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The weight of the crust: Biomass of crustose lichens in tropical dry forest represents more than half of foliar biomass

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Abstract

In recent years, our ecological knowledge of tropical dry forests has increased dramatically. However, the functional contributions of whole ecosystem components, such as lichens, remain mostly unknown. In these forests, the abundance of epiphyte crustose lichens is responsible for the characteristic white bark on most woody plants, conspicuous during the dry season, but the amount of resources that the lichen component represents remains unexplored. We estimated lichen biomass in a Mexican tropical dry forest using the bark area of trees, the dry mass of lichens per unit area and the percentage of bark covered by lichens, together with previously known tree densities. The lowest 2.5 m of the forests main trunks contained 188 kg/ha of lichen biomass, with lichens covering 85% of the available bark for trees <12 cm DBH and 38% for trees >12 cm. Total epiphytic lichen biomass was 1.34–1.99 Mg/ha. Lichen biomass represented 61% of the foliar biomass in the forest. To our knowledge, this is the first time that a lichen biomass estimate is provided for an ecosystem in which crustose lichens are the dominant lichen growth form. Crustose lichens are typically considered to contribute little to the total lichen biomass and to be difficult to include in ecological analyses. The high lichen biomass in this ecosystem implies a significant ecological role which so far is unexplored. We suggest the crustose lichen component should not be underestimated a priori in ecological studies, especially in ecosystems with abundant lichen cover.

Abstract in Spanish is available with online material.

KEYWORDS

Chamela, ecosystem scale, lichenized fungi, Mexico, seasonally dry tropical forest

1 | INTRODUCTION

Lichen contributions to ecosystem functionality are vast and especially important when lichens are abundant, for example, in temperate forests where their biomass can reach 1–4.4 Mg/ha (Berryman & McCune, 2006; Boucher & Stone, 1992; McCune, 1993). As pioneer organisms and primary producers, lichens support an extensive network of microorganisms, invertebrates, and vertebrates by providing habitat, water, and nutrients (Gerson & Seaward, 1977; Ward & Marcum, 2005). Lichens reincorporate nutrients from plant exuviates (Knops, Nash, Boucher, & Schlesinger, 1991) and directly from the atmosphere, which include nutrients from sources outside the ecosystem (Pike, 1978). In turn, the multiple roles of lichens create a cascading effect in which an increase in their biomass is related to increased abundances of top predators, such as spiders (Gunnarsson, Hake, & Hultengren, 2004) and passerine birds (Pettersson, Ball, Renhorn, Esseen, & Sjöberg, 1995) by increasing availability of prey.

Although most of the ecological knowledge about lichens comes from temperate ecosystems, it is expected that some of the contributions from lichens to ecosystem dynamics are present in tropical areas as well. Among the different tropical ecosystems, the tropical dry forest (TDF) (Holdridge, 1967; Olson et al., 2001) is the most extensive and represents 42% of the forested tropical land in the world (Murphy & Lugo, 1986a, 1995). Studies from TDFs in Mexico (Herrera-Campos et al., 2019; Miranda-González, 2012), Colombia (Lücking et al., 2019), Ecuador (Benítez, Aragón, & Prieto, 2019), and from Brazilian caatingas (Cáceres, Lücking, & Rambold, 2008) showed that lichens in this ecosystem are diverse and abundant; for instance, more than 380 species are reported for Mexican TDFs (Herrera-Campos et al., 2014). The abundance of epiphytic lichens in some TDFs is remarkably evident during the extended dry season, when most plants lose their leaves completely. During the dry season, the forest appearance changes from exuberant green to a characteristic "white-bark forest", which is caused by the microlichens that cover most of the bark of most trees (Miranda-González, 2012).

Even though anecdotally abundant, the amount of resources that the lichen component represents has not been quantified for this ecosystem. Even general information about their ecology or their relevance at the ecosystem scale has been neglected. Nonetheless, in an effort to understand forest structure and function, other researchers have focused on plants and calculated their aboveground biomass and net primary productivity at the ecosystem scale. For TDFs, the aboveground net primary productivity of plants was 4.5 Mg ha^{-1} yr^{-1} in Guánica, Puerto Rico (Clark et al., 2001) and 6.1–8.1 Mg ha^{-1} yr^{-1} in Jalisco, Mexico, of which the leaf component represents 2.4–3.1 Mg ha^{-1} yr^{-1} (Martínez-Yrizar, Maass, Pérez-Jiménez, & Sarukhán, 1996; Martínez-Yrízar & Sarukhán, 1990; Vizcaíno, 1983). For aboveground plant biomass, the estimated mean from 22 TDFs across Mexico, Puerto Rico and Venezuela was 77.4 (±30.5 *SD*) Mg/ha (Jaramillo, Martínez-Yrízar, & Sanford, 2011).

