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Research article

Anthropogenic disturbances simplify frugivory interactions in Amazonia

Liana Chesini Rossi[1,2,3], **Carine Emer**[1,3], **Alexander Charles Lees**[2,4], **Erika Berenguer**[5,6], **Jos Barlow**[6], **Joice Ferreira**[7,8,9], **Filipe M. França**[8,10], **Yan Gabriel Ramos**[11], **Paulo Tavares**[8] and **Marco Aurelio Pizo**[1]

[1]Departamento de Biodiversidade, Centro de Pesquisa em Dinâmica da Biodiversidade e Mudanças do Clima (CBioClima), Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil
[2]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK
[3]Rio de Janeiro Botanical Garden Research Institute, Rio de Janeiro, RJ, Brazil
[4]Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 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), Universidade Federal do Pará, Belém, PA, Brazil
[9]Programa de Pós-Graduação em Ciências Ambientais (PPGCA), Universidade Federal do Pará, Belém, PA, Brazil
[10]School of Biological Sciences, University of Bristol, Bristol, UK
[11]Aiuká Consultoria em Soluções Ambientais, Rio das Ostras, RJ, Brazil

Correspondence: Liana Chesini Rossi (lianachesinibio@gmail.com)

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Frugivory interactions are essential ecological processes for the regeneration of tropical forests, ensuring ecosystem resilience following disturbances. However, little is known about how frugivory interactions are shaped by anthropogenic disturbances, especially in Amazonia – one of the most biodiverse ecosystems on Earth. We investigate how selective logging and forest fires impact both arboreal and terrestrial frugivory interactions in Amazonian forests. We focus on four forest classes: Undisturbed, Logged, Logged-and-17y-burned (burned 17 years before sampling) and Logged-and-3y-burned (burned three years before sampling). We recorded 4670 frugivory interactions at the community level, in a sampling effort of 31 484 h. Undisturbed forests sustained a significantly higher number of species and interactions when compared to Logged-and-17y-burned forests, and similar numbers to Logged and Logged-and-3y-burned. Selective logging and forest fires did not alter significantly the structural properties of the frugivory networks, which were highly modular, moderately specialised, poorly connected and non-nested. Regarding community composition, we detected high β-diversity of plant species, frugivore species, and their interactions between all study areas, as well as within and between forest classes, mainly driven by species turnover. Logged-and-17y-burned forests hosted the most unique interaction composition compared to Undisturbed forests. Our study provides novel evidence that anthropogenic disturbances, particularly selective logging and forest fires, negatively

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affect frugivory interactions in Amazonian forests. These effects may persist for years after the initial disturbance events and could be exacerbated due to the predicted increase in forest fires driven by climate change.

Keywords: β-diversity, forest fires, frugivory networks, seed dispersal, seed predation, tropical forests

Introduction

In the Amazon, 38% of forest habitats have already been impacted by different types of anthropogenic disturbances, often acting synergistically (Díaz et al. 2019, Lapola et al. 2023). For example, between 2001 and 2018, selective logging affected 120 000 km^2 in the region (Lapola et al. 2023). Selectively logged forests are hotter and drier due to the greater amount of clearings, thus making them more vulnerable to forest fires (Uhl and Kauffman 1990, Cochrane 2003). The increase in frequency, intensity and length of extreme droughts across the region also result in more flammable forests (Cochrane 2003, Nepstad et al. 2004, Jiménez-Muñoz et al. 2016). As a consequence, forest fires are estimated to become extremely widespread in the 21st century (Brando et al. 2020, Lapola et al. 2023), with some megafires, i.e. those affecting an area ≥ 10 000 ha, already being reported (Withey et al. 2018).

Given that Amazonian forests have not evolved under conditions of regural natural fire disturbance (Uhl and Kauffman 1990), such events cause high tree mortality (Berenguer et al. 2021). Post-fire plant communities are often dominated by pioneer species with low wood densities and small seeds (Barlow et al. 2003, Barlow and Peres 2004, Hawes et al. 2020). These pioneer species are also common colonists of forests that have recently undergone selective logging (Costantini et al. 2016). In the long term, these shifts in species composition may jeopardise the availability of fruits for forest fauna, potentially leading to a decrease in frugivore visitation rates (Moegenburg and Levey 2003, Brando et al. 2024). Such changes in fruit availability can also alter the composition of frugivore communities, particularly affecting strict frugivore species. Indeed, avian frugivore communities in disturbed tropical forests have been shown to be less diverse and differ in species composition when compared to undisturbed forests (Moura et al. 2013, Bregman et al. 2016). Such shifts in plant and frugivore communities are likely to disrupt essential ecological processes such as seed dispersal and seed predation, which in turn will influence natural regeneration and, ultimately, the post-disturbance community dynamics (Valiente-Banuet et al. 2015, Neuschulz et al. 2016, Rogers et al. 2021).

Despite these advances in our understanding of the effects of anthropogenic disturbances on plant and frugivore communities, there are no studies addressing these impacts on frugivory interactions at the community level in Amazonian forests (Ballarin et al. 2024). To date, studies in the region have primarily focused on describing the interactions of either single species, such as tapirs (Fragoso and Huffman 2000, Tobler et al. 2010, Paolucci et al. 2019), or specific groups such as macaws (Baños-Villalba et al. 2017), tortoises and fish (Guzmán and Stevenson 2008, Weiss et al. 2016), keystone plants (Stevenson et al. 2015), and/or guilds of medium-to large-bodied diurnal vertebrates (Hawes and Peres 2014). Studies involving the whole frugivore community, including both arboreal and terrestrial frugivores, pose significant challenges, given the wide range of both fruit-eating vertebrates and the morphological fruit types they exploit (Hawes and Peres 2014, Todeschini et al. 2020, Scabin and Peres 2021).

