Fuel bed variation in coastal tropical freshwater forested wetlands in three disturbance regimes at La Encrucijada Biosphere Reserve, Mexico

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Abstract

Tropical freshwater forested in coastal regions are rapidly disappearing as a result of wildfires caused by high accumulations of forest fuels, which can vary in quantity and availability. Therefore, the objective of this study was to characterize fuel beds in tropical freshwater forested wetlands with three levels of disturbance at El Castaño, La Encrucijada Biosphere Reserve. Seventeen sampling units were used to describe the structure of the forest's fuel beds (canopy, sub-canopy, understory). Fallen woody material, surface litter, and fermented litter were characterized using the planar intersection technique. Diversity was composed of eight species of trees, two shrubs, five lianas, and two herbaceous species. The vertical strata were dominated by trees between 2 to 22 m high. The horizontal structure had a higher percentage of trees with a diameter at breast height between 2.5 and 7.5 cm (61.4%) of the total. The non-disturbed sites presented the highest arboreal density (2686 ind. ha −1). The richness and diversity of species showed that the Fisher, Margalef, Shannon, and Simpson α indices were higher in the undisturbed sites. The Berger-Parker index exhibited greater dominance in the site's with high disturbance. Pachira aquatica showed the highest importance value index and was the largest contributor to fuel beds. The sites with the greatest disturbance had a greater accumulation of dead fuel beds, with the greatest accumulations of woody fuels in classes 1, 10, and 1000 h (rotten). This study contributes to defining the areas prone to fire in these ecosystems and designing prevention strategies.

1. Introduction

In tropical regions, tropical freshwater forested coastal wetlands (TFFCW) are regularly found close to mangrove forests in swampy terrain, with gentle slopes near the river bank, where freshwater has the most influence (via flood pulses) (Ewel 2010, Infante et al. 2011a, Torres et al. 2018). These plant communities group a large number of trees, shrubs, and lianas (Moreno and Infante 2016). Because they develop in a transition zone, they play an important role in nutrient and biogeochemical processes in addition to other ecosystem services (Moreno and Infante 2009). TFFCWs function as natural filters for pollutants and as refuges for wildlife (Infante et al. 2011a). In addition, they are an important carbon (C) sink, and even store greater amounts of C in the soil than mangroves (Moreno and Infante 2016). However, TFFCW are an understudied tropical ecosystem.

TFFCW are located in freshwater-influenced areas where one or two species commonly dominate (Infante et al. 2011a, Infante 2014). One of these species is *Pachira aquatica* Aubl. (water zapote), a floating tree that forms a false forest floor with produced and retained organic matter (Infante 2011). TFFCW dominated by *P. aquatica* only share their space with certain flood-tolerant species (Barrios-Calderón 2019). In Mexico and Mesoamerica, the only TFFCW dominated by *P. aquatica* are those distributed in Huimanguillo, Tabasco (Ascencio 1994), Ciénaga del Fuerte, Laguna Chica, El Apompal in Veracruz (Infante et al. 2011b), and La Encrucijada in Chiapas (Rincón 2014, Barrios-Calderón 2015). In La Encrucijada, the TFFCW of *P. aquatica* becomes associated with mangrove species (Moreno and Infante 2016), however, human influence has caused the gradual disappearance of these ecosystems.

One of the disturbance threats leading to the loss of plant communities in TFFCW is forest wildfires, either from natural or anthropogenic causes. These play an important role in vegetation dynamics and land-use change (Jardel et al. 2000, Rodríguez and Fulé 2003, FAO 2006). Therefore, these coastal wetlands are considered vulnerable ecosystems that are threatened by the frequency and magnitude of fires (Page et al. 2009, García et al. 2014, Williams-Jara et al. 2022). Although TFFCWs remain flooded most of the year, they are highly productive and store woody forest fuels (i.e., branches, twigs, logs, fallen trees) and layers of litterfall. Leaf litter is found at different levels of decomposition on the soil surface (Sales et al. 2020). In dry seasons, litter can lead to combustion processes, when the water level fades, the soil dries out, and all accumulated organic matter can burn (Goldammer 1999, Kaal et al. 2011). This explains why this ecosystem presents recurrent fires, largely managed by the quality and quantity of woody fuel and litterfall.

Forest fuels are the energy source that, in combination with topography, climate, and source of ignition, they can cause fires to vary in magnitude and spread (Scott et al. 2014). Because fires are an important environmental driver of ecosystem processes and biogeochemical cycles, studies that characterize and estimate forest fuels are of great relevance for fire management and prediction (Rodríguez et al. 2002). Fuel bed characterization integrates the analysis of the quantity and quality of forest fuel, considering both vertical and horizontal spatial distributions (Dentoni and Muñoz 2001). To characterize fuel beds, both live (Flores 2001, Sandberg 2001) and dead (Villers 2006) fuels are considered in different categories or strata (Turner et al. 2001), among other factors that have caused the fragmentation of these forest ecosystems. Additional information to be considered is the frequency of fires due to anthropogenic activities, such as illegal wood extraction, the use of fire for poaching, and the proximity of the population center. Particularly in areas such as La Encrucijada Biosphere Reserve (LEBRE), Chiapas, these disturbing agents are a threat to ecosystems, such as TFFCW. CONANP (2018) and CONAFOR (2018) have collected information on fires in LEBRE since 1998 and have observed at least 20 fires in El Castaño, which have affected freshwater marshes (1200 ha), mangroves (800 ha), and *P. aquatica* TFFCW (450 ha).

The study of fuel beds has been developed worldwide in different ecosystems (Sandberg et al. 2001, Ottmar et al. 2007, Ricardi et al. 2007, Arroyo et al. 2008, Donato et al. 2013, Keane 2013, Bernau et al. 2018), temperate (Villers and López 2004, Bautista et al. 2005, Muñoz et al. 2005, Wong and Villers 2007) and tropical (Rodríguez et al. 2011, Adame et al. 2013, 2015, Barrios-Calderón et al. 2018). However, few studies have focused on exploring TFFCWs with different levels of disturbance. Therefore, the objective of this research was to characterize the structure and composition of living and dead fuels in a TFFCW dominated by *P. aquatica* in El Castaño (LEBRE), in a disturbance gradient (high, medium, no). The following hypotheses were put forward: (i) As a result of decreased species richness in highly disturbed sites, *P. aquatica* has a higher importance value, and (ii) despite having a lower stratification and species mix, the accumulation of dead fuels is greater in sites with high disturbance.

