Fire frequency drives structural changes in bat-mediated seed dispersal networks in Neotropical dry forests

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Research Article

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Abstract

Fire is a major driver of biodiversity change, influencing ecosystem composition, structure, and function. In Colombian tropical dry forests (TDF), however, its effects on ecological interactions remain largely unknown. We evaluated the effects of fire frequency changes over the structure of bat-mediated seed dispersal networks by analyzing connectance, specialization, modularity, and nestedness across three sites with contrasting fire histories. Connectance increased from 0.38 in unburned forests to 0.52 in high-frequency fire sites, while network specialization (H_2') decreased from 0.41 to 0.29 and modularity declined from 0.48 to 0.33, indicating a shift toward more generalized and less compartmentalized networks. Conversely, nestedness rose from 0.56 to 0.71, suggesting greater overlap in interactions among species. These structural shifts appear to be driven by the proliferation of super-generalist species, particularly *Carollia perspicillata* and *Piper marginatum*, which assumed central roles as connections from other species declined. Such dynamics highlight a trade-off between robustness and vulnerability: while generalist species sustain key ecosystem services under recurrent disturbance, the dependence on a few central taxa may increase long-term instability. To our knowledge, this is the first study to examine the effects of fire frequency on bat-mediated seed dispersal networks, offering novel perspectives on species resilience and the ecological functioning of fire-affected ecosystems.

Keywords: Fire Ecology; Mutualistic Networks; Ecological Resilience; Restoration Strategies; Pyrodiversity.

Introduction

Fire is a major ecological disturbance shaping biodiversity across multiple levels of organization (Pausas 2015). Climate change and the increase in anthropogenic fires have modified fire regime parameters such as frequency, severity and seasonality, with major ecological consequences (Puig-Gironès et al. 2025). For instance, higher frequency changes have been linked to defaunation processes (Maciel et al. 2021), and to declines in small mammal abundances (Mendes-Oliveira et al. 2012). Regarding plant communities, altered fire regimes have reduced species richness, and have favored fire-resilient plant species thus affecting functional diversity (Meza et al. 2023; Tirado 2024). Beyond species-level responses, fire also affects ecological interactions by promoting generalist species and reducing mutualistic networks modularity and specialization (Peralta et al. 2017). And while the effects of fire on biodiversity have been explored, the punctual effects of fire frequency on mutualistic seed dispersal networks remain poorly understood, particularly in highly threatened ecosystems such as tropical dry forests (TDF, González- M et al. 2018). Addressing this gap is crucial for understanding biodiversity resilience and guiding restoration strategies under changing disturbance regimes (Schröder et al. 2021).

In the context of mutualistic networks, contrasting scenarios have been described regarding changes in fire regimes, with both positive and negative effects on biodiversity. For example, interactions such as rodent-mediated seed dispersal through seed burial have been reported to benefit from fire (Moore and Van der Wall 2015; Peterson and Parker 2016). Conversely, highly disturbed ecosystems with severe defaunation show declines in ecological interactions (Del Claro and Dirzo 2021). Bats are some of the species that may benefit from fire (Loeb and Blakey 2021), and although they are tolerant to disturbances such as forest fragmentation (Laurindo et al. 2019), the effects of fire on the dynamics of bat-mediated mutualistic networks have been poorly studied, particularly in the Neotropics (Loeb and

Blakey, 2021). Plant-bat mutualistic networks tend to be robust when subjected to disturbances such as habitat loss, owing to the capacity of different bat species to assume central roles within plant-bat interaction networks (Castaño et al. 2020; Laurindo et al. 2020; Regolín et al. 2020), however, this apparent robustness must be interpreted with caution when considering the impacts of other disturbances like fire in highly perturbed ecosystems (Peralta et al. 2017).

The case of the Colombian TDF is particularly important in this context, as it is considered one of the most threatened ecosystems worldwide (Schröeder et al. 2021). It is currently at critical risk of extinction, with less than 8% of its original cover remaining (Etter et al. 2017). Despite this severe level of endangerment, TDFs continue to face increasing pressures from the rising frequency and intensity of forest fires, a trend that has also been documented at a global scale in forest fires (González-M et al. 2018; Ruiz et al. 2023). While the Colombian TDF may have a historical relationship with fire (Berrío et al. 2002), and there is evidence of positive selection for fire-resilient plants thus supporting this hypothesis (Gutiérrez-Rincón and Parrado-Rosselli 2020) the effects of fire on its ecological structure and processes remain unknown. Given the current rise in forest fires in Colombian TDFs (Armenteras-Pascual et al. 2011; Pausas and Ribeiro 2017), it is essential to understand how altered fire regimes may disrupt ecological interactions that are critical for the regeneration and resilience of these threatened ecosystems, to guide effective conservation and management strategies.