Biomass estimates for epiphytes of TDFs are available for Guánica, Puerto Rico where vascular epiphytes contribute 0.14 Mg/ha of the 44.9 Mg/ha of above ground plant biomass (Murphy & Lugo, 1986b), and for a dry oak forest in the Macanal Reserve in Colombia where vascular epiphytes contribute up to 0.54 Mg/ha (Higuera & Wolf, 2010). Although vascular epiphytes in TDFs do not reach the up to 3.2 Mg/ha reported for wetter tropical oak forests (Wolf, 2005) or the 4.7 Mg/ha reported for cloud forests (Nadkarni, 1984), they still are important contributors to the total plant biomass (Martínez-Yrízar et al., 1992) and increase water availability and food for other organisms (Andrade, 2003; Reyes-García, Griffiths, Rincón, & Huante, 2008; Sáyago et al., 2013). To our knowledge, no biomass estimates are currently available for non-vascular epiphytes of TDFs.

In this study, we aim to provide the first estimate of epiphytic lichen biomass for a TDF. This is a necessary step in order to incorporate lichens into our understanding of ecosystem processes, including their roles as primary producers, nutrient cyclers, and habitat providers, among others. In particular, we: (a) estimated the cover and mass of lichens present in the lowest 2.5 m of trees of different sizes; (b) estimated the total epiphytic lichen biomass per ha of TDF; and (c) discussed the implications of abundant lichen resources at the ecosystem level.

2 | METHODS

2.1 | Study area

The study took place at the Chamela-Cuixmala Biosphere Reserve, located 2 km inland from the Pacific Coast of Mexico (20°N, 105°W). The tropical dry forest component of the Reserve is characterized by a warm sub-humid climate with summer rains (García, 2004) and an extended dry season during which more than 95% of the vascular plants lose their leaves completely. The wet season is marked by the fast greening of the canopy and short, intense rains intercalated with dry periods. The mean annual precipitation is highly variable, ranging from 340 to 1,329 mm, with a mean of 800 mm (1983–2015 period). About 87% of the rain falls between the months of June and October. The area has a strong oceanic influence that maintains mean monthly values of relative humidity above 75% year-round, dew formation for roughly 100 days per year, mean annual temperature of 24.6°C and elevation of 20–180 m a.s.l. (Barradas & Glez-Medellín, 1999; García-Oliva, Camou, & Maass, 2002; Maass et al., 2002, 2018; Sánchez-Azofeifa et al., 2013).

The mature forest consists of trees 4–15 m tall in a dense pattern of up to 4,500 trees per ha (Figure 1a), with more than 50% of the stems having a diameter at breast height (DBH) <5 cm (Lott, Bullock, & Solís-Magallanes, 1987). The Reserve sustains 1,149 species of plants including 229 species of trees. The most representative plant families are Fabaceae and Euphorbiaceae (Lott & Atkinson, 2006). Lichen communities cover most of the bark on most trees and are predominantly crustose species in the families Arthoniaceae, Graphidaceae, and Pyrenulaceae. Macrolichens are few and usually limited to the canopy (Miranda-González, 2012).

The TDF in the Reserve is considered well conserved and is immediately surrounded by a matrix of well conserved, secondary forest, and agricultural land (Flores-Casas & Ortega-Huerta, 2019; Sánchez-Azofeifa, Quesada, Cuevas-Reyes, Castillo, & Sánchez-Montoya, 2009). Nonetheless, the area was severely damaged by hurricane Jova in 2011 and especially by hurricane Patricia in 2015. Most of the damage was concentrated in the forest canopy, which reduced its mean tree height from 6.8 m to only 3.5 m (Parker, Martínez-Yrízar, Álvarez-Yépiz, Maass, & Araiza, 2018).

2.2 | Lichen biomass estimation

Our biomass estimate focused on the lowest 2.5 m of the main trunk of trees, in order to avoid the hurricane effect. Using available