2. Materials And Methods

Study area

La Encrucijada Biosphere Reserve (LEBRE) is a natural protected area and is also a RAMSAR site (RAMSAR 1999), located on the southeastern Pacific coast of Mexico. The surface area of LEBRE is 144,868 ha, 24% (36,216 ha) are classified as core areas, while 75.1% (108,651 ha) are classified as buffer areas (DOF 1995). *P. aquatica* TFFCWs surround mangroves, freshwater marshes, and other coastal ecosystems (Fig. 1), and these ecosystems are connected through a complex hydrological network. In this wetland system, *P. aquatica* is far from the saltwater inlets of the estuaries, and the main source of water is freshwater from the San Nicolas River. The climate is tropical, warm-humid with summer rainfall Am (w). The mean annual temperature is 28°C, and annual precipitation ranges from 1300 to 3000 mm (INE 1999). The dry period is from February to May, during this period, the water level is below the soil surface (Rincón 2014).

Field study

Based on hydroperiod data (Rincón 2014), field campaigns for this study were planned from February to April in 2017 and 2018. Following a stratified randomized experimental design, 17 circular 600 m^2 (radius = 13.8 m) sampling units (SUs) were established in the TFFCW, with three different disturbance levels (Fig. 1). Disturbance levels were defined based on the following criteria: 1) canopy openness, 2) distance from roads, 3) human activities, 4) illegal extraction of wood, 5) hurricane/wind impact, 6) fires, and 7) forest cover (Table 1). Based on this information, field assessment sites were classified as no disturbance (n = 7 sites), medium disturbance (n = 5 sites), and high disturbance (n = 5 sites) (Fig. 2).

Table 1 Site classification criteria of no, medium, and high disturbance.

Level	Criteria						
	Canopy openness	**Distance to roads (km)**	**Human activities**	**Illegal extraction wood**	**hurricane/wind impact**	**Fires (1998–2018)**	**Forest cover (%)**
No disturbance	0 to 25%	0.6 to 1	None	Very low	No fallen trees	None	75–100
Medium disturbance	25 to 50%	0.2 to 0.6	Dirt road	Low to Medium	fallen trees (1 to 3)	Low frequency (5 events)	50–75
High disturbance	> 50%	< 0.2	Dirt road, poaching	High to Very high	fallen trees (>3)	High frequency (>15 events)	< 50

Structural and composition analysis of fuel beds

Live fuel

In each SU, measurements of trees, shrubs, and lianas (normal diameter, ND > 2.5 cm) were performed. Height was measured with a hypsometer (Vertex III), and the canopy diameter of 20% of the trees was measured following Valdez (2002). To describe the horizontal structure, 10 diameter classes were established starting at 2.5 cm with 5 cm intervals (Corella et al. 2001). Measurements were used to estimate density and basal area (Ramos et al. 2004), relative coverage (Zarco et al. 2010), relative frequency, density, and dominance of species (Gentry and Ortiz 1993). Furthermore, three structural indices were estimated: the importance value index (IVI) (Villavicencio and Valdez 2003), forestry value index (FVI) (Zarco et al. 2010), and Holdridge complexity index (HCI) (Holdrige 1971). The understory was characterized by herbs, shrubs, and trees (height < 50 cm and ND < 2.5 cm) that are part of natural regeneration. To measure this forest stratum, a 60 m^2 (diameter = 8.7 m) sub-circle was established in the middle of the SU, records included height, diameter, and coverage.

Dead fuels: woody fuel and litterfall

Woody dead fuel was characterized using the planar intersections technique (Brown 1974, Sánchez and Zerecero 1983, Flores et al. 2018), adapted by Barrios-Calderón et al. (2018). Four 10-m linear transects were established in each SU, from the site center to each cardinal point (N, S, E, W). The woody fuel was classified according to the "timelag," i.e., the time necessary for the fuel to lose or gain 66% of its humidity, according to the ambient temperature (Rodríguez et al. 2002). Therefore, the timelag/diameter ratio was used (1 h [0–0.6 cm], 10 h [0.61–2.5 cm], 100 h [2.5–7.5 cm], and 1000 h [> 7.5 cm]) (Table 2). Transect measurements were performed as follows: 1 h of fuels in the first 2 m, 10 h up to 4 m, 100 h up to 7 m, and 1000 h up to 10 m. Fine fuels (1 and 10 h), and medium fuels (100 h) were counted based on the number of intersections on the horizontal plane. Thick fuels (1000 h) were classified according to their state or condition (firm or rotten), and their diameters were measured.

Table 2 Equations to estimate woody fuel at each sampling unit (SU) at El Castaño according to Brown (1974).

Fuel class	Equation
1 h	P = (0.484 * *f * c) / (N* l)*
10 h	P = (3.369 * *f * c) / (N* l)*
100 h	P = (36.808 * *f * c) / (N* l)*
1000 h firm (no rot)	P = (1.46 * *f * c) / (N* l)*
1000 h (rotten)	P = (1.21 * *f * c) / (N* l)*
Where: *P = fuel weight (t ha^{-1}).* *F = frequency or number of intersections* *c = slope correlation factor* *d^2 = sum of the squared diameter of branches or logs > 7.5 cm.* *N = number of intersection lines* *l = line longitude or sum of the longitude (2 m = 6.56 feet) (4 m = 13.12 feet) (7 m = 22.96 feet) (10 m = 32.8 feet)*	

Litterfall was collected at the end of each planar intersection line in four 0.2 x 0.2 m quadrants, where the depth of the layer was measured and separated into surface litterfall (SL) and fermented litterfall (FL). Subsequently, litterfall was transferred to the laboratory, and the dry biomass was obtained after 24 h in a drying oven (IKA OVEN) at 105°C.

Data processing and calculations

Average woody fuel beds were estimated following standardized procedures for each diameter class (Brown 1974, Barrios-Calderón et al. 2018). Litterfall dry weight biomass was determined following the methodology of Morfín et al. (2012). For this, it was necessary to obtain the bulk density (ρ) at SL and FL depths and subsequently determine the litterfall layer load:

$$\rho = \left(\frac{P}{a * h}\right) x\ 10$$

where ρ = bulk density (t ha^{-1} mm^{-1}), P = dry weight (g), a = surface area (cm^2), h = litterfall depth average (mm), 10 = constant for conversion of litterfall density (g cm^{-3}) to (t ha^{-1} mm^{-1}). Subsequently, the litterfall fuel load (C) was estimated (Ottmar et al. 2004, Barrios-Calderón et al. 2018):

$$C = \frac{\sum_{i=1}^{8}(hi)(d)}{8}$$

where C = litterfall fuel load (t ha^{-1}), hi = litterfall layer (mm) (SL or FL), and d = bulk density (t ha^{-1} mm^{-1}).

Statistical analysis

Paleontological Statistics software (Past 3.26) (Hammer 2016) was used to analyze diversity, considering the disturbance level for all fuel components (trees, shrubs, herbs, and lianas) studied here. Species richness was estimated using the Margalef index (DMg). At the structural level, Fisher's alpha (α) and Shannon–Wiener (H') indices were used to assess proportional abundance, and Berger–Parker (d) and Simpson (D) indices were used to calculate species dominance for each disturbance level. Differences among disturbance levels were evaluated with an analysis of variance (ANOVA) and Tukey–Kramer test at 95% confidence for comparison of means, using the Statistical Analysis System, version 14 (SAS 2018). To define possible differences between dead fuel loads (woody and litterfall), an ANOVA and Tukey–Kramer mean comparison test was also applied, with a significance level of 0.05 using the SAS statistical package.

