Jan Mc P.; ELSTON, David A.; SCOTT, E. Marian; SMITH, Rognvald I.; SOMERFIELD, Paul J.;

- WATT, Allan D. Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. **Trends in Ecology and Evolution**, vol. 25, no. 10, p. 574–582, Oct. 2010. <https://doi.org/10.1016/j.tree.2010.06.016>.
- MATRICARDI, Eraldo Aparecido Trondoli; SKOLE, David Lewis; COSTA, Olívia Bueno; PEDLOWSKI, Marcos Antonio; SAMEK, Jay Howard; MIGUEL, Eder Pereira. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. **Science**, vol. 369, no. 6509, p. 1378–1382, 1 Sep. 2020. <https://doi.org/10.1126/SCIENCE.ABB3021>.
- METCALF, Oliver C; BARLOW, Jos; MARSDEN, Stuart; GOMES DE MOURA, Nárgila; BERENGUER, Erika; FERREIRA, Joice; LEES, Alexander C. Optimizing tropical forest bird surveys using passive acoustic monitoring and high temporal resolution sampling. **Remote Sensing in Ecology and Conservation**, vol. 8, no. 1, p. 45–56, 2022. DOI 10.1002/rse2.227. Available at: www.phylopic.org.
- OLIVEIRA, Hernani F. M.; PINHEIRO, Rafael Barros Pereira; VARASSIN, Isabela Galarda; RODRÍGUEZ-HERRERA, Bernal; KUZMINA, Maria; ROSSITER, Stephen J; CLARE, Elizabeth L. The structure of tropical bat–plant interaction networks during an extreme El Niño–Southern Oscillation event. **Molecular Ecology**, vol. 00, p. 1–15, 2022. <https://doi.org/10.1111/mec.16363>.
- PIVELLO, Vânia R.; VIEIRA, Ima; CHRISTIANINI, Alexander V.; RIBEIRO, Danilo Bandini; DA SILVA MENEZES, Luciana; BERLINCK, Christian Niel; MELO, Felipe P.L.; MARENGO, José Antonio; TORNQUIST, Carlos Gustavo; TOMAS, Walfrido Moraes; OVERBECK, Gerhard E. Understanding Brazil’s catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. **Perspectives in Ecology and Conservation**, vol. 19, no. 3, p. 233–255, 2021. DOI 10.1016/j.pecon.2021.06.005. Available at: <https://doi.org/10.1016/j.pecon.2021.06.005>.
- PRESCOTT, Graham W.; GILROY, James J.; HAUGAASEN, Torbjørn; MEDINA URIBE,

- Claudia A.; FOSTER, William A.; EDWARDS, David P. Reducing the impacts of Neotropical oil palm development on functional diversity. **Biological Conservation**, vol. 197, p. 139–145, 2016. <https://doi.org/10.1016/j.biocon.2016.02.013>.
- RIVAS-ROMERO, Javier A.; SOTO-SHOENDER, Jose Roberto. Filling in the Gaps: Evaluating the Use of Camera Traps in the Canopy to Examine Frugivore Visits to *Oreopanax echinops* in the Highlands of Guatemala. **Southwestern Naturalist**, vol. 60, no. 4, p. 366–397, 2015. <https://doi.org/10.1894/0038-4909-60.4.366>.
- ROGERS, Haldre S; DONOSO, Isabel; TRAVESET, Anna; FRICKE, Evan C. Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. **Annual Reviews**, vol. 52, p. 641–666, 2021. .
- SILVA JUNIOR, Celso H.L.; PESSÔA, Ana C.M.; CARVALHO, Nathália S; REIS, João B.C.; ANDERSON, Liana O; ARAGÃO, Luiz E.O.C. The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. **Nature Ecology and Evolution**, vol. 5, no. 2, p. 144–145, 2021. DOI 10.1038/s41559-020-01368-x. Available at: <https://doi.org/10.1038/s41559-020-01368-x>.
- SLIK, J. W.F.; VAN BALEN, S. Bird community changes in response to single and repeated fires in a lowland tropical rainforest of eastern Borneo. **Biodiversity and Conservation**, vol. 15, no. 14, p. 4425–4451, 2006. <https://doi.org/10.1007/s10531-005-4385-1>.
- SRIVASTAVA, Diane S.; CADOTTE, Marc W.; MACDONALD, A. Andrew M.; MARUSHIA, Robin G.; MIROTECHNICK, Nicholas. Phylogenetic diversity and the functioning of ecosystems. **Ecology Letters**, vol. 15, no. 7, p. 637–648, 2012. <https://doi.org/10.1111/j.1461-0248.2012.01795.x>.
- ZHU, Chen; LI, Wande; GREGORY, Tremaine; WANG, Duorun; REN, Peng; ZENG, Di; KANG, Yi; DING, Ping; SI, Xingfeng. Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. **Remote Sensing in**

Ecology and Conservation, vol. 8, no. 1, p. 92–104, 1 Feb. 2022.

<https://doi.org/10.1002/rse2.232>.

ZHU, Chen; LI, Wande; WANG, Duorun; DING, Ping; SI, Xingfeng. Plant-frugivore interactions revealed by arboreal camera trapping. **Frontiers in Ecology and the Environment**, no. March, p. 149–151, 2021. <https://doi.org/10.1002/fee.2321>.