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

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Research

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Abstract

**Background:** Tropical freshwater forested wetlands in coastal regions are rapidly disappearing, one of the causes is forest fires. This is caused by high accumulation of fuel beds that can vary in origin and type. Therefore, the objective of this study was to characterize the fuel beds in tropical freshwater forested wetlands with three different level of disturbance at El Castaño, La Encrucijada Biosphere Reserve.

**Methods:** Seventeen sampling units were used to described the strates of forest fuel beds (canopy, sub-canopy and understory) in both the vertical and horizontal stratum. Quantity and quality of dead (fallen woody material, surface litterfall and fermented litterfall) fuels were characterized using the planars intersections technique.

**Results:** A total of eight tree species, two shrubs, five lianas and two herbaceous species were found in tropical freshwater forested wetlands. The vertical structure concentrates the highest proportion of trees between 2 and 12 m high, including the first two defined height classes. The horizontal structure denotes a higher percentage of trees with a normal diameter between 2.5 to 7.5 cm (61.4%) of the total. The sites none disturbance presented the highest arboreal density (2,686 ind. ha$^{-1}$), however the highest basal area was found in the sites with medium disturbance (39.41 m$^2$ ha$^{-1}$). The richness and diversity of species shows that the Fisher, Margalef, Shannon and Simpson α indices were higher in the sites undisturbed, while the Berger-Parker index shows greater dominance in the sites high disturbance. *Pachira aquatica* Aubl. was the species with the highest importance value index, and contributes the most to the fuel beds. The average accumulation of dead fuel beds was higher in sites with high disturbance (222.18 ± 33.62 t ha$^{-1}$), with the largest accumulations of woody fuels occurring in the 1 h, 10 h and 1000 h classes, the latter in a state of fermentation.

**Conclusions:** It’s important to consider the probability of occurrence of surface fires is high. In these tropical freshwater forested wetlands, independent of disturbance, underground fires have the same probability and the intensity will depend on the depth of the organic matter layer. This study contributes define fire-prone areas in these ecosystems. The results are of great importance to design fire prevention strategies.

**Background**

Tropical freshwater forested wetlands (TFFW) are regularly found close to mangrove forests within tropical regions occupying swampy terrain, gently sloping and near the river bank, where freshwater influence is greatest (flood pulses) (Ewel, 2010; Infante et al. 2011a; Torres et al. 2018). These plant communities group a large number of tree, shrub and climbing species (Moreno and Infante, 2016). Its complexity is very high, since in addition to providing numerous environmental services, they significantly favor the natural processes of nutrient supply (Moreno and Infante, 2009). In hydrological and terrestrial cycles, TFFWs function as a natural filter for pollutants and as an important refuge for wildlife (Infante et al. 2011a). They also constitute important carbon (C) sinks and even store greater amounts of C in the soil than mangroves (Moreno and Infante, 2016), but unlike these, TFFW are a type of tropical arboreal vegetation that has been little studied.

TFFW are located in freshwater-influenced areas where one or two species commonly dominate (Infante et al. 2011a; Silva et al. 2012). A species of great importance in TFFW is *Pachira aquatica* Aubl. (water zapote), which by its physiological and morphological characteristics could belong to the mangrove group, since they have the particularity of being floating trees that form a false forest floor with organic matter produced and retained (Infante Mata et al. 2011). TFFW dominated by *P. aquatica* are pure communities that only share their space with certain
species tolerant to floods (Barrios-Calderón, 2019). In Mexico and Mesoamerica, the only flood forests 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 (Infante et al. 2011; Rincón, 2014; Barrios-Calderón, 2015). In this last, the TFFW of *P. aquatica* come to be associated with mangrove species (Moreno and Infante, 2016), however human influence has caused the gradual disappearance of these ecosystems.