3. Results

Structure and composition of fuel beds

The tree stratum registered eight species in the TFFCW studied at LEBRE, where *P. aquatica* was dominant. The associated species were *Zygia conzattii* (Standl.), *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F. Gaertn., *Cynometra oaxacana* Brandegee, *Leucaena leococephala* (Lam.) de Wit, *Tabebuia rosea* (Bertol.), and *Hampea macrocarpa* Lundell. The shrub stratum had the following composition: *Solanum tampicense* Dunal, and *Malvaviscus arboreus* Cav. Lianas were comprised of *Paullinia pinnata* L., *Serjania mexicana* (L.) Willd, *Entadopsis polystachya* (l.) Britton, *Mansoa hymenaea* (DC.) A.H. Gentry, *Machaerium kegelii* Meisn, and *Cissus cacuminis* Standl.

In the understory, there were young trees of *P. aquatica* (average height of 0.76 m, and average ND of 0.5 m), *R. mangle* (average height of 1.2 m, and average ND of 0.7 m), and *L. racemosa* (average height of 1.34 m, and average ND of 0.6 m). Other understory species included *Cynometra oaxacana, Zygia conzattii,* and *Leucaena leucocephala.* The herb stratum was mostly composed of *Acrostichum aureum* L. (average height 1.95 m, ND max 1.42 and min 0.98 m) and *Crinum americanum* (average height 0.85 m, ND max 0.66 and min 0.34 m).

Vertical structure of fuel beds

In sites with high disturbance, there was a higher number of trees with heights between 2 and 7 m (75%). In the no and medium disturbance sites, 65% and 49% of trees, respectively, belonged to the 2–7 m category. Therefore, this was the dominant height class in the disturbance gradient (Table 3). The percentage for the 7 to 12 m height class varied across sites, in which only 20, 25, and 32% of the trees were in this category at sites with high, medium, and no disturbance, respectively. Sites with medium disturbance had the highest percentage for classes 12–17 m (14.48%), 17.1–22 m (6.43%), and > 22 m (6.43%), compared to no and high disturbance sites (Table 3). Therefore, the sum of the percentages of these three classes corresponds to 24%, while in the other two disturbance conditions (high and null), height classes greater than 12 m represent only 3.29 and 3.16%, respectively.

Table 3 Structural characterization based on height class, percentage by species for each class and disturbance level.

Species	Height class (%)						Total
	> 22 m	17–22 m	12–17 m	7–12 m	2–7 m	< 2 m	
No disturbance							
Pachira aquatica	-	0.09	1.25	28.27	51.80	-	81.41
Zygia conzattii	-	-	-	0.62	5.52	-	6.14
Cynometra oaxacana	-	-	-	1.07	2.14	-	3.21
Entadopsis polystachya	-	-	-	0.27	2.49	-	2.76
Rhizophora mangle	-	0.53	0.71	0.18	0.27	-	1.69
Laguncularia racemosa	-	0.09	0.53	0.27	0.62	-	1.51
Hampea macrocarpa	-	-	-	0.61	0.44	-	1.05
Leucaena leucocephala	-	-	-	0.19	-	-	0.19
Paullinia pinnata	-	-	0.09	0.44	0.53	-	1.06
Serjania mexicana	-	-	-	-	0.53	-	0.53
Lianas	-	-	-	-	0.06	-	0.06
Combretum decandrum	-	-	-	-	0.03	-	0.03
Tabebuia rosea	-	-	-	0.09	0.00	-	0.09
Total	-	0.71	2.58	32.10	64.61	-	100.00
Medium disturbance							
Pachira aquatica	2.39	6.06	13.94	22.21	37.25	1.83	83.68
Cynometra oaxacana	-	-	-	1.65	9.17	-	11.00
Zygia conzattii	-	-	-	0.55	2.02	-	2.57
Entadopsis polystachya	-	-	-	0.37	0.92	-	1.29
Rhizophora mangle	0.73	0.37	0.18	-	-	-	1.28
Laguncularia racemosa	-	-	0.18	-	-	-	0.18
Total	3.12	6.43	14.48	24.78	49.36	1.83	100.00
High disturbance							
Pachira aquatica	0.21	0.11	0.53	18.02	70.39	0.84	90.10
Laguncularia racemosa	-	0.84	1.16	0.95	0.63	-	3.58
Zygia conzattii	-	-	-	-	3.06	-	3.06
Rhizophora mangle	0.11	0.11	0.11	0.53	1.16	0.32	2.32
Lianas	0.00	0.00	0.00	0.32	0.42	0.00	0.74
Hampea macrocarpa	0.00	0.00	0.00	0.00	0.21	0.00	0.21

Total	0.32	1.05	1.79	19.81	75.87	1.16	100.00

Legend: * Lianas include*: Mansoa hymenaea, Cissus cacuminis, Machaerium kegelii, Combretum decandrum*

Horizontal structure of fuel beds

The analysis of fuel beds based on diameter classes of each disturbance level showed that sites with high disturbance had the highest percentage of ND between 2.5 and 7.5 cm (61.45%). Furthermore, the no disturbance sites had a higher percentage (32.7%) in the 7.5 to 12.5 cm category. However, sites with medium disturbance had the highest percentages in all classes greater than 12.5 cm (Fig. 3). Overall, the average percentage for each ND class, including the three disturbance conditions, was as follows: 2.5–7.5 (41.5%), 7.5–12.5 cm (26.2%), 12.5–17.5 cm (18.5%), and 17.5–22.5 cm (8.3%).

The average tree density was higher in no disturbance sites, with 2686 individuals ha^{-1} and an average basal area of 26.59 m^2 ha^{-1}. The highest basal area was observed in sites with medium disturbance (39.41 m^2 ha^{-1}). The species with the highest IVI was *P. aquatica* (171.35%) at no disturbance sites, followed by *R. mangle* (29.53%) and *Z. conzattii* (24.73%). At sites with medium disturbance, *P. aquatica* (178.07%) had the highest IVI, followed by *C. oaxacana* and *R. mangle*, at 35.36 and 34.44%, respectively. At sites with high disturbance, *P. aquatica* (207.47%) had the highest IVI, while *Hampea macrocarpa* (4.84%) had the lowest (Table 4). Species composition decreased with disturbance, in this sense, sites with no disturbance had more species (n = 12) than sites with high disturbance (n = 5). Regardless of the disturbance level, 33% of the species were present across all sites. In order of importance, these species were *P. aquatica*, *Zygia conzattii, Laguncularia racemosa*, and *Rhizophora mangle,* while *Hampea macrocarpa* was present only at sites with high and no disturbance*. Pachira aquatica* was registered at all three disturbance levels, and it became more dominant as the disturbance increased, which was reflected in its forest value index. The Holdridge index showed that as the number of species decreased, complexity decreased (Table 4).