Ecological networks are often employed to understand how frugivory interactions are structured (Delmas et al. 2019). The use of networks also provides valuable insights into how disturbances reshape ecological interactions (Tylianakis and Morris 2017, Emer and Timóteo 2020). Following an anthropogenic disturbance, several network structural properties are expected to change (Menke et al. 2012, de Assis Bomfim et al. 2018). For example, network connectance – understood as the proportion of realised interactions relative to all possible pairwise species combinations in the system (Dunne et al. 2002) – is expected to increase following anthropogenic disturbances, as the number of species usually declines and therefore the possibility of realised interactions among the remaining ones is likely to increase (Heleno et al. 2012, Menke et al. 2012). Network nestedness – which represents the extent to which the interactions of specialist species are subsets of those involving generalists, while interaction between generalist species are uncommoly (Bascompte et al. 2003, Almeida-Neto et al. 2008) is also predicted to increase, as generalist species tend to become hyperabundant in disturbed ecosystems (Emer et al. 2020). Modularity – the measure of whether groups of species have stronger interactions among themselves than with species from other groups (Olesen et al. 2007) – is expected to decrease after a disturbance event, as specialist interactions tend to vanish (Schleuning et al. 2014). Lastly, network specialisation – which reflects how exclusively species interact with each other (Vázquez and Aizen 2004, Blüthgen et al. 2006) – is also expected to decline as generalist interactions tend to become more prevalent in disturbed forests (Menke et al. 2012, Palacio et al. 2016). In addition to network analysis, the effects of anthropogenic disturbances can also be assessed by examining species dissimilarity among different areas – β-diversity (Poisot et al. 2012, Burkle et al. 2022). For example, the replacement of original species or changes of species interactions can result in ecological turnover (e.g. β-turnover), including cases where the remaining species are a nested subset of the original species (β-nestedness, Baselga 2010).

Here, we use both network structural properties and β-diversity metrics to quantify the impacts of selective logging and forest fires on frugivory interactions in Amazonian forests. Our sampling design focuses on the community level, including both arboreal and terrestrial frugivores, to sample the entire functional group of vertebrate frugivores. We sampled frugivory interactions across four forest classes: 1) undisturbed forests, 2) selectively logged forests, 3) selectively logged forests that burned at least 17 years before sampling, and 4) selectively logged forests that burned three years prior to sampling. For ease of reference, these forest classes are referred to as Undisturbed, Logged, Logged-and-17y-burned and Logged-and-3y-burned, respectively. Specifically, we investigated how selective logging and forest fires affect:

1) the number of plants and frugivore species, and their interactions;
2) the frugivory network structural properties (i.e. connectance, nestedness, modularity and specialisation);
3) the β-diversity of plants, frugivores and their interactions.

We hypothesise that there will be a decline in the number of plants and frugivore species following selective logging and forest fires (Moura et al. 2013, Berenguer et al. 2021), with direct implications for frugivory interactions (Albert et al. 2020), reducing their frequencies and altering pairwise species associations. We predict that impacts will be stronger in forests selectively logged and burned recently, where we expect fewer species and interactions compared to undisturbed forests due to the recent fires. In contrast, we expect that selectively logged forests and forests selectively logged and burned nearly two decades ago will harbour more species and interactions than forests that burned more recently, given the extended period of post-fire recovery. In the case of logged forests, we expect that they will be the least impacted, given the absence of fire events. Further, we hypothesise that the remaining interactions in forests which were selectively logged and burned recently will result in more connected, more nested, less modular, and less specialised network structures compared to undisturbed forests (Sebastián-González et al. 2015, Tylianakis and Morris 2017). This is because generalist species are expected to prevail in these areas, contributing disproportionately to the pairwise interactions, while reducing the number of specialist species (Burivalova et al. 2014, Hawes et al. 2020). Finally, we predict high β-diversity values for species and interactions between study areas and between forest classes. The highest values were expected between forests selectively logged and burned recently and undisturbed forest, due to the compositional dissimilarity of species and interactions resulting from recent forest fires events. These fires drive species and interaction replacement, i.e. β-turnover (see Burkle et al. 2022 for pollination interactions). Regarding forests selectively logged and selectively logged and burned nearly two decades ago, we expect these to be more similar to undisturbed forests given nearly two decades of recovery time. This extended recovery period facilitates the presence of not only generalist species but also species associated with undisturbed forests.

Material and methods

Study area

The study was conducted in the eastern Brazilian Amazon, in the municipalities of Belterra, Mojuí dos Campos and Santarém (Supporting information). The region comprises a mosaic of land uses, including undisturbed primary forests, degraded primary forests, varyingly-aged secondary forests, croplands and pastures (Gardner et al. 2013). Selective logging and forest fires represent some of the primary threats to remaining forested areas (Lapola et al. 2023). During 2015 and 2016, an extreme drought, caused by a strong El Niño event, led to fires extending over one million hectares of forests in the study region. Forests selectively logged and burned recently (Logged-and-3y-burned forest) in this study are those forests that were burned during this El Niño event (Withey et al. 2018).

Sampling design

We studied 17 areas across four forest classes: 1) Undisturbed forests – i.e. primary forests with no evidence of anthropogenic disturbances (n = 5), 2) Logged forests – i.e. selectively logged primary forests (n = 4), 3) Logged-and-17y-burned forests – i.e. selectively logged primary forests that burned at least 17 years before sampling (n = 4), 4) Logged-and-3y-burned forests – i.e. selectively logged primary forests that burned three years before sampling (n = 4, Supporting information). When present, selective logging occurred at least 30 years prior to the study. The type and timing of anthropogenic disturbances affecting each study area were determined through field assessments and visual inspection of satellite images from 1988 to 2010 (Gardner et al. 2013). In each study area, we installed a single 1-km long transect, ensuring that each transect was separated from others by at least 1.5 km to minimize spatial autocorrelation (Supporting information).