One of the disturbance agents that promote the loss of plant communities in TFFW are forest fires, either by natural or anthropogenic causes. These play an important role in the dynamics of vegetation and the change of land use (Rodríguez y Fulé, 2003; FAO, 2007; Jardel et al. 2009). Therefore, these coastal wetlands are considered fragile ecosystems, which are threatened by the frequency and magnitude of fire (Page et al. 2009; García et al. 2014). Although TFFW remain flooded for most of the year, they are highly productive and store woody forest fuels (i.e. branches, twigs, logs, fallen trees) and litterfall accumulated. This latter is at different levels of decomposition on the soil surface (Sales et al. 2020). It's precisely in the dry seasons that these ecosystems can lead to combustion processes when the water level fades, the soil dries and all accumulated organic material is available to burn (Goldammer, 1999; Kaal et al. 2011). This explains why this ecosystem has presented fires on a recurring basis, largely managed by the quality and quantity of woody fuel and litterfall.

Forest fuels are the source of energy, in combination with topography, climate and a source of ignition that control the magnitude and fire spread (Scott et al. 2014). Because fires are an important environmental driver for ecosystem processes and biodiversity losses, studies to characterize and estimate forest fuels are of great relevance to fire management and prediction (Rodríguez et al. 2002). The characterization of fuel beds integrates the analysis of the quantity and quality of forest fuel, taking into account the spatial distribution both vertical and horizontal (Dentoni and Muñoz, 2001).

A first step towards this is the description of the fuel beds resulting from the stratification of live fuels (Flowers, 2001; Sandberg et al. 2001) and the quantification of dead fuels (Villers, 2006). 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 population center (Turner et al. 2001), among others that have caused the fragmentation of these forest ecosystems.

Particularly in areas such as the La Encrucijada Biosphere Reserve (LEBRE) Chiapas, these disturbance agents are a threat to ecosystems such as TFFW. CONANP (2018) and CONAFOR (2018) have collected fire information in LEBRE since 1998, have observed at least 20 fires in El Castaño, which have affected freshwater marshes (1,200 ha), mangroves (800 ha) and TFFW of *P. aquatica* (450 ha).

The study of fuel beds has been developed worldwide in different ecosystems (Sandberg et al. 2001; Ottmar et al. 2007; Riccardi et al. 2007; Arroyo et al. 2008; Donato et al. 2013; Keane, 2013; Bernau et al. 2018), tempered (Villers y López, 2004; Bautista et al. 2005; Muñoz et al. 2005; Wong and Villers, 2006) and tropical (Rodríguez-Trejo et al. 2011; Adame et al. 2013; Barrios-Calderón et al. 2018). However, few studies have focused on exploring tropical freshwater forested wetlands with different levels of disturbance. Therefore, the objective of this research was to characterize the structure and composition of living and dead fuels, from a study approach to fuel beds of TFFW dominated by *Pachira aquatica* in El Castaño (LEBRE), with different levels of disturbance (high, medium, none). The following hypotheses were raised: (i) Species diversity will be greater in undisturbed sites with respect to sites of medium and high disturbance. In addition, (ii) *P. aquatica* will have higher importance value and major
dominance in tropical freshwater forested wetlands with high disturbance, this as a result of decreased in species richness in these conditions. (iii) Despite having less stratification and mixing of species, the accumulation of dead fuels is greater in sites with high disturbance.

Methods

Study area

The natural protected area La Encrucijada (LEBRE) is also a RAMSAR site (1996), located in the southeast Pacific coast of Mexico. The surface area of the 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 (Diario Oficial de la Federación, 1995).

TFFW of *P. aquatica* are found surrounding mangroves, freshwater marshes and other coastal ecosystems (Fig. 1), these ecosystems are connected through a complex hydrology network. In this wetland system, *P. aquatica* is far from the salt water inlets of the estuaries and the main source of water is freshwater from the San Nicolas River. Climate is tropical warm-humid with summer rains Am(w), mean annual temperature is 28 °C, and annual precipitation ranges from 1300 mm to 3000 mm (INE, 1999). The dry period goes from February to May, during this period water level is below the soil surface (Rincón, 2014).