Recent fire ecology research on Colombian TDF has revealed important variations in fire frequency. While some preserved areas have remained fire-free for over 60 years, other patches have experienced between one and five fire events in the last 20 years, demonstrating an altered fire regime (Díaz-Timoté 2019). The maintenance and regeneration of highly disturbed ecosystems depend on ecological interactions such as seed dispersal (Wunderle Jr 1997; Kim et al. 2022). Considering the potential resilience of some bat species to disturbances, and the apparent robustness of bat-plant seed dispersal networks, understanding how these networks function in Colombian TDF may provide insights into their capacity to withstand changes in fire regimes and help identify species that can guide conservation efforts (Nielsen and Totland 2014, Castaño et al. 2020).

Mutualistic networks have been widely used to describe the structure of ecological interactions and to evaluate the effects of disturbances on them (Valdovinos 2019; Laurindo et al. 2020). In the case of TDF under modified fire regimes, studying these networks is expected to clarify the roles of different species as generalists or specialists. Moreover, assessing how species roles and network structure change under fire disturbance can reveal shifts in subgroup formation (a metric known as modularity), the number of interactions (also called connectance), and the degree of nestedness between these interactions (Valdovinos 2019). This approach will make it possible to assess the tolerance of TDF to altered fire regimes and to determine the level of disturbance these ecosystems can endure without losing their functionality (Bascompte 2009).

This study aims to evaluate the effect of changes in fire frequency on the structure of bat-plant seed dispersal mutualistic networks in a Colombian TDF. Specifically, we examined variation in connectivity, degree of specialization, modularity, and nestedness. Network structure was analyzed across a fire frequency gradient: null frequency (no fires in the last twenty years), intermediate frequency (one fire in the last twenty years), and high frequency (two fires in the last twenty years). We expected that an increase in fire frequency would reduce the diversity and specialization of these networks (Bascompte and Jordano 2006). In addition, we anticipated a reduction in modularity (Garay-Narváez et al. 2013; Ramos-Robles et al. 2018). By contrast, we expected no significant changes in nestedness or connectance (Castaño et al. 2020).

Materials and methods

Field site

Our study was conducted in a TDF located in the upper Magdalena River basin, specifically in the municipality of Honda (5º9'N, 74º470'W), Tolima department, Colombia (Corredor-Ospina et al. In press). The climate is characterized by marked seasonality, with two pronounced dry seasons: the first between December and February, and the second one between July and September (García-Herrera et al. 2015; Aguilar-Cano 2016). The annual mean temperature was 26.5 ± 1 ºC, with maximum values reaching 30 ºC in July, August, and September (González-M et al. 2018). The annual mean precipitation is 291.23mm, with April being the wettest month (mean precipitation of 380mm) and February and March being the driest months (mean precipitation of 200mm; IDEAM, 2024). There is also a marked fire seasonality between August and September, coinciding with the period of highest temperatures and greatest hydric stress (Díaz-Timoté, 2019; IDEAM, 2024).

The TDF in the area is a matrix of forest relics in different successional stages interspersed with cattle pastures, fruit crops and herbs (Pizano et al. 2014). The main botanical families include Leguminosae, Lecythidaceae, and Euphorbiaceae (Aguilar 2016). Although information on the mammal fauna of the region is limited, at least 126 species have been reported, with bats (Chiroptera) being the most representative group, comprising up to 99 species in the Tolima Department (García-Herrera et al. 2015; Díaz-Pulido 2016; García-Herrera et al. 2019a). Among them, *Carollia perspicillata* is one of the most abundant species (García-Herrera et al. 2015).