Table 4 Forest fuel bed characterization and structural indices.

Species	D_A	D_R (%)	F_A	F_R (%)	BA ($m^2\ ha^{-1}$)	Do_R (%)	IVI (%)	FVI (%)	HCI
No disturbance									
Pachira aquatica	2171	80.85	1.17	15.56	23.72	74.95	171.35	110	148.05
Rhizophora mangle	69	2.57	1.17	15.56	3.61	11.40	29.53	45	
Zygia conzattii	164	6.12	1.17	15.56	0.97	3.06	24.73	53	
Entadopsis polystachya	74	2.75	1.00	13.33	0.76	2.39	18.47	25	
Laguncularia racemosa	43	1.60	0.83	11.11	0.89	2.81	15.51	23	
Cynometra oaxacana	86	3.19	0.33	4.44	1.14	3.59	11.23	19	
Paullinia pinnata	29	1.06	0.33	4.44	0.36	1.15	6.66	8	
Serjania mexicana	14	0.53	0.33	4.44	0.05	0.15	5.13	5	
*Lianas	12	0.44	0.33	4.44	0.05	0.17	5.06	6	
Hampea macrocarpa	12	0.44	0.33	4.44	0.03	0.08	4.97	4	
Tabebuia rosea	2	0.09	0.17	2.22	0.06	0.20	2.52	-	
Leucaena leucocephala	7	0.27	0.17	2.22	0.01	0.03	2.52	2	
Combretum decandrum	2	0.09	0.17	2.22	0.01	0.02	2.33	-	
Total	2686	100	7.5	100	26.59	100	300	300	
Medium disturbance									
Pachira aquatica	1900	81.72	1.00	21.05	29.67	75.30	178.07	146	102.59
Cynometra oaxacana	250	10.75	1.00	21.05	1.40	3.55	35.36	77	
Rhizophora mangle	29	1.25	0.75	15.79	6.86	17.40	34.44	29	
*Lianas	54	2.33	0.75	15.79	0.30	0.75	18.87	12	
Zygia conzattii	58	2.51	0.75	15.79	0.22	0.55	18.85	21	
Entadopsis polystachya	29	1.25	0.25	5.26	0.85	2.15	8.67	9	
Laguncularia racemosa	4	0.18	0.25	5.26	0.12	0.30	5.74	6	
Total	2325	100	4.75	100	39.41	100	300	300	
High disturbance									
Pachira aquatica	2386	90.61	1.00	27.27	25.60	89.59	207.47	195	72.03
Rhizophora mangle	53	2.00	0.83	22.73	1.74	6.08	30.81	29	
Laguncularia racemosa	89	3.38	0.67	18.18	0.65	2.26	23.82	37	
Zygia conzattii	81	3.06	0.67	18.18	0.51	1.78	23.02	25	
*Lianas	19	0.74	0.33	9.09	0.06	0.21	10.04	11	

Hampea macrocarpa	6	0.21	0.17	4.55	0.02	0.08	4.84	3
Total	2633	100	3.67	100	28.57	100	300	300

Legend: Absolute (D_A) and relative (D_R) densities, absolute (F_A) and relative (F_R) frequencies, basal area (BA), Importance value index (IVI), forest value index (FVI), and Holdridge complexity index (HCI).

Species richness was highest for no disturbance sites (19), followed by medium disturbance (14) and high disturbance (9) sites. Alpha Fisher index, Margalef, Shannon, and Simpson were all higher in non-disturbed sites. The Berger–Parker index was higher for *P. aquatica* in highly disturbed sites (Table 5).

Table 5 Fuel beds, live-fuel characterization.

FB	S	α	D_{Mg}	*H'*	*D*	*D*
No disturbance	19	2.91±0.75	2.39±0.41	1.06±0.01	0.77±0.003	0.39±0.02
Medium disturbance	14	1.8±0.3	1.54±0.19	0.91±0.11	0.78±0.04	0.37±0.007
High disturbance	9	1.16±0.08	1.01±0.58	0.56±0.22	0.87±0.02	0.22±0.05

Legend: Average and standard deviation of each index. S = richness, α = Alpha Fisher, D_{Mg} = Margalef, H' = Shannon–Wiener, d = Berger–Parker, D = Simpson.

Dead fuels

The woody fuel stratum of fuel beds in TFFCW was different among the 1, 10, and 1000 h (rotten) classes. The highest fuel load was observed at sites with high disturbance, while in the remaining categories, there were no significant differences. However, litterfall fuels (SL and FL) did not show differences in the disturbance gradient studied (Table 6). The results of the total woody fuel load (including all classes) showed that the highest average amount was 176.22 ± 31.48 t ha^{-1} (high disturbance), followed by medium disturbance (130.15 ± 21.75 t ha^{-1}), and no disturbance (121.36 ± 27.15 t ha^{-1}). The average total litterfall fuel load (which included the two evaluated categories) was similar among high disturbance (45.96 ± 8.42 t ha^{-1}), medium disturbance (46.51 ± 5.11 t ha^{-1}), and no disturbance (43.83 ± 3.86 t ha^{-1}) sites. Finally, the total amount of dead forest fuels (woody and litterfall) was significantly higher in sites with high disturbance (222.19 ± 13.37 t ha^{-1}), while the lowest load corresponded to sites with no disturbance (165.2 ± 34.92 t ha^{-1}) (Fig. 4).

Table 6 Average value of woody fuels by diameter class and litterfall.

Tropical Freshwater Forested Wetlands / disturbance level				
Level	**Fuel beds stratum**			
	Average (t ha^{-1})	**S.D.**		
0–0.6 cm (1 h)				
No disturbance	4.33	1.21	ab	$F_{2,14}$ =4.94
Medium disturbance	3.26	0.23	b	p = 0.02
High disturbance	5.93	0.65	a	
0.61–2.5 cm (10 h)				
No disturbance	10.72	0.93	b	$F_{2,14}$ = 19.92
Medium disturbance	11.82	1.21	b	p = <0.0001
High disturbance	15	1.54	a	
2.51–7.5 cm (100 h)				
No disturbance	42.86	5.65		$F_{2,14}$ = 1.45
Medium disturbance	51.28	11.95		p = 0.26
High disturbance	55.55	19.9		
> 7.5 cm rotten (1000 h)				
No disturbance	48.7	26.89	b	$F_{2,14}$ = 8.47
Medium disturbance	47.08	13.42	b	p = 0.0039
High disturbance	90.34	12.98	a	
> 7.5 firm (1000 h)				
No disturbance	14.42	9.33		$F_{2,14}$ = 1.57
Medium disturbance	15.71	3.17	n.s.	p = 0.24
High disturbance	11.55	2.86		
Surface litterfall				
No disturbance	27.85	3.47		F2,14 = 0.13
Medium disturbance	28.42	4.59	n.s.	p = 0.87
High disturbance	25.66	3.73		
Fermentation litterfall				
No disturbance	15.97	8.54		F2,14 = 0.50
Medium disturbance	18.08	7.81	n.s.	p = 0.61
High disturbance	20.3	6.54		

Legend: Significant differences are shown with different letters, as determined by the Tukey–Kramer test ($p < 0.05$). (± SD = standard deviation). n.s. = not significant.