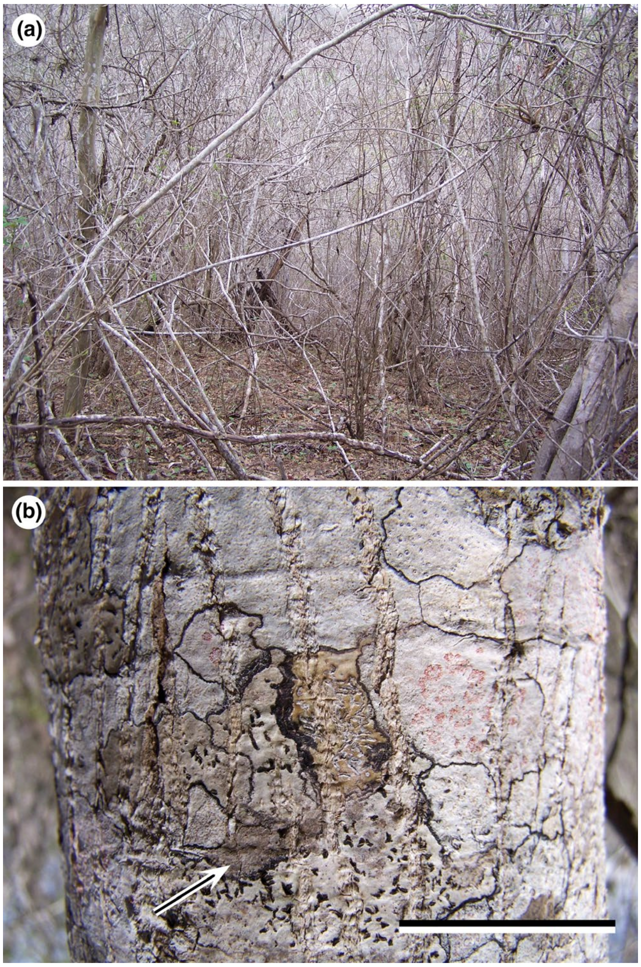

FIGURE 1 View of the study area (a) Typical dense pattern of thin trees just before the start of the rainy season, (b) Close up of the bark of *Helliocarpus pallidus* showing lichen cover close to 100%. Notice the small brown area (arrow) representing the original color of the bark, the rest of the bark is covered by gray to brownish-gray crustose lichens. Scale = 2 cm

studies, we extrapolated the biomass estimate to include the canopy strata. The analysis was based on the variables lichen dry mass per unit area, percent of lichen cover on bark, and surface area of bark, all at three different categories: lowest 2.5 m of individual trees, lowest 2.5 m of all trees per hectare, and all tree strata (whole main trunk and canopy) of all trees per hectare. This last category is equivalent to the typical estimation of biomass per hectare reported in the literature.

2.3 | Lichen dry mass per unit area

Lichen tissue on top of a 2 cm^2 area of bark was carefully scraped from each of 20 previously collected pieces of bark, representing 20 common lichen species in the forest (Miranda-González, 2012). Collection technique for these bark pieces consisted of using a knife to remove, from a living tree, a small and thin piece of the outer bark with the lichen of interest on it. Each cut was made carefully to avoid reaching into the cambium layer of the tree. The 20 lichen samples in this study represent twice the amount of the recommended minimum of 10 destructive samples needed to estimate biomass of vascular epiphytes per functional group (Wolf, Gradstein, & Nadkarni, 2009). To account for different lichen community compositions of TDFs, the samples included a range of lichen thallus thickness from thin and endoperidermic to thick and epiperidermic, individuals from the main trunk of trees and from the canopy, a mix of crustose and microfoliose lichens, and samples from smooth and rugose bark. Loss of material was avoided by continuously dampening each bark sample and scraping it with a single razor blade under the stereoscope. Special care was taken to avoid removing the bark layer which has a different texture and color than the wet lichens. The collected tissue was heated for 24 hr at 60°C and weighed immediately to the nearest 0.1 mg with an Ohaus Analytical Plus balance. All measurements were transformed to g/m^2. Given that lichen cover is a good indicator of lichen biomass (McCune, 1990), we used the mean value of lichen dry mass per unit area as a proxy to transform field data of lichen cover into lichen biomass.

2.4 | Lichen biomass and cover estimations per tree

We measured the bark surface area of 62 randomly selected trees that did not branch below 2.5 m. Trees were haphazardly selected a few meters to the side of a sinuous transect of 2.5 km that followed three trails inside the Reserve. The selected trees were a typical representation of the species present in the Reserve and included different DBH sizes and percentages of lichen cover. This sample size is larger than the recommended 35 trees to estimate biomass of epiphyte vascular plants (Wolf et al., 2009) or the 50 trees recommended to estimate aboveground biomass with allometric models (Ramírez-Ramírez, Ramírez y Avilés, Solorio-Sánchez, Navarro-Alberto, & Dupuy-Rada, 2019). For each tree, we measured the bark surface area on the lowest 2.5 m of the main trunk using the formula for the lateral surface area of a truncated cone with diameter measurements at 0.3 and 2.5 m high. The lichen cover of the measured area was visually estimated as a percentage by dividing the area in at least 8 smaller zones that included the lower and upper parts of the lowest 2.5 m of the main trunk at each cardinal point. The lichen biomass in the lowest 2.5 m of each tree was calculated as the product of the bark surface area in m^2, the lichen cover percentage per tree, and the mean lichen dry mass in g/m^2 described above.

2.5 | Lichen biomass estimation of the lowest 2.5 m of all trees per hectare

We used linear regression to analyze the relationship between DBH and lichen cover on the lowest 2.5 m of the 62 measured trees. After analyzing the residuals, we found a breaking point in the slope around a DBH of 12 cm and therefore divided the regression in two groups: DBH < 12 cm and DBH > 12 cm. Given the approximately constant values within groups, the mean lichen cover on trees per group was used for the analysis of biomass per hectare.

To extrapolate the lichen biomass in the lowest 2.5 m of individual trees to the hectare scale, we used the known tree density per ha in five DBH categories for the Chamela-Cuixmala Biosphere Reserve (Lott et al., 1987). Using linear regression ($R^2 = 0.98$, $p < .001$), we regressed previously published log tree densities against tree size categories to obtain tree densities at each of our new DBH categories, which have a range of 3–32 cm of DBH with increments of 1 cm each (Figure 2a, Table 1), while constraining the distribution to fit the total basal area of the forest and the proportion of trees in each DBH category (Lott et al., 1987). The upper limit of 32 cm DBH accounts for the majority of individuals and species in the study area (Bullock, 2000; Lott et al., 1987).