Sample site identification

To estimate fire frequency, we used as a baseline event a 800 ha TDF fire in 2019 (Alonso and Montealegre 2021). Previous fires within the same area were identified through annual polygons (375m resolution, FIIRMS; Schöeder et al. 2014) generated in Google Earth Engine, centered on recorded thermal anomalies. Three categories were defined: (1) *Unburned site*, permanent plots established by the Instituto de Investigaciones Biológicas Alexander von Humboldt, undisturbed for over 60 years (Gonzáles-M et al. 2018); (2) *Low - frequency*, one fire in the last 23 years (2019); and (3) *High-frequency*, two fires in the last 23 years (2006, 2009). Due to spatial and historical fire constraints, sampling replicates were restricted within these treatment categories rather than across additional TDF areas.

Bats and seed characterization

For each fire frequency treatment, two field trips were conducted: one during the rainy season and one during the dry season. Within each treatment, we established one replicate in the same forest fragment due to difficulties in finding different forests with the same fire history; replicates were located at least 1 km apart, selected based on accessibility and similarities in vegetation. For the three fire treatments (Unburned site, Low frequency, and High frequency), each replicate contained three mist nets (12 m x 3 m; mesh size 1.5 x 1.5 mm; Laurindo et al. 2020), which were operated simultaneously over three consecutive nights per season. Nets were set at both ground and subcanopy levels and remained fixed in the place between sampling nights. Nets were opened daily from 17:30 to 02:30 and checked every 20 minutes resulting in a total sampling effort of 324 m^2·hours per fire frequency treatment).

After capture, frugivorous bats (Phyllostomidae family) were placed in individual cotton bags for 30 minutes to obtain fecal samples, with additional samples collected when removing individuals from the nets (Casallas-Pabón et al. 2017). Fecal samples were preserved in 97% ethanol (Laurindo et al. 2020). Taxonomic identification and nomenclature followed Solari et al. (2013), López-Baucells et al. (2016), Díaz et al. (2021), and Ramírez-Chávez et al. (2022) (Table 1). All individuals were released after being marked to avoid recapture (Medellín et al. 2000)

Seed samples were examined under a stereoscope and separated into morphotypes. To aid identification, botanical samples of plants from the study area were collected along phenological transects located 1 km from each net site (Stevenson, 2004). Seeds were washed and identified through comparison with reference collections and published descriptions (Aramendiz and Valencia, 2020). Identification was made to the species level when possible, or otherwise to the genus level (Table 1).

Mutualistic Network Analysis

We analyzed bat-plant interactions using quantitative bipartite networks constructed from matrices in which plant species were arranged in rows and bat species in columns. Interaction frequency was defined as the number of dispersed seeds recorded in bat fecal samples with zeros indicating the absence of interaction. Independent interaction matrices were constructed for each fire frequency treatment.

To characterize network structure, we calculated the following metrics: (I) connectance (C), defined as the proportion of realized interactions relative to all possible links, with higher values indicating a greater connectivity among network nodes (Valdovinos 2019); (II) nestedness (by using the quantitative index Weighted NODF (WNODF)), which measures the extent to which interactions of specialists (species with few links) are subsets of those of generalists (highly connected species). Values close to 0 indicate the absence of nestedness, while values close to 100 represent perfectly nested networks (Laurindo et al. 2020); (III) Complementary specialization (H_2), which quantifies the degree of specialization across the entire network, with values ranging from 0 (completely generalized) to 1 (completely specialized; Ramírez-Burbano et al. 2017); (IV) modularity (Q), describing the extent to which species form cohesive subgroups of species that interact more strongly within modules than with species outside them. Values near 0 indicate low modularity, while values close to 1 indicate strong modularity and a clear grouping pattern (Dormann and Strauss 2014); and (V) interaction diversity (Shannon index, H’), which combines species richness and evenness interactions, with higher values of H’ reflecting networks with more evenly distributed interactions, and lower values indicating a dominance of few interactions (Da Silva et al. 2024).

The differences in frequency metrics were assessed using a Kruskal-Wallis test, followed by Wilcoxon post hoc comparisons (Falcão et al. 2024). Sampling intensity was evaluated with an interaction accumulation curve for each fire frequency (Moreno et al. 2014; Carrillo-Villamizar et al. 2022). To test the significance of the analyzed network metrics, we applied a Monte Carlo procedure by comparing the observed values with those obtained from 2,000 randomized networks (Dormann et al. 2009; Muylaert and Dodonov 2015). All analyses were conducted in R (R Development Core Team 2009), using the bipartite (Becket 2016), vegan, and NetworkD3 packages (Dormann et al. 2009; Browning et al. 2022).