4. Discussion

Despite the controversy about how disturbance influences diversity (Mackey and Currie 2001), there is some evidence that less disturbance leads to higher species diversity (Laurance et al. 2012). Forested tropical coastal freshwater wetlands in the southeastern Mexican Pacific are sensitive to disturbance. In this study, we observed that sites with medium to no disturbance had higher diversity and were richer with up to 12 species. However, the number of species was low compared to other forested tropical freshwater coastal wetlands in the Gulf of Mexico (Díaz et al. 2002, Zamora et al. 2008, Maldonado and Maldonado 2010, Maldonado et al. 2016). For instance, in Calakmul, Campeche, the number of species can be as high as 56 (Chiquini et al. 2017). It is possible that the lower diversity in El Castaño (Pacific) is related to the high dominance of *P. aquatica* (Rincón 2014). In this region, *P. aquatica* is a very adaptive species that grows in association with some mangrove species (Barrios-Calderón et al. 2018).

The dominance of *P. aquatica* was potentially associated with its germination requirements, which can have up to 18 practical salinity units (SPU) in the Pacific, in contrast to the Gulf of Mexico (Rincón 2014). The surface of TFFCW in El Castaño and the region has decreased in recent years due to anthropogenic activities, such as tree harvesting, agriculture, livestock, and villages (Romero et al. 2015, Barrios-Calderón 2019). This pressure on the ecosystem could lead to a successional stage, where the tree stratum cover decreases while the shrub and herb stratum may be more abundant (Kellogg et al. 2003). From this perspective, the characterization of the structure and composition of forest fuel beds is of great interest and should be studied in the long term. Precisely, an important field of application for studies related to the structural composition of forests is fire ecology, mainly in the TFFCW. These ecosystems have been affected by an irresponsible fire use regime (Chen 2006) and fire dynamics have also contributed to changes in their vegetation (Randerson et al. 2006, Parisien et al. 2010, Carmenta et al. 2011, Mistry et al. 2016), thus reducing their diversity.

In this study, the Shannon–Wiener (H') indices in undisturbed forest areas were similar to those of other TFFCWs (Díaz et al. 2002, Pérez et al. 2005, Ramírez 2006), while the values obtained in high disturbance regions were low, as expected. In the Gulf of Mexico, the *P. aquatica* TFFCW can be low (4 m) and grow up to 30 m, as indicated by Moreno and Infante (2009). In contrast, in the Pacific, the same type of species grows as much as 17 m (Rincón 2014), values similar to those reported in this study. Furthermore, 59.1% of the canopy strata were 6 to 17 m, while smaller trees represented only 6%. However, this was not the case in high disturbance areas, where the most abundant height (76%) ranged from 2 to 7 m, thus verifying that disturbance had an effect on the vertical structure.

Medium disturbance in the Pacific TFFCW caused *P. aquatica* to grow higher than in undisturbed sites. This suggests that low fire frequency could be beneficial to the ecosystem (Keane and Karau 2010, Bowman et al. 2011), acting as a renewal mechanism. In areas with high disturbance, *P. aquatica* was more dominant but did not have a great height. Therefore, the level of disturbance influenced the vertical and horizontal structure, and in sites with a higher density of *P. aquatica,* the forest will not be as tall. The most common diameter class of live fuels on the horizontal plane ranged from 2.5 to 7.5 cm, independent of disturbance. Similar observations have been reported at other sites of the LEBRE, e.g., El Jicaro (Rincón 2014). Similarly, in TFFCW from the Gulf of Mexico in Veracruz, the most frequent class was from 3 to 13 cm (Infante et al. 2011a). This was especially observed in El Castaño in high disturbance sites. The density of trees made up of the live fuel stratum was higher in this study and had a similar range to that reported in sites in the Gulf of Mexico (Intante 2011). However, in other LEBRE sites with a higher state of conservation, such as Brisas del Hueyate, the density can go up to 3310 ind. ha^{-1} and the IVI of *P. aquatica* (285.28%) was higher (Barrios-Calderón 2015).

In the present study, the density of trees comprising the live fuel's stratum was higher in the less disturbed sites, while woody and litter fuels showed the opposite pattern, having more accumulation in sites with greater disturbance. However, the average value of dead fuels (woody and litterfall) reveals that TFFCWs from the Pacific coast can have more fuel than other forested ecosystems in the tropics (Reyes and Coli 2009, Adame et al. 2015) and temperate regions (Amiro et al. 2001, Flores and Omi 2003, Martínez et al. 2018). In the study carried out by Barrios-Calderón et al. (2018) in the Brisas del Hueyate area within the LEBRE, loads were reported for the classes of 1 (2.75 ± 0.45 t ha^{-1}), 10 (7.01 ± 1.65 t ha^{-1}), and 100 h (18.58 ± 7.22 t ha^{-1}) that are less than those obtained in this study. However, for the class of 1000 h rotten (20.67 ± 16.22 t ha^{-1}) and firm (14.18 ± 9.33 t ha^{-1}), these same authors reported loads similar to those obtained at no disturbance TFFCW sites in the present study. Thus, TFFCW with medium and high disturbance represent a greater potential to present fires under favorable temperature and weather conditions. Mainly high disturbance sites that would represent hot spots for fires with the worst implications for the ecosystem (Flores 2017).

Litterfall fuels, especially the surface litterfall (SL) from all studied sites, are higher than those reported by Rodríguez et al. (2011) in Quintana Roo, Campeche, and Yucatan, with loads up to 17.2 t ha^{-1}. Litterfall productivity in TFFCW from the Gulf of Mexico (Veracruz) ranged from 9.3 ± 0.5 t ha^{-1} (Apompal) to 14.9 ± 1.0 t ha^{-1} (Chica) (Infante et al. 2011b), which is similar to that observed in this study. In both the Gulf of Mexico and the southeast Pacific (LEBRE, El Castaño), litterfall fuels are the result of tree and liana productivity. As suggested by Souza et al. (2019), high litterfall accumulation is determined by climatic factors that affect the vegetative phenology of tree species. Thus, the amount of litterfall fuels in the soil of the study area is twice that accumulated in Veracruz TFFCWs in the Gulf of México, thus, the accumulation rate is higher in the southeastern Pacific. In terms of fire potential, this also represents a greater threat for the El Castaño area, due to the high accumulation of these litterfall fuels (Westcott et al. 2014, Varner et al. 2015). However, the litterfall fuels in the fermented layer are lower compared to studies in the Yucatan Peninsula (Rodríguez et al. 2011), with maximum loads of 53.89 t ha^{-1}. This layer is especially important because combustion is low, but energy is high, so underground fires are more severe than surface fires (Neri et al. 2009). Observations of this fuel layer in this study show no significant differences in the three conditions evaluated, so regardless of the disturbance level, TFFCW are vulnerable to underground fires in the LEBRE.