To calculate the bark surface area in the lowest 2.5 m of all trees per hectare, we multiplied the bark surface area of individual trees in each DBH category by their respective tree densities. Given that our 62 measured trees did not include samples from all the DBH categories (3–32 cm), we estimated the bark surface area for trees in each DBH category using linear regression ($R^2 = 0.99$, $p < .001$) from the 62 measured trees (Figure 2b). The small error in this relationship derives from the rather limited variation in the taper of the truncated cone representing the lower trunk of trees of a given DBH.

Following these calculations, lichen biomass estimations per DBH category were calculated as the product of the bark surface area in the lowest 2.5 m of all trees per hectare at each DBH category, and the previously generated percentage of lichen cover and lichen dry mass per unit area. Then, to estimate lichen biomass in the lowest 2.5 m of the forest, we added the values from all the DBH categories using the following formula:

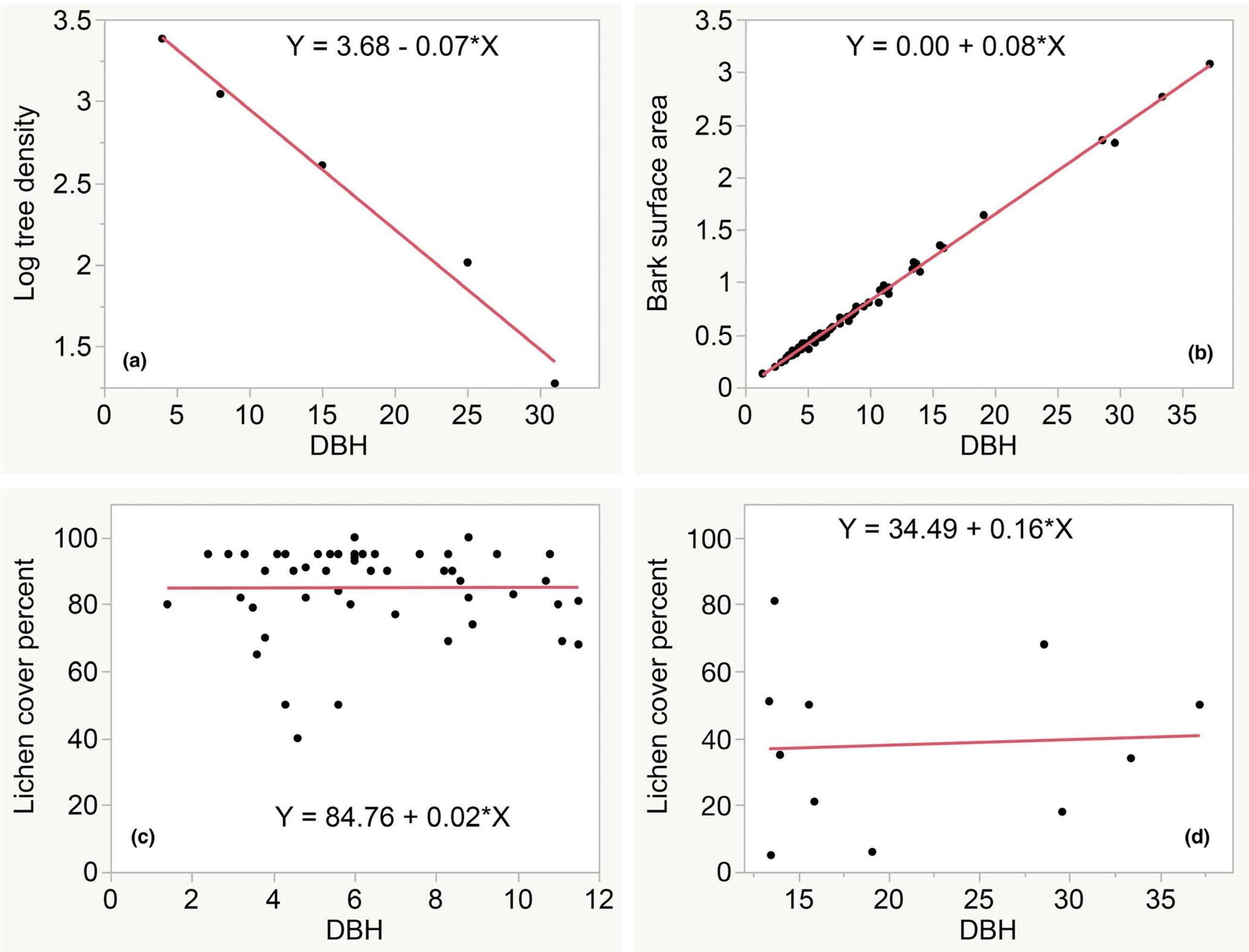

FIGURE 2 Linear regressions in this study. (a) Relationship between the five DBH categories described in Lott et al. (1987) and the number of trees per hectare in a logaritmic scale ($R^2 = 0.98$, $p < .001$), used to interpolate tree densities for each of our new DBH categories, (b) relationship between DBH and the bark surface area in m^2 for the lowest 2.5 m of the main trunk of trees ($R^2 = 0.99$, $p < .001$) used to generate a new bark surface area estimation for trees at each DBH category, (c, d) relationship between DBH and percentage of lichen cover on the lowest 2.5 m of the bark of trees, (c) DBH of 3–11.9 cm ($R^2 < 0.001$, $p = .97$), and (d) DBH of 12–37 cm ($R^2 = 0.003$, $p = .85$). Note a break point in lichen cover for trees larger than 12 cm of DBH