Sampling frugivory interactions

From February 2019 to March 2020, we recorded frugivory interactions between fleshy-fruited plants and frugivorous birds and mammals (except bats). Frugivory interactions were recorded at the community level without focusing on specific taxonomic groups of plants or frugivores species. The following feeding behaviours were considered as frugivory interactions: seed swallowing – the frugivore swallows the entire seed; pulp consumption – the frugivore eats the fruit piecemeal but does not swallow the seed; seed carried away – the frugivore takes the fruit away from the plant instead of immediately swallowing it; and seed predation – the frugivore damages the seeds (Jordano and Schupp 2000). For each interaction, we recorded the plant and frugivore species, as well as the number of individuals interacting with the fruits.

Frugivore visits to individual plants were sampled using three complementary methods to maximize the diversity of interactions recorded, including arboreal and terrestrial functional groups. To combine the three methods, we standardised the data by considering each frugivory visit as the frequency of interaction. The three weighted matrices (one for each method), weighted by the frequency of interactions, were merged by directly summing the datasets (Quintero et al. 2022). Although the methods had different sampling efforts when compared to one another, we estimated the sampling effort for each study areas and standardized it across forest classes to the greatest extent feasible, ensuring similar forest class-level sample effort (Supporting information).

The three sampling methods were:

1) Walking censuses. Frugivory interactions were recorded along 1-km transects between 6:00 a.m. and 6:00 p.m., with no surveys taking place during periods of rainfall. Frugivory records were obtained viewing plants situated within 25 m of either side of the transects, totalling 50 000 m^2 sampled per transect. Each study area was sampled twice a month. The sampling effort for the walking censuses was 1053 h.
2) Focal census. Focal samples were undertaken opportunistically during walking censuses. When plants with ripe fruits were observed, we paused the walking census and started focal observations. Focal plants were observed for a minimum of 15 min. If a frugivore visited the plants during this period, an additional 30 min of focal observation time was added. The sampling effort for the focal censuses was 503 h.
3) Camera trapping. We established 88 camera trapping points (14 arboreal and 74 terrestrial) using APEMAN 16MP cameras with Infrared Night Vision detecting movement up to 20 m away. We installed 3–6 cameras per study area on plants during the ripe fruit period, removing them when no more fruits were available. Cameras were installed facing the fruits to maximize the likelihood of recording interactions (Zhu et al. 2022). Arboreal cameras were set 5–15 m from the ground, while terrestrial cameras were placed 30 cm above the ground. Cameras were active 24 h day^{-1}, recording 20-s videos when triggered by movement, with a 20-s interval between consecutive recordings. Consecutive videos of the same species were considered independent if more than an hour had passed between them (Rivas-Romero and Soto-Shoender 2015). When more than one individual was recorded in a single video, each individual was counted as a separate event. Sampling effort was calculated as the sum of hours each camera trap was active, totalling 29 928 h.

Plant species were identified by parabotanists from Embrapa Amazônia Oriental to the lowest possible taxonomic level. Bird species were primarily identified by LCR with help from ACL and MAP, and small mammals were identified by YGR with inputs from local researchers (Acknowledgments).

Network structural properties

For each study area, we built frugivory networks from a_{ij} matrices, where i represents plant species, j represents frugivore species, and the ij component describes the weighted links among them, i.e. the frequency of interactions between plant i and frugivore j. We then calculated several network descriptors for each study area, namely: the number of plant and frugivore species, the network size (i.e. total number of species), the number of unique pairwise interactions, and the total number of interactions. We then estimated a set of metrics with $r < 0.7$ correlation among themselves (Supporting information) to maximise complementary information about the structure of the frugivory networks, as follows:

1) Connectance (*C*). The proportion of realised interactions in relation to the total number of possible ones (Dunne et al. 2002);
2) Weighted nestedness (*wNODF*). A quantitative measure of nestedness, hereafter referred to as network-nestedness, which considers the decreasing matrix filling according to the frequency of interactions. It represents whether the organisation of the frugivory interactions is set by a core of generalist species that interact with each other and also with subsets of more specialist ones (Ulrich et al. 2009, Almeida-Neto and Ulrich 2011);
3) Weighted modularity. The presence of groups of plant and frugivores species that strongly interact among themselves, but interact either less frequently or not at all with species in other groups (Olesen et al. 2007). We used the *DIRT_LPA_wb_plu* algorithm (Beckett 2016) to estimate the level of modularity and the number of modules;
4) Specialisation (*H2'*). Quantifies the deviation of observed interactions from those expected given interaction frequencies (Blüthgen et al. 2006). The more unique the interactions, the higher the *H2'* value, indicating a more specialised network.

Finally, to test whether the observed network properties differed from those expected by chance, we contrasted the observed values for each network property against 100 randomizations generated using the Vaznull algorithm (Vázquez et al. 2007). This algorithm randomises the interaction frequencies while preserving the observed number of species and interactions, thereby maintaining constant connectance (Vázquez et al. 2007). We then calculated the respective z-scores for each observed network property value by subtracting the mean of the null model and dividing by its SD (Dormann et al. 2009). These z-scores and observed values were used as the response variable in the statistical models. Network metrics and null models were estimated using the 'bipartite' package (Dormann et al. 2009).

β-diversity of species and interactions

We measured the β-diversity of plant species (β_{plants}), frugivore species (β_{frug}), and their interactions (β_{int}) at three levels to capture different scales of dissimilarity. First, at the study study area level, we accessed dissimilarity between study areas, treating each study area as a replicate, regardless of its forest class. This reflects the dissimilarity across geographic locations. Second, at the intra-forest class level, we evaluated dissimilarity within the same forest class, using study areas within that forest class to replicate. This captures the dissimilarity among study areas that share the same forest class. Finally, at the inter-forest class level, we quantified dissimilarity between different forest classes, treating each forest class as a replicate. This measures the magnitude of the dissimilarity between forest classes.