Field study

Based on hydroperiod information by Rincón (2014), the field campaigns for this study were planned from February to April in 2017 and 2018. Following a stratified randomized experimental design, 17 circular sampling units (SU) of 600 m² (radius = 13.8 m) were established in TFFW with three different disturbance levels (Fig. 1). Disturbance levels was defined based on the following criteria: 1) canopy openness, 2) distance from roads, 3) human activities, 4) illegal extraction wood, 5) hurricane/wind impact, 6) fires, and 7) forest cover (Table 1). Based on this information and field validation sites were categorized as None disturbance (n = 7), Medium disturbance (n = 5), and High disturbance (n = 5) (Fig. 2).

| Level                      | Criteria                  | Canopy openness | Distance to roads (km) | Human activities | Illegal extraction wood | hurricane/wind impact | Fires (1998–2018) | Forest cover (%) |
|---------------------------|---------------------------|-----------------|------------------------|------------------|------------------------|---------------------|-------------------|------------------|
| None 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

Lives-fuel

At 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 canopy diameter of 20% of the trees was measure following methods from Valdez (2002). To describe horizontal structure, 10 diameter classes were established starting at 2.5 cm with 5 cm interval (Corella et al. 2001). Furthermore, measurements were used to estimate density and basal area (Ramos et al. 2004), relative coverage (Zarco, Valdez, Ángeles and Castillo, 2010), relative frequency, density and dominance (Gentry and Ortiz, 1993) of the species. Furthermore, three structural indexes were estimates: importance value index (IVI) (Villavicencio and Valdez, 2003), forestry value index (FVI) (Zarco et al. 2010), and Holdridge complexity index (HCI) (Holdridge et al. 1971). 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 sub-circle of 60 m² (diameter = 8.7 m) 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 planars 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 center of the site to each cardinal point (N, S, E, W). The woody fuel was classified according to the “timelag”, that is, 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 to 0.6 cm], 10 h [0.61 to 2.5 cm], 100 h [2.5 to 7.5 cm] y 1000 h [> 7.5 cm]) (Table 2). Measurements in the transect were performed as follow 1 h fuels in the first 2 m, 10 h up to 4 m, 100 h up to 7 m, 1000 h up to 10 m. Fine fuels (1 and 10 h), and medium fuels (100 h), were counted based on the numbers of intersections on the horizontal plane. Thick fuels (1000 h) were classified according to their state or condition (firm or rotten), and their diameter was measured.
Table 2
Equations to estimate woody fuel at each sampling unit (SU) at El Castaño

| Fuel class                  | Equation                                      |
|-----------------------------|-----------------------------------------------|
| 1 h                         | \( P = \frac{(0.484 \times f \times c)}{(N \times l)} \) |
| 10 h                        | \( P = \frac{(3.369 \times f \times c)}{(N \times l)} \) |
| 100 h                       | \( P = \frac{(36.808 \times f \times c)}{(N \times l)} \) |
| 1000 h firm (none rotten)   | \( P = \frac{(1.46 \times f \times c)}{(N \times l)} \) |
| 1000 h (rotten)             | \( P = \frac{(1.21 \times f \times c)}{(N \times l)} \) |

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)

The litterfall was collected at the end of each planar intersection line in four quadrants of 0.2 × 0.2 m, where the depth of the layer was measured and separated into superficial litterfall (SL) and fermented litterfall (FL). Later, the litterfall was carried to the laboratory and dry biomass was obtained after 24 h in 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 Morfin-Ríos et al. (2012). For this, it was necessary to obtain the apparent density (\( \rho \)) at the depths of SL and FL and subsequently determine the load of the litterfall layer:

\[
\rho = \left( \frac{P}{a \times h} \right) \times 10
\]

Where: \( \rho \) = apparent 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, 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), \( d \) = apparent density (t ha\(^{-1}\) mm\(^{-1}\))
Statistical analysis