TABLE 1 Estimated tree density and lichen biomass on trees per DBH category. Notice that smaller trees have less lichens, but, given their higher densities, they contribute more to the total biomass per hectare. Estimates for "all tree strata" were based on the 1:5 ratio (trunk:canopy)

		Lowest 2.5 m of the trees		All tree strata
DBH of trees (cm)	Tree density per ha	Lichen dry mass per tree (g)	Lichen biomass contribution (kg/ha)	Lichen biomass contribution (kg/ha)
3	1,055	22	23.7	217.5
4	891	29	26.0	240.3
5	752	37	28.1	259.3
6	338	45	15.3	138.3
7	285	53	15.1	134.9
8	241	61	14.6	129.7
9	203	67	13.7	121.8
10	172	74	12.8	117.5
11	87	83	7.2	66.6
12	73	40	3.0	55.3
13	62	46	2.9	49.7
14	52	48	2.5	44.8
15	44	50	2.2	42.2
16	37	55	2.0	37.2
17	31	61	1.9	34.6
18	26	67	1.8	30.0
19	22	65	1.4	27.0
20	19	69	1.3	24.1
21	22	75	1.6	28.5
22	19	76	1.4	26.5
23	16	80	1.3	22.6
24	13	81	1.1	19.9
25	11	88	1.0	17.1
26	9	96	0.9	15.8
27	8	94	0.8	13.7
28	7	95	0.6	12.0
29	6	102	0.6	10.4
30	5	105	0.5	9.3
31	11	112	1.3	21.9
32	10	109	1.0	19.3
Total	4,525		187.7	1,987.9

$$\text{Lichen biomass} = \frac{\sum_{i=3}^{32} (\text{surface area}_i \times \text{lichen dry mass} \times \text{lichen cover}_i)}{1,000}$$

where Lichen biomass is the dry mass of lichens in kg/ha, surface area is the bark surface area in the lowest 2.5 m of all trees in m^2/ha at each DBH category, lichen dry mass is the estimated dry mass constant in g/m^2, lichen cover is the percentage of bark covered by lichens at each DBH category, *i* is the DBH category ranging from 3 to 32 cm, and 1,000 converts from g to kg.

Each component of the calculation has inherent error. Because the ways that these errors combine are potentially very complex, we simulated the total error by resampling and randomization, rather than a theoretical approach. To calculate a standard deviation for our lichen biomass estimate, we recalculated 1,000 times the lichen biomass at each DBH category by taking random draws from a normal distribution (based on *SD* and mean) using the excel formula "=NORM.INV(RAND(),mean,standard_dev)" for each of the following variables: lichen cover percentage, lichen dry mass per unit area, and basal area of the forest. Random numbers were selected independently for the three variables simulating simultaneous but independent errors. Basal area, was obtained from Lott et al. (1987), Martínez-Yrízar et al. (1992), and Jaramillo, Kauffman, Rentería-Rodríguez, Cummings, and Ellingson (2003). We then calculated the total lichen biomass for each set of simulated values. From those 1,000 totals, we then calculated the mean and standard deviation of the lichen biomass in the lowest 2.5 m of all trees per hectare.

2.6 | Lichen biomass estimation for all tree strata per hectare

To account for the lost canopy due to recent hurricanes, we calculated the pre-hurricane canopy bark surface area using the ratios developed by Whittaker (1966) and Whittaker and Woodwell (1967) in their regressions for temperate deciduous forests. These ratios estimate the bark surface area of canopy branches (hereafter called canopy bark area), based on the bark surface area of the whole main trunks (trunk:canopy), or based on the surface area of the ground (ground:canopy). Although trees in TDFs are smaller than trees in temperate deciduous forest they have higher densities per hectare. To reduce a possible overestimation, we applied the ratio values in the lower range of the temperate deciduous forests regressions. To estimate the bark area of whole trees, we first calculated the whole main trunk bark surface area for trees in each DBH category using the formula of a cylinder of 4 m height with radius at breast height. We then added the canopy bark area from Whittaker and Woodwell (1967) ratios of 1:5 (trunk:canopy), or 1:1.19 (ground:canopy).

To obtain the estimated total lichen biomass per hectare, we multiplied the bark surface area of whole trees by their mean percentage of lichen cover, the mean lichen dry mass per unit area, and the known tree densities per DBH category. Standard deviations for the total lichen biomass per hectare were calculated in the same way as in the estimation for the lowest 2.5 m of the forest.