Results

A total of 972m^2 hours of sampling effort was conducted (with 324m^2hours per fire frequency). Sampling success was 8.02 for the Unburned-site, 4.93 in the Low-frequency site, and 12.03 in the High-frequency site, which is consistent with previously reported data for the zone (García-Herrera et al., 2019b). We captured 81 bat individuals, belonging to 4 subfamilies, 9 genera, and 18 species (Table 1). Regarding plants, a total of 9 plant species belonging to 5 botanical families were identified in bat fecal samples (Table 2).

In the Unburned-site, we recorded 10 seed-dispersing bat species with 365 dispersed seeds from 7 plant species (Table1; Table 2). In the Low-frequency site, four seed-dispersing bat species were registered, with 974 dispersed seeds belonging to 7 plant species (Table 1; Table 2). Finally, in the High-frequency site, we recorded 10 seed-dispersing bat species, and 974 dispersed seeds belonging to 8 plant species (Table 1; Table 2).

Table 1. List of seed disperser bats in a Tropical Dry Forests with different fire frequencies in Honda, Colombia.

Subfamilies	SPECIES	Unburned site	Low frequency	High frequency	Total
Carollinae	*Carollia brevicauda*	2	5	1	8
	Carollia perspicillata	7	8	16	31
	Carollia sp.	0	0	4	4
Stenodermatinae	*Artibeus amplus*	1	0	0	1
	Artibeus lituratus	1	0	0	1
	Artibeus obscurus	2	0	1	3
	Artibeus planirostris	0	0	2	2
	Chiroderma trinitatum	1	0	0	1
	Chiroderma vilosum	0	0	1	1
	Dermanura glauca	6	0	8	14
	Sturnira lilium	1	0	5	6
	Sturnira sp.	2	1	0	3
	Uroderma bilobatum	1	0	1	2
Mycronicterinae	*Mycronicteris microtis*	0	1	0	1
Phyllostominae	*Lophostoma brasiliense*	1	0	0	1
	Phyllostomus elongatus	0	1	0	1
	Phyllostomus hastatus	1	0	0	1
	Total	26	16	39	81

Table 2. List of plants dispersed by bats in a Tropical Dry Forest with different fire frequencies in Honda, Colombia.

Families	Species	Unburned site	Low frequency	High frequency
Cactaceae	*Cereus sp.*	115	63	4
Cecropiaceae	*Cecropia peltata*	94	3	20
	Cecropia sp.	0	1	28
Moraceae	*Ficus sp1*	36	0	5
	Ficus sp2	42	62	150
Piperaceae	*Piper marginatum*	270	568	659
	Piper undulatum	54	0	0
	Piper sp1	24	275	74
Solanaceae	*Solanum sp1*	0	2	34

The interaction curve between bats and dispersed plants represented 93.33% of the total possible interactions. Individually, the Unburned-site presented 83.6% (n = 17), the Low-frequency presented 89.28% (n=15), and the High-frequency site presented 100% (n=37) of the interactions.

Null model analyses indicated that all metrics associated with the networks across fire frequencies were significant, except for the weighted nestedness of the Low-frequency Table 4). Which indicates that the observed patterns are the result of species interactions rather than random processes.

In the Unburned site, we observed low connectance (C = 0.23; $p < 0.05$), high specialization (H2 = 0.79; $p < 0.05$), Weighted NODF was low (WNODF = 8.58, $p <0.05$), and high modularity (M = 0.60; $p < 0.05$; Fig. 1), with five well-defined modules (Table 3; Fig. 2). Interaction diversity was also high (H' = 2.41 $p < 0.05$) (Table 3). In contrast, the Low-frequency fire site showed higher connectance (C = 0.53; $p < 0.05$) but the lowest specialization (H2 = 0.23; $p < 0.05$), non-significant nestedness (WNODF = 67.9, $p > 0.05$; Fig. 1) low modularity (M = 0.09; $p < 0.05$) with only three weak modules, and the lowest interaction diversity (H' = 1.51; $p < 0.05$) (Table 3; Fig. 2). In the High-frequency fire site, connectance reached its highest value (C = 0.79; $p < 0.05$), while specialization remained low (H2 = 0.24; $p < 0.05$ and presenting a higher nestedness WNODF = 37.49; Fig. 1). Modularity was also low (M = 0.16; $p < 0.05$), with three weak modules, but interaction diversity was again high (H' = 2.40; $p < 0.05$), like the unburned site (Fig. 2; Table 3).