Some authors, such as Rodriguez (2014) point out that the amount of woody fuels and litterfall decreases with frequent fires. However, despite the fact that, in the last 10 years, two fires of low intensity have been recorded in the study area (CONANP 2018), a limited decrease in dead fuels has been observed in sites with high or medium disturbance. This is due to disturbances caused by timber extraction and the opening of new roads, according to information provided by forest rangers.

Regarding the average load of dead fuels (woody and litterfall), Barrios-Calderón et al. (2018) observed an average load of 225.06 t ha^{-1} at other study sites in the TFFCW of El Castaño. These loadings are very similar to those of high disturbance sites, which represent the highest average accumulation of dead fuels. In another study carried out at the TFFCW in Calakmul, Campeche, Contreras et al. (2006) reported total loads ranging from 43.15 to 154.5 t ha^{-1}, which were within the range obtained for no and medium disturbance sites. However, the total amount of dead fuels was higher than other TFFCW dominated by *P. aquatica* in the Yucatan Peninsula, Mexico (16.46 t ha^{-1}), as shown by Reyes and Coli (2009), as they are the lowest loads that could be considered in relation to those obtained in this work.

Recently, Flores et al. (2018) determined that the load or biomass of these dead fuels contains between 47.5% C for litter and 67% C for 1000 h firm fuels. Consequently, the total amount of C released into the atmosphere when the TFFCW is burned contributes to the amount of greenhouse gases. Thus, the conservation and management of these coastal ecosystems is important for the C cycle at the local and regional scales. Therefore, Mahdizadeh and Russell (2021) pointed out the need not only to estimate degraded areas but also to quantify the amount of C lost in the most disturbed areas in a given year, which can vary greatly.

Irrational logging causes alteration in the vegetation structure, which has led to a greater increase and continuity of forest fuels, resulting in a greater possibility of fires (Gao et al. 2020). Fuel beds in highly disturbed sites have a higher ignition potential and C emissions through fine fuels (1 and 10 h) and litterfall, while the medium fuels (100 h) spread the fire, coarse fuels (1000 h) are related to their intensity. Furthermore, dead fuel available at any level of forest disturbance is related to the potential for fire spread and movement on stairway fuels (Chávez et al. 2016). The latter is the result of the vertical continuity of fuels arranged in these ecosystems, ranging from herbs, grasses, shrubs, lianas, and trees connecting one stratum with the next. In general, sites with higher disturbances will have higher fire potential, these sites will require the implementation of strategies to prevent and mitigate fire. Furthermore, if there is a wide dominance of *P. aquatica*, a type of softwood that grows in tropical regions, conditions increase the decomposition rates of this type of woody material (Hararuk et al. 2015). Finally, the probabilities of underground fires are similar in the three TFFCW conditions, as there are no differences in the depth of the litterfall layer or in the amount of organic material.

The information generated in this study related to the characterization of fuel beds is a starting point for further studies to predict the ignition, spread, and impact of fires in these ecosystems. In general, the potential for fires in the TFFCW conditions evaluated is more evident in areas with high disturbance that require the implementation of management and conservation strategies.

5. Conclusions

Observations show that in undisturbed sites, greater species diversity can be found, while in medium and high disturbance sites, richness decreases. Although the species *P. aquatica* has a high importance value that makes it a dominant species under disturbed conditions, its vertical and horizontal structures do not show optimal development. Large amounts of woody fuels lead to a higher probability of occurrence of high-to-severe fires. The composition of fuel beds in the high and middle disturbance forests showed a greater accumulation of forest fuels. The proximity to the population center, the opening of roads or access routes, the illegal extraction of trees and shrubs, and the historical record of fires have become causes of the high accumulation of forest fuels. Therefore, it is important to consider that the probability of the occurrence of surface fires increases. However, the three TFFCW the evaluated conditions have the same probability of presenting underground fires, where the intensity depends on the depth of the organic material (fermented litterfall) that is equally distributed in the three disturbance conditions evaluated. TFFCWs are an important C sink, which, during a fire event, could release considerable amounts of greenhouse gases into the atmosphere. The information from this study helps to define and prioritize areas that need different management strategies in these ecosystems, for which there are few references.