3 | RESULTS

Most trees in the study area had high cover values of crustose lichens in the lowest 2.5 m of the main trunk (Figure 1b), with few exceptions such as some *Bursera* species that support lichens when young but later lose them from most of their bark. The mean lichen cover was 85% (±13.1 *SD*, $n = 51$) of the available bark area for trees smaller than 12 cm of DBH. Using a regression (Figure 2c), no relationship was detected between DBH and lichen cover percentage for trees with DBH of 1–12 cm ($R^2 < 0.001$, $p = .97$); which represent more than 85% of the trees in a mature forest for the study area (Lott et al., 1987). This lack of relationship resulted from constantly high values of lichen cover percentage on trees throughout the DBH range. Larger trees (DBH of 12–37 cm) were rare and had a mean lichen cover of 38% (±24.5 *SD*, $n = 11$). Similar to the case for smaller trees, a regression (Figure 2d) found no relationship between DBH and lichen cover percentage for trees with DBH of 12–37 cm ($R^2 = 0.003$, $p = .85$).

Lichen dry mass per unit area was estimated as 105 g/m^2 (±59 *SD*, $n = 20$), from a taxonomically diverse set of lichens in ten different families (Table S1). Given that most trees had similarly high values of lichen cover percentage, the lichen biomass per tree was strongly dependent on DBH (Table 1). Due to their higher density, trees with DBH of 3–7 cm had around 50% of the total lichen biomass in the forest (Table 1).

The lichen biomass in the lowest 2.5 m of the forest was estimated as 188 kg/ha (±32 *SD*). We estimated the total lichen biomass per hectare (whole main trunks and canopy) to be 1.99 Mg/ha (±0.28 *SD*) by using the 1:5 ratio (trunk:canopy) and as 1.34 Mg/ha (±0.58 *SD*) by using the 1:1.19 ratio (ground:canopy); both ratios developed by Whittaker and Woodwell (1967).

Lichens in the forest covered a total bark area of 1,755 m^2/ha (± 103 *SD*) in the lowest 2.5 m of the forest. When the canopy was included, lichens covered 18,618 m^2/ha (±880 *SD*) after using the 1:5 ratio (trunk:canopy) or 12,639 m^2/ha (±1,395 *SD*) after using the 1:1.19 ratio (ground:canopy). This values represent a lichen area index (projected area of lichens over a unit of land) of 1.2–1.8.

4 | DISCUSION

4.1 | Lichen biomass estimate per hectare

This is the first time that the lichen biomass of a tropical dry forest has been estimated. Our estimate of 1.34–1.99 Mg/ha of lichen biomass represents the epiphytic lichen component of a mature TDF from the Chamela-Cuixmala Biosphere Reserve in Mexico, before the area was devastated by hurricanes Jova and Patricia.

As expected for all estimates, ours include components that overestimate or underestimate lichen biomass in addition to those explicitly modeled here. The most probable main sources of overestimation are the fraction of recent canopy branches that are bare of lichens and the presence of a few species of trees with few to no lichens. The main sources of underestimation are the following three: (a) Trees smaller than 3 cm of DBH, although abundant and typically well covered with lichens, were not included because their density was unknown; (b) the few foliose and fruticose lichens in the canopy were not measured. Even though they are infrequent, their mass per bark unit area can be higher than that of crustose lichens; and (c) our method only estimates the lichen component that grows outside the bark and not the endoperidermic component present in crustose lichens (Tucker, Matthews, & Chapman, 1991), i.e., fungal hyphae that penetrate the upper layers of the bark. We consider that these two types of over and under estimations compensate each other to some extent and leave a useful and reasonable estimate of lichen biomass for the study area.

Two sources of error require further discussion. Canopy destruction by recent hurricanes prevented us from measuring the lichen cover percentage in the canopy. We extrapolated the values from the main trunks following pre-hurricane observations by the first author that showed high percentage of lichen cover in the canopy (around 95%). This was particularly evident in larger trees that had a depauperate lichen cover in the lower part of the main trunk but an abundant cover in the canopy.

The second source of error was that the ratios to estimate the canopy bark area were developed by Whittaker (1966) and Whittaker and Woodwell (1967) using regressions on a series of temperate deciduous forests. Extrapolations to TDFs are not ideal, however, in all their differences, both ecosystems share many useful metrics. For instance, in our study area, the values of aboveground plant biomass, basal area, and foliage productivity per year are well in the range of the values present in the temperate deciduous forests used by Whittaker & Woodwell in their regressions. We consider that by using the lower range of ratios developed for temperate deciduous forests, we can provide a conservative estimate of lichen biomass for TDFs. The fact that our estimates based on two independent ratios (trunk:canopy and ground:canopy) provided similar results, further supports the viability of our adoption of Whittaker's ratios.