We then partitioned β-diversity into two components: β-turnover and β-nestedness, both estimated for plant and frugivore species, as well as for frugivory interactions (Baselga 2010). The analyses were performed employing the *beta.multi* function from the 'betapart' package (Baselga and Orme 2012). This function computes multiple-site dissimilarities using Sorensen dissimilarity (β_{SOR}). It further distinguishes between the contributions of species and interactions replacement (i.e. β-turnover – β_{SIM}), computed using Simpson dissimilarity, and species and interactions loss or gain (i.e. β-nestedness – β_{NES}), measured using nestedness-resultant dissimilarity derived as the difference between β_{SOR} and β_{SIM} (Baselga 2010). Additionally, we used non-metric multidimensional scaling (NMDS, two dimensional) to graphically represent the dissimilarity in species and interaction composition. We used Bray–Curtis dissimilarity matrices to ordinate study areas and forest classes according to their dissimilarity in species and interaction composition. The NMDS ordination was created using the *metaMDS* function in the 'vegan' package (Oksanen et al. 2015).

Statistical analyses

To test the effects of selective logging and forest fires upon network properties, we used generalised linear models (GLM) with the *glm* and *glm.nb* functions from the 'lme4' package (Bates et al. 2015). We checked for overdispersion with the 'DHARMa' package (Hartig 2016). An individual model was fitted for each network structural property as the response variable and the forest class as the predictor variable. We fitted a Poisson distribution with a log link function to model count data, including the number of plant and frugivore species and network size. For variables exhibiting overdispersion (i.e. the number of unique pairwise interactions and the total number of interactions), we applied a negative binomial distribution. For continuous responses (i.e. observed and null model for connectance, network-nestedness, modularity and specialisation), we used Gaussian distributions. We did not detect spatial autocorrelation among study areas (Supporting Information). We fit a full model using maximum likelihood estimation and selected the best fixed-effects structure based on the Akaike information criterion corrected for small sample sizes (AICc), using the 'lme4' package (Bates et al. 2015). To control for differences in sampling effort among forest classes, we calculated the square root of the number of interactions divided by the square root of the network size, and included these values as a fixed covariate in all models (Schleuning et al. 2012). Models with delta AICc < 2 were selected as plausible explanations for the observed patterns (Supporting information). We used the Akaike weight of evidence (wAICc) to rank the relative importance for each model (Burnham and Anderson 2001). Then, we presented the coefficients of each predictor, the variance explained, and the confidence intervals (CIs) for the best linear model. We estimated the CIs of the models using the *confint* function from the 'lme4' package (Bates et al. 2015). All analyses were carried out in R (www.r-project.org).

Results

Frugivory interactions

We recorded 4670 interactions involving 991 unique pairwise associations between 165 plant and 174 frugivore species, summing up 31 484 sampling hours (Supporting information). Eighty-six percent of frugivory interactions recorded were arboreal while only 14% were recorded on the ground. Out of the frugivore pool, 146 were identified as bird species, accounting for 3665 interactions (78.5%), while 28 were mammal species, which performed 1005 interactions (21.5%).

Plants from the Melastomataceae, Moraceae and Urticaceae families were involved in 52% of the total number of interactions (18.3%, 17.8% and 15.8%, respectively). The plant species most commonly involved in interactions with frugivores were *Coussapoa tessmannii* (Urticaceae, 9.7%), followed by *Ficus* morphotype 1 (Moraceae, 8.7%), *Brosimum acutifolium* (Moraceae, 7.1%), and *Miconia pyrifolia* (Melastomataceae, 5.3%).

Birds from the families Ramphastidae (18.2%), Thraupidae (13.7%) and Pipridae (11%) accounted for 43% of the total number of interactions. The most common frugivores included three bird species: *Ceratopipra rubrocapilla* red-headed manakin (8.9%), *Ramphastos vitellinus* channel-billed toucan (5.1%), *Ramphastos tucanus* white-throated toucan (3.9%) and *Pteroglossus bitorquatus* red-necked aracari (3.9%), and one mammal, *Dasyprocta leporina* red-rumped agouti (4.3%). Additionally, we recorded threatened species interacting with plants, including *Lepidothrix iris* opal-crowned manakin (classified as Vulnerable by the IUCN), found in Undisturbed and Logged forests, as well as *Aburria cujubi* red-throated piping guan (Vulnerable), *Penelope pileata* white-crested guan (Vulnerable), and *Ateles marginatus* white-cheeked spider monkey (Endangered), which were observed in Undisturbed, Logged, and Logged-and-3-year-burned forests (IUCN 2024). None of the globally threatened species were recorded in Logged-and-17-year-burned forests.

Network descriptors and structural properties

Networks showed a reduced number of frugivore species and smaller network size in Logged-and-17y-burned forests (Frugivores: mean = 28.5 ± SD = 6.5, Network size: mean = 44 ± SD = 6.0) in comparison to Undisturbed ones (Frugivores: mean = 44.4 ± SD = 8.88, Network size: mean = 59.6 ± SD = 7.12, Table 1, Supporting information). In contrast, no significant differences were detected in

Table 1. Results from generalised linear models testing the effects of selective logging and forest fires, and sampling effort (accounting for the differences in samplings intensity among forest classes with least square weighted, calculated as the square root of the number of interactions divided by the square root of the network size) on frugivory network properties of Amazonian forests. Forest classes from left to right correspond to: Undisturbed forest, Logged forests, Logged-and-17y-burned forests and Logged-and-3y-burned forests. Results are presented for the number of plant species, frugivore species network size (number of plant and frugivore species), number of unique pairwise interactions and interaction frequency. Frugivory interactions in Undisturbed forests served as a baseline for comparison with all other models. *w*AICc – weight that gives an estimate of the probability of that models being the best choice under AICc criteria, and confidence intervals (CIs) not overlapping zero indicate significant results, highlighted in bold.