Table 3. Network metrics of bat–plant mutualistic networks in a Tropical Dry Forest under different fire frequencies in Honda, Colombia. Asterisks (*) indicate significant values ($p < 0.05$).

Network metric	Unburned site	Intermediate frequency	High frequency
	Index	Index	Index
Connectance (C)	0.24*	0.53*	0.79
Modularity 0Q	0.6*	0.09*	0.16*
Weighted NODF (WNODF)	*8.58**	67.9	37.49*
Specialization (H_2)	*0.79**	0.23*	0.24*
Diversity	*2.41**	1.51*	2.4*

Figure 1. Mutualistic networks of interactions between frugivorous bats and dispersed plants in a Tropical Dry Forests exposed to different fire frequencies in Honda, Colombia. Three interaction networks are shown, corresponding to Uburned site (no fires in the last 23 years), Low-frequency (one fire in the last 23 years), and High-frequency (two fires in the last 23 years). Yellow bars represent bat species that disperse seeds, while red bars represent plant species dispersed by bats. Connections between two network nodes are shown as grey lines, whose thickness indicates the frequency or intensity of the interactions.

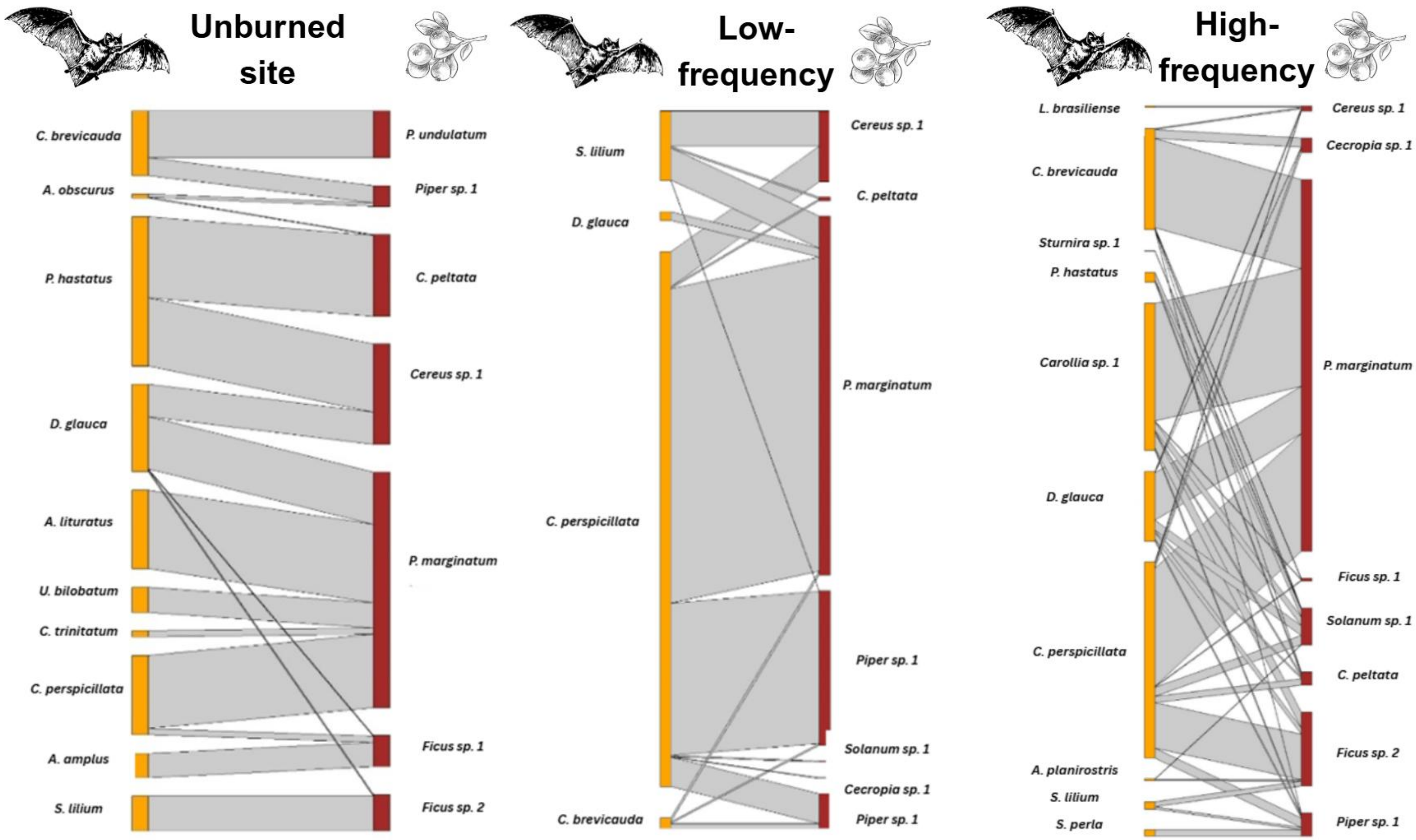