Declarations

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Figures

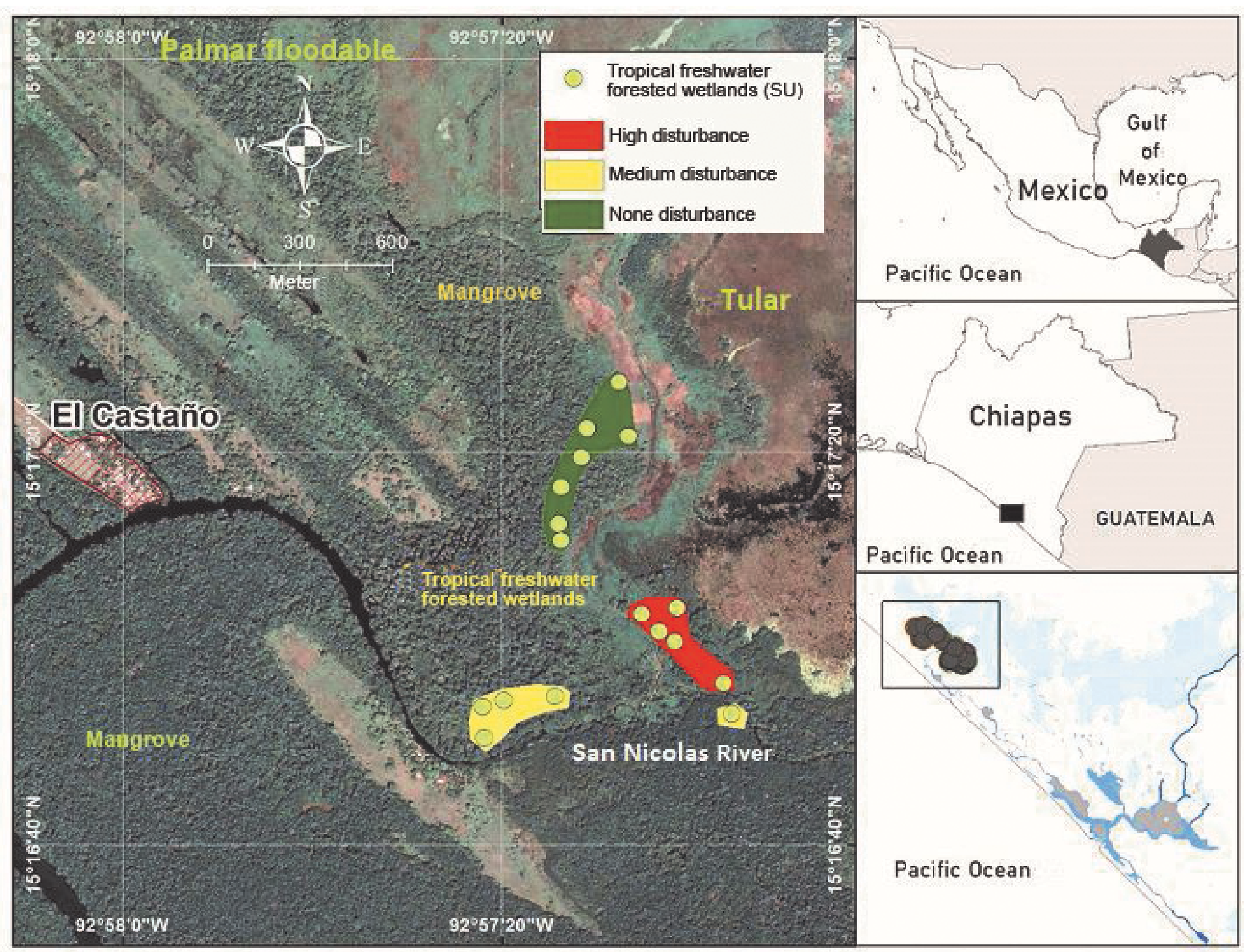

Figure 1

Location of the study area in the Encrucijada Biosphere Reserve, México. Legend: The study site is on the Pacific coast of Mexico, and the tropical freshwater forested coastal wetlands (TFFCW) polygons show three levels of disturbance

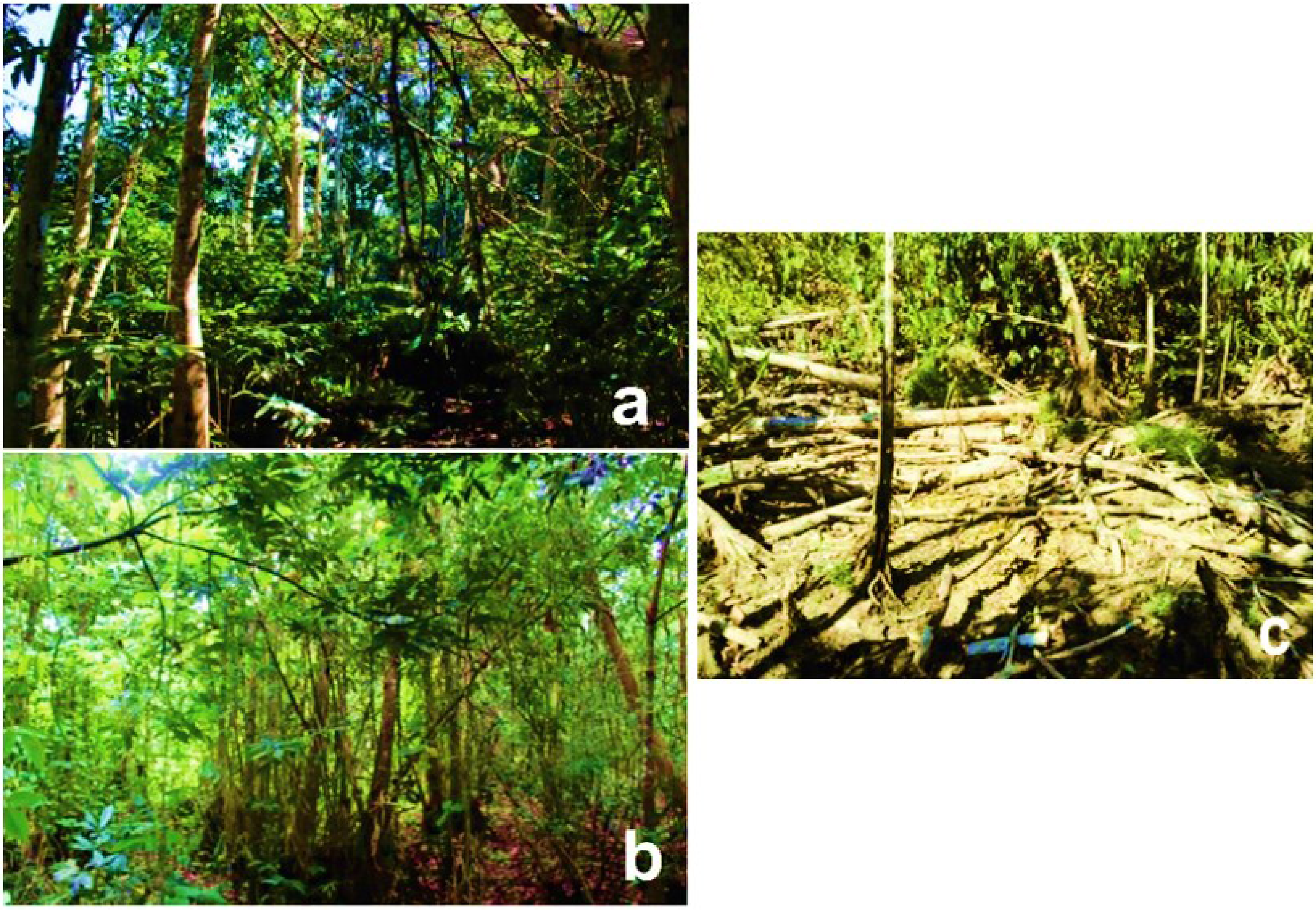

Figure 2

Tropical freshwater forested coastal wetlands of *Pachira aquatica*: a) no disturbance, b) medium disturbance, and c) high disturbance