Network metrics	Best model	*w*AICc	Est	SE	95% CI	z
Number of plant species	Sampling	0.73				
	Intercept		3.61	0.33	**2.95, 4.26**	10.82
	Sampling		−0.36	0.16	**−0.68, −0.05**	−2.28
Number of frugivores species	Forest treatment + Sampling	0.86				
	Intercept		3.12	0.30	**2.53, 3.69**	10.56
	Undisturbed – Logged		0.08	0.10	−0.12, 0.28	0.75
	Undisturbed – Logged-and-17y-burned		−0.31	0.13	**−0.56, −0.05**	−2.36
	Undisturbed – Logged-and-3y-burned		0.20	0.12	−0.03, 0.43	1.65
	Sampling		0.28	0.12	**0.04, 0.50**	2.36
Network size	Treatment	0.62				
	Intercept		4.09	0.06	**3.97, 4.19**	70.56
	Undisturbed – Logged		0.06	0.09	−0.10, 0.22	0.70
	Undisturbed – Logged-and-17y-burned		−0.30	0.10	**−0.49, −0.11**	−3.19
	Undisturbed – Logged-and-3y-burned		0.12	0.08	−0.04, 0.28	1.44
	Forest treatment + Sampling	0.38				
	Intercept		3.85	0.24	**3.36, 4.32**	15.74
	Undisturbed – Logged		0.08	0.09	−0.09, 0.25	0.92
	Undisturbed – Logged-and-17y-burned		−0.26	0.11	**−0.46, −0.04**	−2.42
	Undisturbed – Logged-and-3y-burned		0.17	0.10	−0.02, 0.37	1.73
	Sampling		0.10	0.10	−0.09, 0.29	0.99
Number of unique interactions	Forest treatment + Sampling	0.77				
	Intercept		3.67	0.23	**2.93, 4.25**	16.29
	Undisturbed – Logged		0.17	0.08	−0.04, 0.42	1.15
	Undisturbed – Logged-and-17y-burned		−0.32	0.10	**−0.57, −0.02**	−3.19
	Undisturbed – Logged-and-3y-burned		0.34	0.09	−0.08, 0.63	1.72
	Sampling		0.26	0.09	**0.02, 0.54**	2.91
Total number of interactions	Forest treatment + Sampling	0.82				
	intercept		−302.07	88.19	**2.94, 4.00**	−3.43
	Undisturbed – Logged		−9.71	32.91	−0.09, 0.29	−0.30
	Undisturbed – Logged-and-17y-burned		−70.13	36.10	**−0.47, −0.04**	−1.94
	Undisturbed – Logged-and-3y-burned		16.12	37.03	−0.03, 0.41	0.44
	Sampling		279.49	35.62	**0.75, 1.17**	7.85

Logged (Frugivores: mean = 45 ± SD = 4.5, Network size: mean = 63.25 ± SD = 7.25) and Logged-and-3y-burned forests (Frugivores: mean = 46.4 ± SD = 4.0, Network size: mean = 67.25 ± SD = 4.62) when compared to Undisturbed forests (Table 1). Similarly, the total number of interactions was also lower in Logged-and-17y-burned (mean = 168 ± SD = 65.30), but it did not differ significantly between Logged (mean = 298.75 ± SD = 64.22), and Logged-and-3y-burned forests (mean = 239 ± SD = 43.50) when compared to Undisturbed forests (mean = 369.40 ± SD = 184.57, Table 1, Supporting information). In addition, Logged-and-17y-burned forests had a lower number of unique frugivory interactions (mean = 47.25 ± SD = 7.08, Table 1), whereas Logged (mean = 82.50 ± SD = 11.68), and Logged-and-3y-burned forests (mean = 89.75 ± SD = 15.91) were similar to Undisturbed forests (mean = 74.00 ± SD = 19.40, Table 1).

Overall, frugivory networks were significantly more modular and less nested than expected by the null models while the significance of connectance and specialization varied among networks (Fig. 1, Supporting information). Nevertheless, there was no significant effect of treatment in any of the network metrics (Supporting information). The 17 modular networks consisted of 159 modules, ranging from 4 to 15 across the networks. Undisturbed forests had the lowest number of modules (mean = 8.00 ± SD = 3.4), while Logged-and-3y-burned forests had the highest (mean = 11.50 ± SD = 2.6, Supporting information). Individual modules varied in the number of species, ranging from two to 45 species per module (mean = 12 ± 6 SD). The number of plant species per module ranged from one to eight (mean = 2 ± 1 SD), while frugivore species ranged from one to 33 (mean = 4 ± 1 SD). Among all modules, 39% (n = 48) were small modules, consisting of a single plant species interacting with a single frugivore.

β-diversity of species and interactions

We found high dissimilarity (β_{sor}) between study areas for plant species ($\beta_{Plants} = 0.94$), frugivore species ($\beta_{Frug} = 0.86$),