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

Results

Structure and composition of fuel beds

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

The understory had presence of Pachira aquatica saplings (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 species in the understory include Cynometra oaxacana, Zygia conzattii, and Leucaena leucocephala. While, herb stratum was mostly composed by 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 larger number of trees with heights between 2 and 7 m (75%). While, in sites with none disturbance, 65% of trees belonged to the same as above category, and in medium disturbance only 49%. Thus, this was the dominant height class in the three levels of disturbance evaluated (Table 3). The percentage for the 7 to 12 m height class varies in sites where the high disturbance has only 20% of the trees in this category, in sites with medium disturbance 25%, and in sites with none disturbance the percentage increases to 32%. Sites with medium disturbance have the highest percentage for classes 12–17 m (14.48%), 17.1–22 m (6.43%), and >22 m (6.43%), with respect to none disturbance and high disturbance sites (Table 3). So much so that the sum of the percentages of these three classes corresponds to 24%, while in the other two disturbance conditions (high and null), the height classes greater than 12 m only represent 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 |
| None disturbance      |        |         |         |        |       |      |
| *Pachira aquatica*    | 0.00   | 0.09    | 1.25    | 28.27  | 51.80 | 0.00 |
| *Zygia conzattii*     | 0.00   | 0.00    | 0.00    | 0.62   | 5.52  | 0.00 |
| *Cynometra oaxacana*  | 0.00   | 0.00    | 0.00    | 1.07   | 2.14  | 0.00 |
| *Entadopsis polystachya* | 0.00  | 0.00    | 0.00    | 0.27   | 2.49  | 0.00 |
| *Rhizophora mangle*   | 0.00   | 0.53    | 0.71    | 0.18   | 0.27  | 0.00 |
| *Laguncularia racemosa* | 0.00  | 0.09    | 0.53    | 0.27   | 0.62  | 0.00 |
| *Hampea macrocarpa*   | 0.00   | 0.00    | 0.00    | 0.61   | 0.44  | 0.00 |
| *Leucaena leucocephala* | 0.00  | 0.00    | 0.00    | 0.19   | 0.00  | 0.00 |
| *Paullinia pinnata*   | 0.00   | 0.00    | 0.09    | 0.44   | 0.53  | 0.00 |
| *Serjania mexicana*   | 0.00   | 0.00    | 0.00    | 0.00   | 0.53  | 0.00 |
| Lianas                | 0.00   | 0.00    | 0.00    | 0.00   | 0.06  | 0.00 |
| *Combretum decandrum* | 0.00   | 0.00    | 0.00    | 0.00   | 0.03  | 0.00 |
| *Tabebuia rosea*      | 0.00   | 0.00    | 0.00    | 0.09   | 0.00  | 0.00 |
| Total                 | 0.00   | 0.71    | 2.58    | 32.10  | 64.61 | 0.00 |
| Medium disturbance    |        |         |         |        |       |      |
| *Pachira aquatica*    | 2.39   | 6.06    | 13.94   | 22.21  | 37.25 | 1.83 |
| *Cynometra oaxacana*  | 0.00   | 0.00    | 0.18    | 1.65   | 9.17  | 0.00 |
| *Zygia conzattii*     | 0.00   | 0.00    | 0.00    | 0.55   | 2.02  | 0.00 |
| *Entadopsis polystachya* | 0.00  | 0.00    | 0.00    | 0.37   | 0.92  | 0.00 |
| *Rhizophora mangle*   | 0.73   | 0.37    | 0.18    | 0.00   | 0.00  | 0.00 |
| *Laguncularia racemosa* | 0.00  | 0.00    | 0.18    | 0.00   | 0.00  | 0.00 |
| Total                 | 3.12   | 6.43    | 14.48   | 24.78  | 49.36 | 1.83 |
| High disturbance      |        |         |         |        |       |      |
| *Pachira aquatica*    | 0.21   | 0.11    | 0.53    | 18.02  | 70.39 | 0.84 |
| *Laguncularia racemosa* | 0.00  | 0.84    | 1.16    | 0.95   | 0.63  | 0.00 |
| *Zygia conzattii*     | 0.00   | 0.00    | 0.00    | 3.06   | 0.00  | 3.06 |