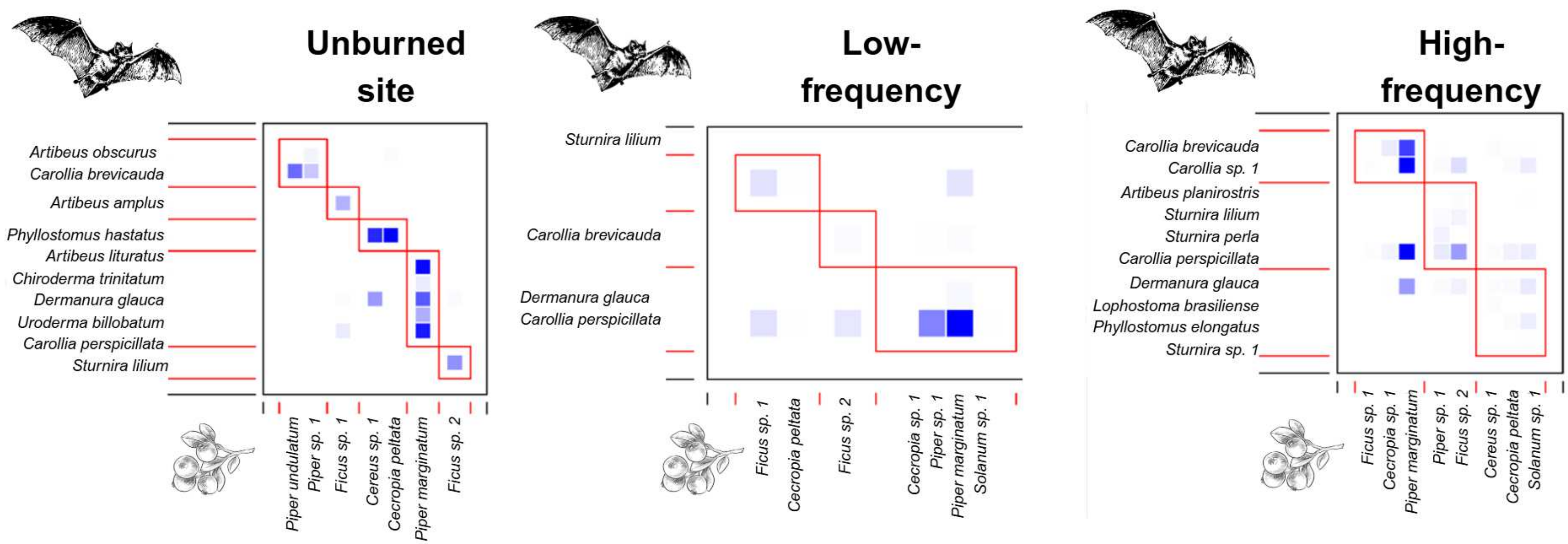

Unburned site
C. brevicauda
A. obscurus
P. hastatus
D. glauca
A. lituratus
U. bilobatum
C. trinitatum
C. perspicillata
A. amplus
S. lilium
P. undulatum
Piper sp. 1
C. peltata
Cereus sp. 1
P. marginatum
Ficus sp. 1
Ficus sp. 2
Low-frequency
S. lilium
D. glauca
C. perspicillata
C. brevicauda
Cereus sp. 1
C. peltata
P. marginatum
Piper sp. 1
Solanum sp. 1
Cecropia sp. 1
Piper sp. 1
High-frequency
L. brasiliense
C. brevicauda
Sturnira sp. 1
P. hastatus
Carollia sp. 1
D. glauca
C. perspicillata
A. planirostris
S. lilium
S. perla
Cereus sp. 1
Cecropia sp. 1
P. marginatum
Ficus sp. 1
Solanum sp. 1
C. peltata
Ficus sp. 2
Piper sp. 1

Figure 2. Matrix of between frugivorous bats and dispersed plants in a Tropical Dry Forests exposed to different fire frequencies in Honda, Colombia. Three interaction networks are shown, corresponding to Uburned site (no fires in the last 23 years). Blue squares indicate strong interactions between bats and dispersed plants, whereas lighter or thinner blue squares represent weaker interactions. Modules are outlined in red.