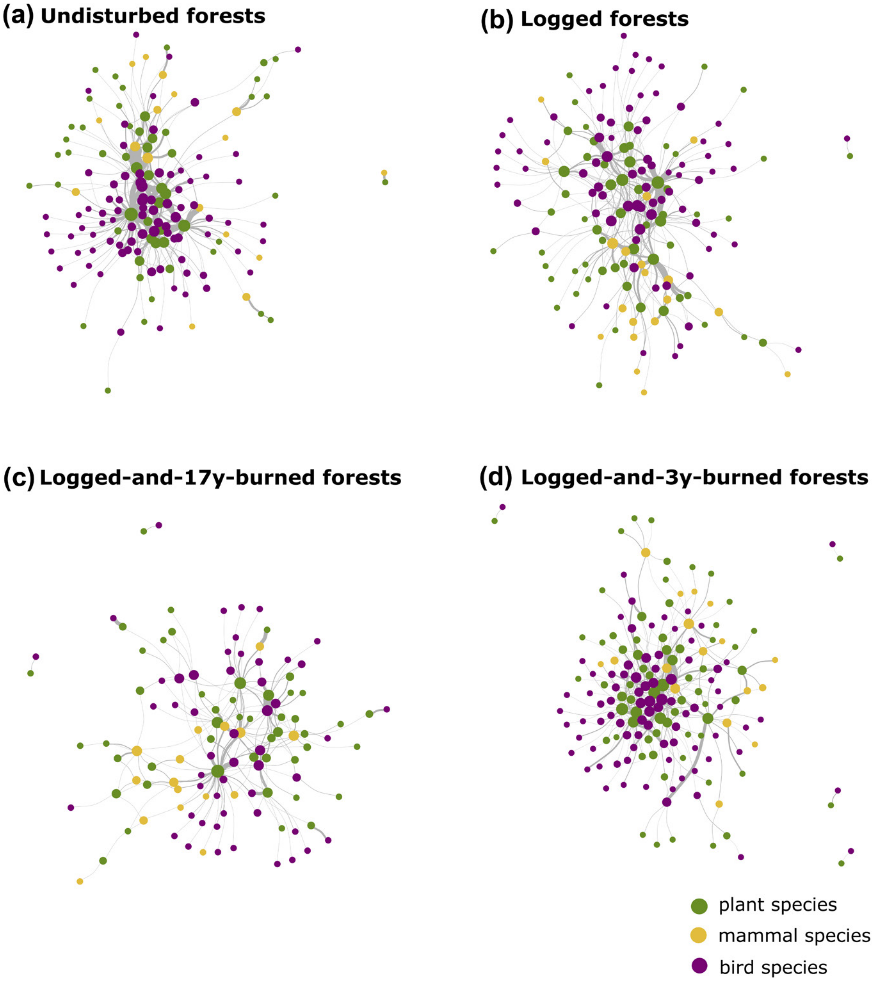

Figure 1. The structure of the frugivory networks surveyed in (a) Undisturbed forests, (b) Logged forests, (c) Logged-and-17y-burned forests and (d) Logged-and-3y-burned forests in the eastern Brazilian Amazon. The size of the dots is proportional to the number of interactions performed by each species. The frequencies of frugivory interactions are denoted by weighted grey lines connecting two nodes. Isolated nodes and their interactions form modules separated from the core of the network, and point towards higher modularity. The structure of the frugivory networks for each study area are provided in the Supporting information.

and frugivory interactions (β_{Int}= 0.97, Fig. 2, Supporting information). Although high differences in the composition of species and interactions were also observed in the intra-forest classes, these differences were smaller compared to those inter-forest classes (Supporting information). This pattern was consistent across all pairwise comparisons for plants, frugivores, and interactions (Supporting information). Species turnover was the main driver of changes in species and interaction composition between study areas. β-turnover (β_{sim}) was high for plant species (β_{Plants} = 0.92) and frugivore species (β_{Frug} = 0.83), as well as for interactions (β_{Int} = 0.97). In contrast, β-nestedness (β_{nes}) was low for plant species (β_{Plants} = 0.01), frugivore species (β_{Frug} = 0.04), and for interactions (β_{Int} = <0.01). Species β-turnover was also the primary component driving dissimilarity in species and interaction compositions intra- and inter-forest classes, with β-nestedness remaining consistently low (Supporting information).

Plant species dissimilarity was high, with only three species (i.e. *Didymopanax morototoni*, *Laetia procera* and *Virola michelii*) found across all forest classes (Supporting information). For frugivores, from 174 species recorded, 68 were exclusive to a single forest class while 29 species (21 birds and eight mammals, or 16.6% of all species) were present in all forest classes (Supporting information). Out of 991 unique interactions, only one single pairwise plant–frugivore interaction was recorded in all forest classes, i.e. *Virola michelii* and its associated frugivore, *Ramphastos tucanus* white-throated toucan (Supporting information).

Species and interaction dissimilarities were reflected in both axes of the two-dimensional NMDS (Fig 3). Study areas within the same forest class exhibited closer axis distributions for species and interactions, indicating greater similarity intra-forest classes. Regarding dissimilarities inter-forest classes, Logged-and-17y-burned forests exhibited negative scores for plants and were nearly fully separated from Undisturbed forests, which had positive scores (Fig. 3a). For frugivore species, Logged-and-17y-burned forests were positively associated with the first NMDS axis, while Undisturbed forests were negatively associated with it (Fig. 3b). These results indicate contrasting communities

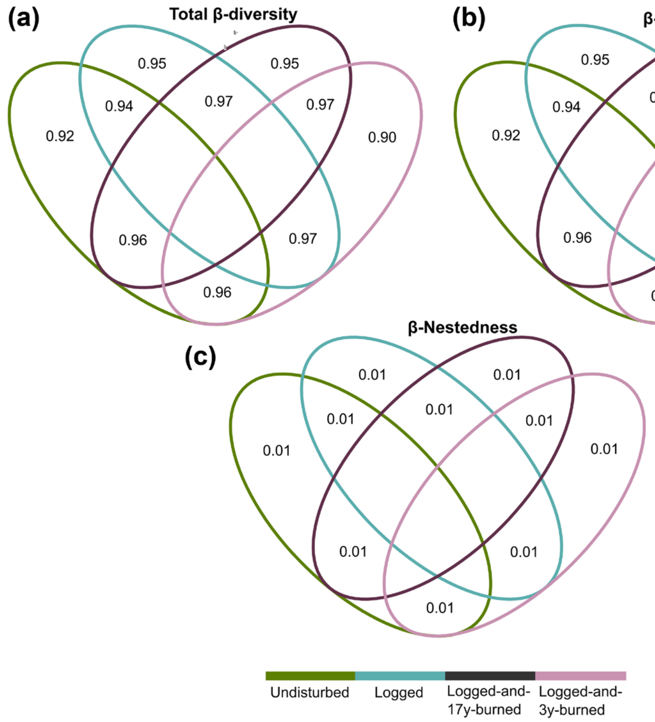

Figure 2. Venn diagrams showing the overlap in β-diversity of frugivory interactions in the Amazonian forest. Values inside overlapping represent the dissimilarity of frugivory interactions between forest classes, while nonoverlapping are the dissimilarity among study areas both measured using Sorensen coefficient. The diagrams show (a) total β-diversity and the combination of its two main components: (b) β-turnover, and (c) β-nestedness. At each diagram, forest classes from left to right correspond to: Undisturbed forest, Logged forests, Logged-and-17y-burned forests and Logged-and-3y-burned forests.

composition for both plants and frugivores. Similarly, frugivory interactions in Logged-and-17y-burned forests exhibited negative scores along the first axis, contrasting with Undisturbed forests, which were associated with positive scores along the second axis (Fig. 3c). These patterns indicate that Logged-and-17y-burned forests had higher dissimilarity in species and interactions compared to Undisturbed forests (Fig 3). In contrast, Logged and Logged-and-3y-burned forests exhibited associations with the NMDS axes similar to those of Undisturbed forests, suggesting greater similarity of plant and frugivore species composition and their interactions (Fig 3).