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, shows that sites with high disturbance have the most percentage of ND between 2.5 to 7.5 cm (61.45%). Furthermore, the none disturbance sites have higher percentage (32.7%) in the category 7.5 to 12.5 cm. However, sites with medium disturbance have 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 were as follows: 2.5 to 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 none disturbance sites with 2,686 individuals ha$^{-1}$ and 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 none disturbance sites, followed by *R. mangle* (29.53%) and *Z. conzattii* (24.73%). At sites with medium disturbance again *P. aquatica* (178.07%) has the highest IVI, followed by *C. oaxacana* and *R. mangle*, with 35.36% and 34.44%, respectively. At sites with high disturbance *P. aquatica* (207.47%) had the highest IVI, while *Hampea macrocarpa* (4.84%) the lowest (Table 4). The species composition decreases with disturbance, in this way, sites with none disturbance have more species (n = 12) than sites with high disturbance (n = 5). 33% of the species are present across all sites independent from the disturbance level. In order of importance, these species were *P. aquatica, Zygia conzattii, Laguncularia racemosa,* and *Rhizophora mangle* while *Hampea macrocarpa* is present only in sites with high and none disturbance. *P. aquatica* was registered at all three disturbance levels and it becomes more dominant as disturbance increases, which is reflected in its forest value index. Holdridge index shows that as the number of species decreases, complexity is less (Table 4).
Table 4
Forest fuel beds characterization and structural indexes

| Species                       | $D_A$ | $D_R$ (%) | $F_A$ (%) | $F_R$ (%) | BA (m² ha⁻¹) | $D_oR$ (%) | IVI (%) | FVI (%) | HCI     |
|-------------------------------|-------|-----------|-----------|-----------|--------------|------------|---------|---------|---------|
| None 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   |

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 Holdrige complexity index (HCI)
| Species            | DA  | DR  | FA  | FR  | BA   | DOR | IVI  | FVI  | HCI  |
|-------------------|-----|-----|-----|-----|------|-----|------|------|------|
| 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 (DA) and relative (DR) densities, absolute (FA) and relative (FR) frequencies, basal area (BA), Importance value index (IVI), forest value index (FVI) and Holdridge complexity index (HCI)

Species richness, was highest for none disturbance sites (19), followed by medium disturbance (14), and finally high disturbance (9) sites. Alpha Fisher index, as well as Margalef, and Shannon and Simpson were all higher in none disturbed sites. While, the Berger-Parker index was higher for P. aquatica in high disturbed sites (Table 5).

Table 5
Fuel beds, live-fuel characterization

| FB                | S    | α    | DMg  | H'   | D    | D    |
|-------------------|------|------|------|------|------|------|
| None 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; DMg = Margalef, H' = Shannon-Wiener; d = Berger-Parker; D = Simpson

Dead fuels

The woody fuels stratum of fuel beds in TFFW different among classes 1 h, 10 h, and 1000 h (rotten). The highest fuel load was presented in sites with high disturbance, while in the remaining categories there are no significant differences. For its part, the litterfall fuels (SL and FL) did not show differences in the three disturbance conditions studied (Table 6). The results of the total load of woody fuels (including all classes) show than 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 none disturbance (121.36 ± 27.15 t ha⁻¹). The average load of total fuel litterfall (which includes the two evaluated categories) was similar among sites high disturbance (45.96 ± 8.42 t ha⁻¹), medium disturbance (46.51 ± 5.11 t ha⁻¹), and none disturbance (43.83 ± 3.86 t ha⁻¹). 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 corresponds to sites with none 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 | Fuel beds stratum | S.D. |     |
|----------------------------------------------------------|-------------------|------|-----|
|                                                          | Average (t ha\(^{-1}\)) |     |     |
|                                                          | Level             |      |     |
|                                                          | 0-0.6 cm (1 h)    |      |     |
|                                                          | None disturbance  | 4.33 | 1.21| ab  |
|                                                          | Medium disturbance| 3.26 | 0.23| b   |
|                                                          | High disturbance  | 5.93 | 0.65| a   |
|                                                          | 0.61-2.5 cm (10 h)|      |     |     |
|                                                          | None disturbance  | 10.72| 0.93| b   |
|                                                          | Medium disturbance| 11.82| 1.21| b   |
|                                                          | High disturbance  | 15   | 1.54| a   |
|                                                          | 2.51-7.5 cm (100 h)|      |     |     |
|                                                          | None disturbance  | 42.86| 5.65| F2,14 = 1.45 |
|                                                          | Medium disturbance| 51.28| 11.95| p = 0.26 |
|                                                          | High disturbance  | 55.55| 19.9 |
|                                                          | > 7.5 cm rotten (1000 h)|      |     |     |
|                                                          | None disturbance  | 48.7 | 26.89| b   |
|                                                          | Medium disturbance| 47.08| 13.42| b   |
|                                                          | High disturbance  | 90.34| 12.98| a   |
|                                                          | > 7.5 firm (1000 h)|      |     |     |
|                                                          | None disturbance  | 14.42| 9.33 | F2,14 = 1.57 |
|                                                          | Medium disturbance| 15.71| 3.17 | p = 0.24 |
|                                                          | High disturbance  | 11.55| 2.86 |
|                                                          | Surface litterfall|      |     |     |
|                                                          | None disturbance  | 27.85| 3.47 | F2,14 = 0.13 |
|                                                          | Medium disturbance| 28.42| 4.59 | p = 0.87 |
|                                                          | High disturbance  | 25.66| 3.73 |
|                                                          | Fermentation litterfall|      |     |     |
|                                                          | None disturbance  | 15.97| 8.54 | F2,14 = 0.50 |