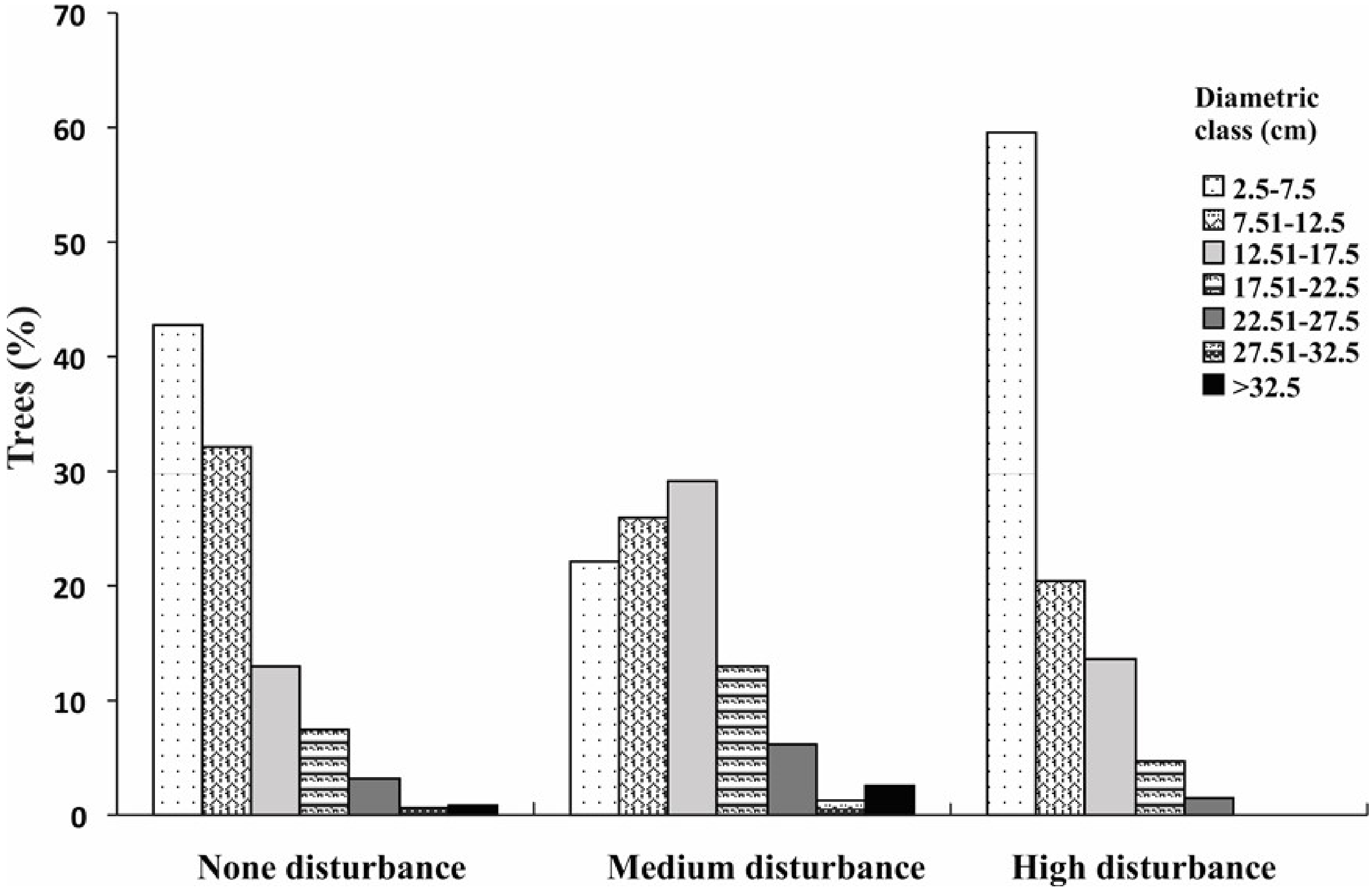

Figure 3

Relative histogram by diameter class for each disturbance level

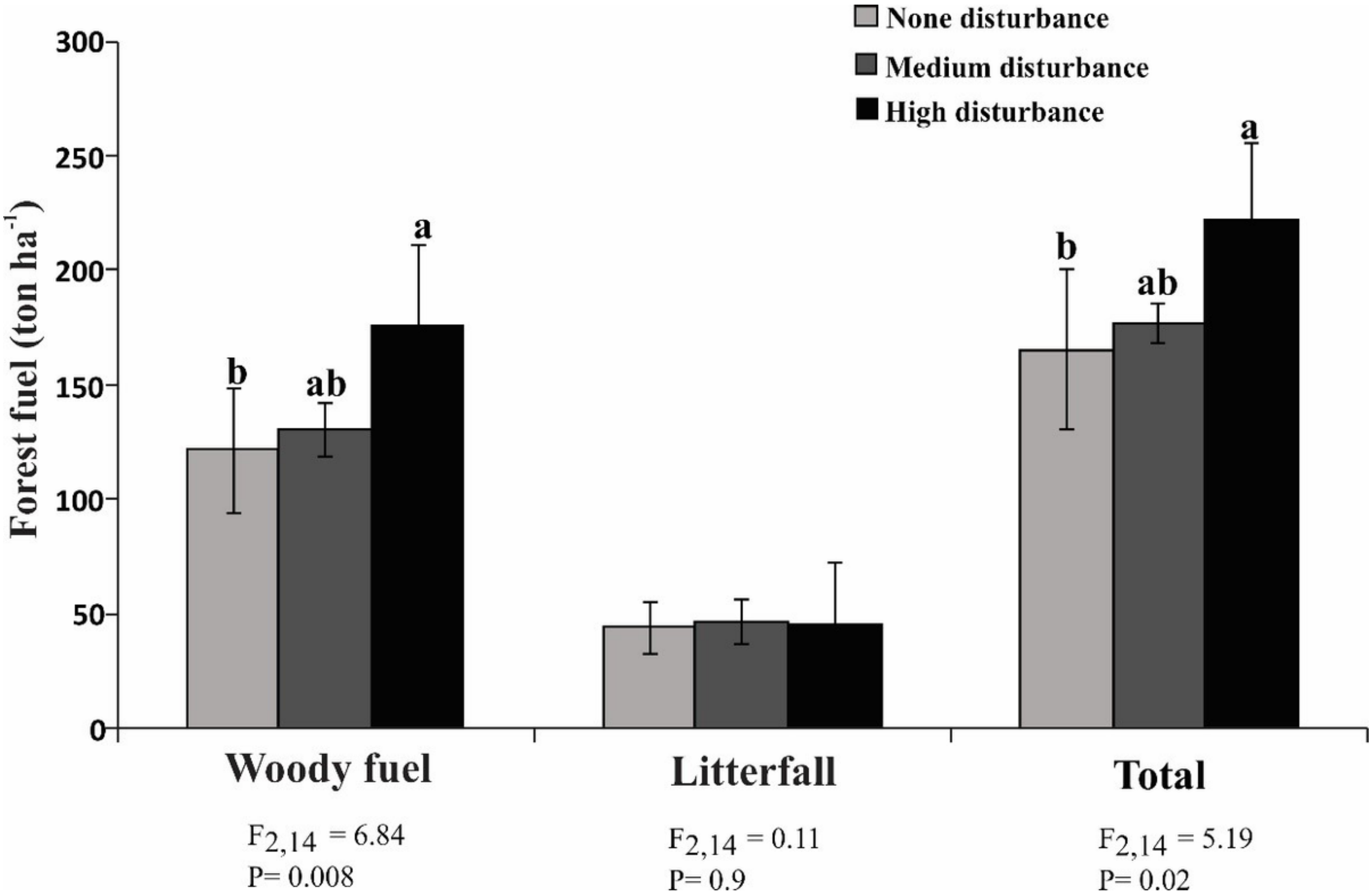

Figure 4

Woody fuel, litterfall, and total forest fuel load. Legend: Significant differences are shown with different letters, as determined by the Tukey-Kramer test ($p < 0.05$), (± standard deviation)

Supplementary Files

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- AppendixA.docx