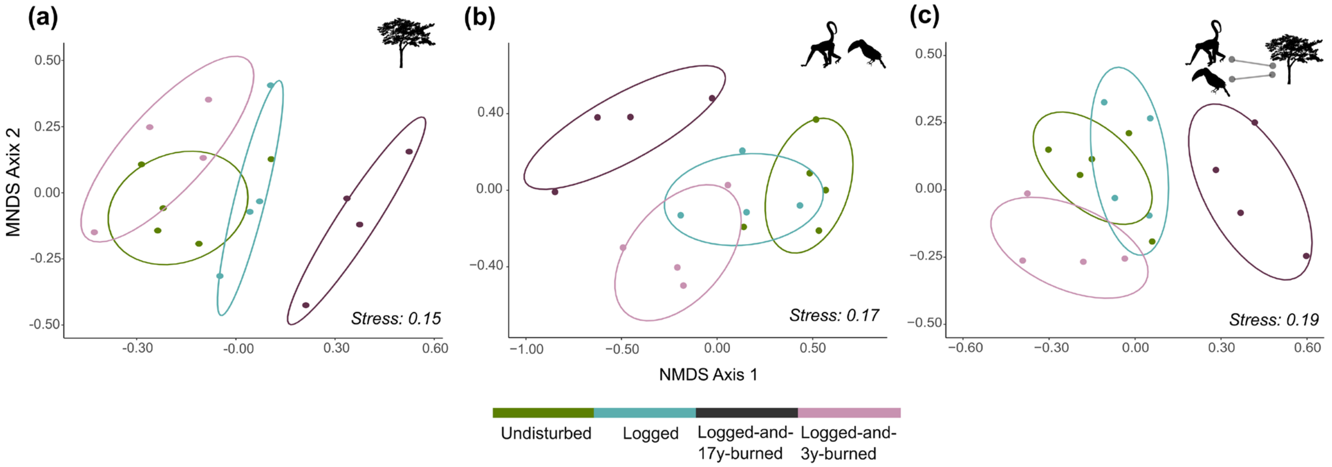

Figure 3. Non-metric multidimensional scaling (NMDS) ordination plot with stress values constructed with weighted Bray–Curtis dissimilarities showing the differences in (a) plant species, (b) frugivore species, and (c) frugivory interactions among forest classes. Each dot represents one of the 17 study areas while ellipses depict the forest classes. Forest classes correspond to: Undisturbed forest, Logged forests, Logged-and-17yburned forests and Logged-and-3y-burned forests.

Discussion

Our study describes community-wide frugivory interactions across undisturbed and human-modified Amazonian forests. We found significant loss of species and interactions in forests selectively logged and burned nearly two decades ago, but no changes in forests that were either selectively logged or selectively logged and burned recently. However, neither selective logging nor forest fires changed the structural properties of frugivory networks, which remained highly modular and specialised, non-nested and poorly connected across forest classes. All forest classes, regardless of the type of anthropogenic disturbance, showed high levels of β-diversity of species and interactions. Dissimilarity was higher between undisturbed forests and those selectively logged and burned nearly two decades ago, driven mainly by species turnover in species and interaction composition.

Impacts of selective logging and fire on species and interactions

According to expectations, forests that were selectively logged and burned had fewer species and interaction compared to undisturbed forests. In particular, forests selectively logged that burned nearly two decades ago exhibited lower numbers of species, as well as a fewer number of total and unique interactions, relative to undisturbed forests. Specifically, forests with such a type of disturbance exhibited a 16% reduction in the number of species, a 65.6% decline in the number of interactions, and a 34.5% reduction in unique interactions, relative to undisturbed forests. This reduction in species and interactions might result in the loss of irreplaceable sets of traits and evolutionary history, which may further compromise ecological functions related to forest dynamics (Emer et al. 2019, Souza et al. 2022). Moreover, the absence of key species, including globally threatened ones, in forests selectively logged and burned nearly two decades ago highlights the inability of these forests to support species sensitive to anthropogenic disturbances. For example, although we found opal-crowned manakin and white-cheeked spider monkey in other forest classes, they were absent from forests selectively logged and burned nearly two decades ago. These results suggest a potential time lag between selective logging and forest fires and their cascading effects on species and, subsequently, on interactions. This extended period likely reflects the response time of different species to disturbances, highlighting that response times often are not immediate. For instance, in the Amazon, fire-induced plant mortality can persist for up to eight years following forest fires (Brando et al. 2014, Silva et al. 2018). While plants in recently burned forests may continue to produce fruit and may even boost production in the short term, ongoing tree mortality is likely leading to an overall drop off in production (Barlow and Peres 2006, Brando et al. 2024), which could explain the eventual loss of species and interactions over longer time-scales (Herrera 1985, García et al. 2011).