Legend: Significant differences are shown with different letter Tukey-Kramer (p < 0.05). (± SD = Standard deviation).
Tropical Freshwater Forested Wetlands / disturbance level

| Disturbance Level  | Mean   | SD    | p     |
|-------------------|--------|-------|-------|
| Medium disturbance| 18.08  | 7.81  | 0.61  |
| High disturbance  | 20.3   | 6.54  |       |

Legend: Significant differences are shown with different letter Tukey-Kramer (p < 0.05). (± SD = Standard deviation).

Discussion

Despite the fact that there is controversy on how disturbance will influence diversity (Mackey and Currie, 2001), there is some evidence that less disturbance results in higher species diversity (Laurance et al. 2012). Tropical freshwater forested wetlands in the Mexican Southeast Pacific, are sensitive to disturbance. In this study we observed that sites with medium to none disturbance are higher in diversity and richer with up to 12 species. The amount of species however, is low in comparison to other tropical freshwater forested wetlands from 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 go as high as 56 (Chiquini et al. 2017). It’s possible that the lower diversity in El Castaño (Pacific) is related to the high dominance of *P. aquatica* (Rincón, 2014). Given that in this region, *P. aquatica* is a very adaptive species, so much so that it grows in association with some mangrove species (Barrios-Calderón et al. 2018).

The dominance of *P. aquatica* is potentially associated to its germination requirement, that can go up to 18 salinity practical units (SPU) in the Pacific in contrast with the Gulf of Mexico (Infante et al. 2011b). The TFFW of El Castaño and the region have reduced their surface in recent years, due to anthropogenic activities such as tree harvest, 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 further reduces its cover percentage, while shrubs and herbs may be more abundant (Kellogg et al. 2003). From this perspective, the characterization of the structure and composition of the forest fuels bed is of great interest, so they should be studied over time. Precisely, an important field of application of studies related to the structural composition of forests and jungles is the fire ecology, mainly in the TFFW. These ecosystems have been impacted by a regime of irresponsible use of fire (Chen, 2006) and fire dynamics have also contributed to changes in its vegetation (Randerson et al. 2006; Parisien et al. 2010; Carmenta et al. 2011; Mistry et al. 2016), thereby reducing its diversity.

In this study the Shannon-Wiener (H’) index in none disturbance forest areas are similar to other TFFW (Díaz et al. 2002; Pérez et al. 2005; Ramírez, 2006), while the values obtained in the zones high disturbance are low as expected. In the Gulf of Mexico, TFFW of *P. aquatica* can be so low (4 m) and grow up to 30 m, as indicated by Moreno and Infante (2009). In contrast, in the Pacific same type of species grows as much as 17 m (Rincón, 2014), similar to the values reported in this study. Furthermore, 59.1% of the canopy strata goes from 6 to 17 m, while smaller trees represent only 6%. However, this is not the case in high disturbance areas were the most abundant height (76%) ranges from 2 to 7 m, thereby verifying that the disturbance has an effect on the vertical structure, which is evident with the supression of the trees.