Unburned site
Artibeus obscurus
Carollia brevicauda
Artibeus amplus
Phyllostomus hastatus
Artibeus lituratus
Chiroderma trinitatum
Dermanura glauca
Uroderma billobatum
Carollia perspicillata
Sturnira lilium
Piper undulatum
Piper sp. 1
Ficus sp. 1
Cereus sp. 1
Cecropia peltata
Piper marginatum
Ficus sp. 2
Low-frequency
Sturnira lilium
Carollia brevicauda
Dermanura glauca
Carollia perspicillata
Ficus sp. 1
Cecropia peltata
Ficus sp. 2
Cecropia sp. 1
Piper sp. 1
Piper marginatum
Solanum sp. 1
High-frequency
Carollia brevicauda
Carollia sp. 1
Artibeus planirostris
Sturnira lilium
Sturnira perla
Carollia perspicillata
Dermanura glauca
Lophostoma brasiliense
Phyllostomus elongatus
Sturnira sp. 1
Ficus sp. 1
Cecropia sp. 1
Piper marginatum
Piper sp. 1
Ficus sp. 2
Cereus sp. 1
Cecropia peltata
Solanum sp. 1

Discussion

To our knowledge, this is the first study that evaluates the effects of fire frequency changes over bat-mediated seed dispersal networks in Tropical Dry Forest (TDF). And given global shifts in fire regimes, and the increase of fire frequency, these results are relevant for understanding the potential responses of this highly threatened ecosystem and for designing management strategies based on ecological dynamics. Despite limitations related to replication due to the scarcity of TDF remnants with comparable fire-history, land use, and conservation status (González-M et al., 2018), our sampling effort exceeded that of previous studies in the region (García-Herrera et al., 2015) and revealed consistent non-random effects of fire on network structure and species interaction.

Our analysis of seed-dispersal networks showed that increasing fire frequency significantly altered the network structure and the organization of ecological interactions (Fig. 2; Table 3). As hypothesized, higher fire frequency reduced modularity and specialization, although network diversity was not diminished. These properties indicate a structured, specialized, and compartmentalized network, which is typical of more stable and mature ecosystems (see Bascompte and Jordano 2006). And in contrast, the burned sites showed marked declines in modularity, and specialization, alongside a rise in connectance, and nestedness (Fig. 3; Table 3). These changes show a transition from a modular and functionally diversified network to a more homogenized and nested system, that is mostly dominated by generalist species, such as *Carollia perspicillata* and *Piper undulatum* (Table 1), species capable of maintaining connectivity under disturbance scenarios dispersal (Mello et al. 2011; Castaño et al. 2020; da Silva et al. 2024). While a configuration in which specialist species depend on a subset of generalists may enhance short-term robustness by maintaining connectivity, it also increases long-term vulnerability to the loss of more central species (Laurindo et al. 2020).

The functional restructuring of bat-mediated seed dispersal networks under altered fire frequencies becomes evident when considering species-level patterns such as the absence or reduced interaction of more specialized species such as *Atibteus liturarus, Phyllostomus hastatus,* and *Chiroderma trinitatum*, and the corresponding decline in the interactions with more vulnerable plant species like *Ficus* and *Cereus* (Thies and Kalko, 2004; Velásquez-Roa et al. 2023). These losses align with previous evidence showing that specialized frugivores and late-successional plant species are more sensitive to habitat disturbance (Valle et al. 2021; Roca et al. 2021). Conversely, generalist bats such as *Carollia perspicillata*, *C. brevicauda,* and *Dermanura glauca*, and eearly successionalplants such as *Piper maringatum* increased in abundance and network centrality, sustaining interactions even under higher fire frequencies (Fig. 1). The rise in the abundance of *C. perspicillata,* and its central role in networks from highly disturbed forests is likely supported by the proliferation of *Piper* species which are tolerant to perturbances, and colonize disturbed habitats (Miyinashi and Kellman, 1986; York and Billings, 2009; Da Silva et al. 2024). Given the close relationship between *Carollia* species, and *Piper* species, a rise in either one of these groups, may benefit the other (York and Billings, 2009). Moreover, it has been reported that arthropods may benefit from fire events due to the increase in resources availability and considering that insects are also an important diet component of omnivorous bats like *Carollia*, an increase in these resources may also enhance their survival and functional dominance (Kwon et al. 2013; Pellón et al. 2020: Sil et al. 2024). Thus, mutualistic resilience in burned forests appears to rely on feedback between fire-tolerant pioneer plant species, and flexible generalist seed dispersers.