Impacts of selective logging and fire on network properties

Contrary to our hypothesis, we did not find effects of anthropogenic disturbances on network structure. All frugivory networks were highly modular, indicating that interactions are structured into distinct subgroups. The observed modularity and specialisation suggest low niche overlap and, consequently, low functional redundancy (Cordeiro et al. 2020, Oliveira et al. 2022). This pattern was further reflected by the variability in connectance values and the consistently low levels of network-nestedness. There are three potential and non-mutually exclusive reasons for a lack of strong network-level effects. First, the high modularity and specialisation could reflect a strong niche partitioning among species and their interactions. By occupying distinct ecological niches, species minimise direct competition with one another, potentially facilitating the formation of distinct modules within the network (Ponisio et al. 2019, Cordeiro et al. 2020). In these modules, species interact more frequently with a subset of species, increasing the overall specialisation within the network. Such niche partitioning may also explain why networks maintained modular and specialised structures despite varying species composition across the different study areas (Schleuning et al. 2012, Oliveira et al. 2022). Second, the high diversity of plants and frugivores in Amazonian forests likely contributed to the emergent modular and specialised patterns observed (Donatti et al. 2011, Messeder et al. 2020). For example, Amazonian forests are known to host plant species that bear fruit several times per year, others that reproduce every year, and yet others that may take several years between fruiting episodes (Haugaasen and Peres 2005, Bentos et al. 2008, Mendoza et al. 2018). Nonetheless, the sampling of specific frugivore groups, including birds and mammals, as well as the distinction between terrestrial and arboreal frugivores, may also contribute to the merging of the modular structure. As such, sampling effort might have had minor effects on network properties (Nielsen and Bascompte 2007) – alternative network structures could emerge with sampling effort encompassing several years. This approach could lead to a more comprehensive representation of all possible interactions (Vázquez et al. 2009, Vizentin-Bugoni et al. 2016). Finally, the lack of effects on network properties could reflect the presence of a continuous forest matrix surrounding the study areas (Hagen et al. 2012). The study areas were embedded within an extensive forested landscape and a species-rich matrix which may support the structural properties of the network, particularly in forests that were selectively logged and burned only once. However, while effects may be stronger in regions with less forest cover, this is far from certain as 1) our study region broadly matches changes in plant traits and winner-loser tree species replacement in other human-modified forest regions (Pinho et al. 2024), 2) the effects of forest disturbance were sufficiently strong to influence community composition and other metrics of diversity for both plants and frugivores, and interactions (Barlow and

Peres 2004, Burivalova et al. 2014, Carvalho et al. 2022, Brando et al. 2024, Grau-Andrés et al. 2024).

Impacts of selective logging and forest fires on network β-diversity

As hypothesised, β-diversity was high between study areas and between forest classes for both species and interactions. However, rather than forests selectively logged and burned recently, it was forests selectively logged and burned nearly two decades ago that displayed the most distinct species and interaction composition compared to undisturbed forests. While smaller than the differences between forest classes, high β-diversity values were also observed within each forest class. The persistence of high diversity of species in certain bird families (e.g. Cotingidae, Pipridae, Ramphastidae and Thraupidae) across forest areas might contribute to the maintenance of high β-diversity values (Moura et al. 2013, Acevedo-Quintero et al. 2020). Additionally, the considerable diversity of species in certain plant families like Melostomataceae, which produce small fruits important for many frugivore species, may also play a key role in sustaining high values of β-diversity (Messeder et al. 2021). The elevated β-diversity observed may reflect the elevated functionality of the systems (Mori et al. 2018), highlighting the immense complexity of megadiverse regions (Valiente-Banuet et al. 2015, Solar et al. 2015, Bruno et al. 2024).

The high β-diversity values are predominantly attributed to β-turnover, rather than β-nestedness, suggesting that selective logging and forest fires play an important role in shaping the composition of the frugivory communities (Mestre et al. 2013). This is likely a consequence of changes in forest structure following anthropogenic disturbances (Mestre et al. 2013, Morante-Filho et al. 2016). For example, a more open canopy resulting from selective logging and forest fires may increase the presence of edge and non-forest bird species like *Megarynchus pitangua* boat-billed flycatcher and *Pitangus sulphuratus* great kiskadee, leading to increasing species turnover of both species and interactions (Barlow and Peres 2008, Lees et al. 2013). In addition, over time, pioneer plant species begin to recruit in human-modified forests, altering community composition and therefore contributing to high β-turnover (Barlow and Peres 2008, Carvalho et al. 2022). Lastly, the time elapsed since disturbance events may also play a crucial role in sustaining β-diversity values, as it can result in greater variation in successional pathways (Norden et al. 2015).

Concluding remarks

Our study provides novel evidence that anthropogenic disturbances simplify frugivory interactions in Amazonian forests. Through an extensive sampling effort of 31 484 h of monitoring arboreal and terrestrial interactions, we found that selective logging and forest fires led to a significant loss of species and interactions, with human-modified forests exhibiting distinct taxonomic composition compared to undisturbed ones. These findings underscore the critical role of selective logging and fire in shaping ecological interactions, particularly when acting synergistically. In contrast, the network structure was not affected by these anthropogenic disturbances, suggesting a capability of interaction communities to maintain ecological functions even in human-modified forest. However, the continued loss and change of interactions, combined with the predicted increase in fire frequency and severity due to climate change, as well as the ongoing selective logging, may threaten the resilience of tropical forests. Plant and frugivore species alone may not be sufficient to sustain ecosystem functionality, as most species are not adapted to forest fires, rising temperatures, climate heterogeneity and the associated environmental changes, such as reduced forest areas. It remains unclear how frugivory interactions respond to forest fires in the long term (i.e. over several decades) across the Amazon – if burned forests either continue to lose frugivory interactions or they reach a stable state with simplified frugivory networks, the recovery of these forests would be severely impacted.

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Author contributions

Liana Chesini Rossi: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead). **Carine Emer**: Formal analysis (supporting); Writing – review and editing (equal). **Alexander**

Charles Lees: Funding acquisition; Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Erika Berenguer**: Data curation (supporting); Funding acquisition (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Jos Barlow**: Formal analysis (supporting); Funding acquisition; Supervision (supporting); Writing – review and editing (equal). **Joice Ferreira**: Funding acquisition (lead); Project administration (lead); Resources (lead); Supervision (supporting); Writing – review and editing (equal). **Filipe M. França**: Formal analysis (supporting); Funding acquisition; Writing – review and editing (equal). **Yan Gabriel Ramos**: Methodology (supporting). **Paulo Tavares**: Visualization (supporting). **Marco Aurelio Pizo**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k0p2ngfjx (Rossi et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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