Medium disturbance in the TFFW of the Pacific, results in *P. aquatica* growing higher than in sites none disturbance. This suggests that low fire frequency could be beneficial for the ecosystem (Keane y Karau, 2010; Bowman et al. 2011), acting like a renewal mechanism. In high disturbance areas, *P. aquatica* is more dominant
however does not have great high. Therefore, the level of disturbance will influence vertical and horizontal structure, and in sites with more density of *P. aquatica* the forest will not be as tall. The most common diameter class of live fuels on the horizontal plane goes from 2.5 to 7.5 cm, independent from disturbance. Similar observations have been reported in other sites of the LEBRE e.g. El Jicaro (Rincón, 2014). Similarly, in TFFW from the Gulf of Mexico in Veracruz, the most frequent class is from 3 to 13 cm (Infante et al. 2011a). This is specially observed in El Castaño in high disturbance sites. The density of trees in this study has a similar range to that reported in sites at the Gulf of Mexico (Infante, 2011). However, in other LEBRE sites with a higher state of conservation such as Brisas del Hueyate, the density can go up to 3,310 ind. ha\(^{-1}\) and the IVI of *P. aquatica* (285.28\%) is higher (Barrios-Calderón, 2015).

It is important to note that in the present study, the density of trees that make up the live fuels stratum is higher in less disturbed sites, while woody and litter fuels show an opposite pattern, having more accumulation in sites with greater disturbance. However, the average value of dead fuels (woody and litterfall) reveals that tropical freshwater forested wetlands from the Pacific coast can have more fuel than other forested ecosystems in the tropics (Adame et al. 2015; Reyes and Coli, 2009) 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 h (2.75 ± 0.45 t ha\(^{-1}\)), 10 h (7.01 ± 1.65 t ha\(^{-1}\)), 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 report loads similar to those obtained at no disturbance TFFW sites in the present investigation. Thus, the TFFW 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 worst implication for the ecosystem (Flores, 2017).

Litterfall fuels, especially the superficial litterfall (SL) from all studied sites is higher than the ones reported by Rodríguez et al. (2011) in Quintana Roo, Campeche and Yucatan, with loads up to 17.2 t ha\(^{-1}\). Litterfall productivity in TFFW from the Gulf of Mexico (Veracruz) goes from 9.3 ± 0.5 t ha\(^{-1}\) (Apompa) to 14.9 ± 1.0 t ha\(^{-1}\) (Chica) (Infante et al. 2011b), which are similar to the observed in this study. In both sites Gulf of Mexico and the southeast Pacific (LEBRE, El Castaño), litterfall fuels is the result of the productivity of trees and lianas. As Souza et al (2019) point out, high litterfall accumulation is determined by climatic factors that affect the vegetative phenology of tree species. In this way, the amount of litterfall fuels in the soil of the study area doubles the amount accumulated in TFFW of Veracruz in the Gulf of México, therefore the accumulation rate is higher in the in the southeast Pacific. This in terms of fire potential also represents a greater danger 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 from the fermented layer are lower in comparison with sited in the Yucatan Peninsula (Rodríguez et al. 2011), with maximum loads of 53.89 t ha\(^{-1}\). This layer is especially important because the combustion is low, but the energy is high, therefore underground fires are more severe than the surface fires (Neri et al. 2009). Observations of this fuel layer in this study shows no significant differences in the three conditions evaluated, therefore independent of disturbance level TFFW 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 las 10 years, two fires of low intensity have been recorded (CONANP, 2018), not much of a decrease of down dead fuels was observed in sites with high and medium disturbance. This is due to disturbance caused by wood extraction and 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) came to obtain an average load of 225.06 t ha\(^{-1}\) at other study sites in the TFFW of El Castaño. These loads are very similar to obtained in the sites of disturbance high at the present investigation, which represent the highest average accumulation of dead fuels. In another study carried out at the TFFW in Calakmul, Campeche, Contreras et al. (2006) report total loads ranging from 43.15 to 154.5 t ha\(^{-1}\), which are within the range obtained for none disturbance and medium disturbance sites. However, the total amount of fuels dead is higher than other TFFW dominated by \(P.\ aquatica\) dominated in the Yucatan peninsula, Mexico (16.46 t ha\(^{-1}\)) obtained by Reyes and Coli (2009), which 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% of C (for litter) to 67% of C (in fuels of 1000 h firm). In this way, the total amount of C released when the TFFW are burned contributes a greater amount of greenhouse gases, compared to other ecosystems that have lower amounts of dead fuels (necromass), since the flood forests are important C sinks. Thus, is important role of these coastal ecosystem to the C cycle at local and regional scale.