Although allometric equations to calculate tree biomass based on DBH, basal area, and tree height are well studied for TDFs (Cairns, Olmsted, Granados, & Argaez, 2003; Martínez-Yrízar et al., 1992; Urquiza-Haas, Dolman, & Peres, 2007), the surface area component of trees has received little attention in the last decades and no detailed information is available for this ecosystem. However, Sánchez-Azofeifa, Kalácska, Espírito-Santo, Fernandes, and Schnitzer (2009) estimated the wood area index (projected area of wood in the canopy over unit of land) for our study area with a series of hemispherical photographs at different forest successional stages. They estimated that above 1.5 m, the wood area index is around 1.4 when canopy openness is low. Unfortunately, their study did not specify whether those values represent mature forests or early successional stages. If we recalculate our estimations using a main trunk height of 1.5 m and a wood area index of 1.4 above it, then total lichen biomass estimation is 1.35 Mg/ha (±0.69 *SD*). Those values are very similar to our biomass estimate that calculates the surface area of canopy branches based on the area of ground (ground:canopy), further supporting our results.

4.2 | Ecosystem implications of high lichen biomass

In contrast to the 85 Mg/ha of above ground plant biomass for the same forest (Martínez-Yrízar et al., 1992), our lichen biomass estimate represents a small fraction. Nonetheless, the above ground plant biomass is mostly constituted of non-labile woody components, like branches and trunks, that make it harder for nutrients to move to a different trophic level (Nadkarni, 1984). Foliage on the other hand, has similar turnover rates to lichens (Pike, 1978), and together they are the primary photosynthetic components of this ecosystem. We estimated that lichens have an area index of 1.2–1.8 compared to a maximum (wet season) leaf area index of 3.3–3.8 in the same forest (Maass, Vose, Swank, & Martínez-Yrízar, 1995). Although the maximum rate of net photosynthesis at light saturation per unit of area is lower for lichens than for plants (Palmqvist, 2000), the large area covered by lichens, regardless of seasonality, suggest that they are a significant component in the carbon economy of this ecosystem.

In the study area, the mean foliage biomass estimate from three studies was 2.72 Mg/ha (Martínez-Yrizar et al., 1996; Martínez-Yrízar & Sarukhán, 1990; Vizcaíno, 1983). Our results showed that when the whole canopy is included (using the mean total lichen biomass per hectare from the two ratios described previously), epiphytic lichen biomass represents 61% of the foliage biomass of the forest. An important difference between foliage and lichen biomass in these seasonally deciduous forests is, however, that lichen biomass remains relatively constant and available as trophic and habitat resources throughout the year, whereas foliage is almost completely lost and later renewed every year.

Given the abundance of lichens in TDFs, the resources they contain (carbohydrates, proteins, minerals, and water) are substantial at the ecosystem scale. For instance, Nadkarni (1984) showed that in cloud forests, the mineral capital held by epiphytes represents 45% of that contained in foliage. Furthermore, a high abundance of lichens suggests the existence of specialized organisms that depend on them. For example, a high proportion of caterpillars that feed on lichens, bryophytes and/or dead leaves were found in montane rain forests of Ecuador (Bodner, Brehm, & Fiedler, 2015).

The poikilohydric water relations of lichens allows them to obtain water directly from the humidity of the air (Green, Nash, & Lange, 2008) and to remain metabolically active even during the harsh conditions of the dry season, especially in our study area where dew formation is common as well (Barradas & Glez-Medellín, 1999). This continuous stability in resources can benefit animals that live in this environment. Even though many of these animals enter a diapause to avoid the lack of liquid water in the dry months, at least 231 species of arthropods in the study area are known to occur exclusively during the dry season (Pescador-Rubio, Rodríguez-Palafox, & Noguera, 2002; Rodríguez-Palafox & Corona, 2002). Some of these locally abundant arthropods, such as species of mites and insect orders such as Collembola and Psocoptera, are known to depend on lichen resources to survive (García-Aldrete, 2014; Gerson & Seaward, 1977; Krantz & Walter, 2009; Laundon, 1971). Furthermore, some of the resident (Vega Rivera, Campos-Cerda, & Meiners, 2011) and migratory (Arizmendi, Márquez-Valdelamar, & Ornelas, 2002) insectivorous birds that arrive in the study area during the dry season depend on some of those arthropods. Throughout the wet season, lichens could also provide resources to a subset of invertebrates, but currently, there is no information regarding how big this subset could be.

4.3 | Comparison to other ecosystems

Our lichen biomass estimate is particularly unexpected because TDF lichens are mostly crustose and inconspicuous to the untrained eye. As lichens heavily cover most of the trees, it is easy to confuse them with the bark itself and completely miss them (Barajas Morales & Pérez Jiménez, 1990). To our knowledge, this is the first time that a lichen biomass estimate is provided for an ecosystem in which crustose lichens are the dominant lichen growth form. In other ecosystems and studies, crustose lichens are considered to contribute little to the total lichen biomass and to be too difficult to include in analyses (Esseen, Renhorn, & Pettersson, 1996; Knops et al., 1991), but most of the time they are not considered at all. However, the crustose form is the most abundant and diverse among tropical lichens (Lücking, Rivas Plata, Chaves, Umaña, & Sipman, 2009) and represents a high proportion of the around 20,000 species of lichens known in the world (Lücking, Hodkinson, & Leavitt, 2017).