The high connectance and interaction diversity observed in the High-frequency site suggests that network reassembly mirrors the concept of functional redundancy, where multiple generalist species perform overlapping ecological roles, thereby ensuring the continuity of key ecosystem services such as seed dispersal (Beal-Neves et al. 2020). However, if generalist and central specialist like *C. perspicillata* and *P. Marginatum* were to decline, the simplified and highly nested network could experience a rapid functional collapse (Castaño et al. 2020). This pattern suggests that the resilience of these networks may be a product of resistance through generalization, and an increase in central species abundance, rather than a true recovery of the dynamics of the ecosystem (Valdovinos 2019).

This reduction in modularity and specialization may reflect the fragility and revictual condition of Colombian TDF, an ecosystem already suffering declines in species composition and diversity (González-M, et al. 2018; Moura et al. 2023). Such biodiversity loss can reduce network complexity, as species are unable to cope with these rapid changes in the conditions and dynamics in their habitats (Laurindo et al. 2020). Defaunation and local plant extinctions resulting from altered ecosystem dynamics may thus erode interaction networks (Maciel et al. 2021), lowering their complexity (Aguirre-Gutiérrez e al. 2021), and reducing beta diversity (Kurten, 2013; Del Claro and Dirzo, 2021; Moura et al. 2023; Falcao et al. 2024).

These findings have important implications for ecosystem management and restoration. Identifying fire-resilient species that maintain ecological connectivity, like *Carollia* and *Piper*, can guide the selection of functional groups to prioritize in regeneration and conservation programs (Loeb and Blakey 2021; Ancillotto et al. 2022). Such species sustain essential mutualistic interactions that facilitate forest recovery through seed dispersal and early succession, especially in highly disturbed ecosystems like the Colombian TDF (Muscarella and Flemming 2007; Ruiz et al. 2023). However, long-term ecosystem resilience and regeneration require the gradual return of specialized species and structural heterogeneity, meaning that TDF conservation and management strategies should implement fire-ecology studies, and the maintenance of interaction networks, focusing on the functional continuity and the structural recovery (Ruiz et al., 2023; da Silva et al., 2024).

In conclusion, recurrent fires alter the structure and functional balance of bat-mediated seed dispersal networks in TDF, by simplifying their structure and concentrating ecological roles in a few resilient generalists. While this reorganization sustains short-term ecosystem functioning, it may compromise long-term resilience of the network. Applying mutualistic network analysis to fire ecology provides a powerful framework to identify keystone species and interactions that support ecosystem services under fire regime changes and disturbance increase. These insights highlight the need to design management and restoration plans that are grounded in ecological function, ensuring that conservation efforts in the TDF not only preserve species, but also the web of interactions that sustain their regeneration and persistence over time.

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Declarations

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Conflicts of interest/Competing interests: Not applicable

Ethics approval:

- The conducted research was approved by the Ethical committee of the Faculty of Medio AMbiente y Recursos Natural belonging to the Universidad Distrital Francisco José de Caldas, and followed standardized methods proposed by the American Society of Mammalogists.

Consent to participate:

- Not applicable

Consent to publication:

- Not applicable

Availability of data and materials:

- The datasets, used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability:

- The code, used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

- Corredor-Ospina, N led the project, coordinated field expeditions, performed all data analyses, and wrote the manuscript.
- Rodríguez-Bolaños, A. Co-directed the project, supervised bat sampling and management, reviewed the manuscript, and provided guidance on statistical design.
- Parrado-Roselli, A. Directed the project, supervised its design, statistical analyses, fieldwork, and manuscript preparation.

- Bravo-García, C., Ríos-Cruz, A., Rodríguez-González. R., Andrade-Uriza, C., assisted with data collection during fieldwork.

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