Fuel beds at high disturbance sites have higher ignition potential and C emissions through fine fuels (1 h y 10 h) and litterfall, while the medium fuels (100 h) propagate the fire and coarse fuels (1000 h) are related to its intensity. Furthermore, dead fuel available in any level of forest disturbance, will be related to propagation potential and movement of the fire on stairway fuels (Chávez et al. 2016). The latter is the result of the vertical continuity of the fuels arranged in these ecosystems, which goes from herbs, shrubs, lianas and trees connecting one stratum with the next. In general, sites with higher disturbance will have higher fire potential, these sites will require the implementation of strategies to prevent and mitigate fire. Even more so if you have a wide dominance of \(P.\ aquatica\), a type of softwood that complies with the established by Haruk et al (2020) when developed in humid areas with high temperatures and annual precipitation greater than 1837 mm, and that favor the decomposition rates of this type of woody material. In this way the complex of woody fuels forms the necromass, that is, the dead wood that is available and susceptible to ignite. Finally, the probabilities of underground fire are similar in the three TFFW conditions, because there are no differences in the depth of the litterfall layer and amount of organic material.

The information generated in this study related to the characterization of fuel beds, is a starting point for further studies which will allow predict the ignition, propagation, and impact of fires in these ecosystems. In general, the potential for fires in the TFFW conditions evaluated is more evident in areas with high disturbance that require the implementation of preventive and efficient. This to counteract the possible presence of fires that could spread to adjacent ecosystems (mangroves, freshwater marshes and palmares). All information referring to the study of fuel beds and their composition, constitutes a starting point at the regional level to predict or diagnose the start, spread and impact of fires in these ecosystems, in the face of anthropogenic disturbances that have fragmented the connectivity and ecosystem functionality of these coastal wetlands.

Conclusions

According to the results obtained in the present study, a greater diversity of species was found in undisturbed sites, while in medium and high disturbance sites richness decreases. Although the \(Pachira aquatica\) species has an importance value higher that makes it a dominant species under conditions of disturbance, its vertical and horizontal structure does not show optimal development. Large amounts of woody fuels give a higher probability
of occurrence of high to severe category fires. In this way, the composition of fuel beds in high and middle disturbance forests have greater accumulation of forest fuels. The proximity to population center, the opening of roads or access routes, the illegal extraction of trees, shrubs and the historical record of fires have become causes of the high accumulation of fuels forest. Therefore, it will be important to consider that the probability of occurrence of surface fires increase. However, the three conditions of TFFW evaluated have the same possibility of presenting underground fires, where the intensity will depend on the depth of the organic material (fermented litterfall) that is distributed equally in the three evaluated disturbance conditions. TFFW's of coastal zones are important C sink, that during a fire event could release considerable amounts of greenhouse gases to 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 not many investigation that refer to the topic addressed. However, it will be important in future studies to increase the sampling points to achieve greater precision in the results.

**Abbreviations**

ANOVA: Analysis of variance; BA: basal area; C: carbon; D\textsubscript{A}: absolute density; D\textsubscript{R}: relative density; F\textsubscript{A}: absolute frequency; FB: fuel beds; FL: fermented litterfall; F\textsubscript{R}: relative frequency; FVI: forestry value index; HCI: Holdridge complexity index; IVI: importance value index; LEBRE: La Encrucijada Biosphere Reserve; ND: normal diameter; S: richness; SD: standard deviation; SL: superficial litterfall; SU: sampling units; TFFW: Tropical freshwater forested wetlands

**Declarations**

**Availability of data and materials**

The datasets used and/or analysed during the current study are available from the corresponding autor on reasonable request.

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no competing interests.

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**Authors’ contributions**

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Figure 1

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

Figure 2

Tropical freshwater forested wetlands of P. aquatica: a) None 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 letter Tukey-Kramer (p<0.05), (±standard deviation).

Supplementary Files

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- AppendixA.pdf