Our total lichen biomass estimate for TDF is in the medium range of the estimated biomass for temperate forests; this seems reasonable given the dominance of crustose lichens and the smaller trees present in TDF. On the other hand, lichen biomass in temperate forests of the Pacific Northwest of USA represent 6%–15% of the leaf biomass in the forest (Boucher & Stone, 1992), while in our site they represent 61%. These high values suggest that similar to moist temperate forests, lichens in TDFs do play significant roles in the ecosystem.

Not surprisingly, most studies of lichen biomass are from temperate areas. We could only find four studies from tropical areas that provided a specific estimate for lichen biomass, none of which included crustose lichens (Table 2). Interestingly, all of them are for tropical montane forests and their lichen biomass estimates are between 0.003 and 0.2 Mg/ha (Forman, 1975; Gómez González, Rodríguez Quiel, Zotz, & Bader, 2017; Pentecost, 1998; Werner, Homeier, Oesker, & Boy, 2012). On the other hand, lichen biomass in subtropical forests in China can reach values up to 1.18 Mg/ha (Li et al., 2017). Note that one challenge in interpreting the literature is that some studies dealing with epiphyte biomass in the tropics have included lichens, but did not provide a separate value for each epiphyte group and instead, combined lichens with bryophytes or vascular plants (Edwards & Grubb, 1977; Gehrig-Downie, Obregón, Bendix, & Gradstein, 2011; Hofstede, Dickinson, & Mark, 2001; Nadkarni, Schaefer, Matelson, & Solano, 2004; Wolf, 1993). Other studies provided lichen biomass values for a single tree (Hofstede, Wolf, & Benzing, 1993) or for individual branches (Freiberg & Freiberg, 2000), but not for the hectare level.

We report the highest recorded value of lichen biomass per hectare for a tropical ecosystem. Even though our study area harbors lichen communities of great diversity and abundance, we believe this comparison is the consequence of few studies, and especially, of ignoring the crustose component of biomass. We predict that TDFs that lack a coastal influence will have lower values of lichen biomass than our study area.

We suggest that the crustose lichen component should not be underestimated a priori in ecological studies, especially in areas with significant cover of crustose lichens. Such habitats include the neotropical lowland rainforests (Komposch & Hafellner, 2002), leaves of tropical humid forests (Lücking, 2008), temperate stands of *Alnus rubra* in the Pacific Northwest of North America (Harrington, 2006) or even coastal forests in Florida, USA (Lücking et al., 2011). From the perspective of TDFs, lichens are abundant and diverse, but work is needed to understand their functional roles, their interactions with other organisms (trophic or otherwise), and their variability at different localities within the same ecosystem. In this study, we provide a first and essential step to include lichens as part of integrative studies of ecosystem functioning and trophic webs for TDFs.

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TABLE 2 Lichen studies of biomass at the hectare level with an emphasis in tropical areas. This study (in bold) was the only one that included the crustose lichens component, which contributes strongly toward being the tropical area with the highest lichen biomass per hectare, so far reported

Source	Vegetation type	Country	Measured trees	Lichen biomass (kg/ha)
Edwards, Soos, and Ritcey (1960)	Temperate forest of *Picea engelmannii*	Canada	11–13	756–3,291
Rhoades (1981)	Temperate forest of *Abies lasiocarpa*	USA	10	1,427–2,079
McCune (1993)	Temperate forest (Pacific Northwest)	USA	42	950–1,870
Forman (1975)	Tropical montane rain forest	Colombia	25	6.9
Pentecost (1998)	Tropical upper montane heath forest	Uganda	4	100
Werner et al. (2012)	Tropical montane forest	Ecuador	63	162–204
Gómez González et al. (2017)	Tropical montane forest	Panama	22	3
This study	**Tropical dry forest**	**Mexico**	**62**	**1,340–1,988**
Chen, Liu, and Wang (2010)	Subtropical montane cloud forest	China	77	1
Li, Liu, Wang, Ma, and Song (2011)	Subtropical primary *Lithocarpus* forest	China	n/a	136
Li et al. (2017)	Subtropical primary dwarf mossy forest	China	14	71
Li et al. (2017)	Subtropical primary *Lithocarpus* forest	China	28	150
Li et al. (2017)	Subtropical middle-aged oak secondary forest	China	14	1,105
Li et al. (2017)	Subtropical *Populus bonatii* secondary forest	China	10	862
Li et al. (2017)	Subtropical *Ternstroemia gymnanthera* secondary forest	China	7	1,180

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CONFLICT OF INTEREST

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

AUTHOR CONTRIBUTION

RMG contributed with conceptualization, formal analysis, investigation, methodology, writing – original draft, and writing – review and editing. BM contributed with: conceptualization, formal analysis, methodology, and writing – review and editing.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.djh9w0vxj (Miranda-González & McCune, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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