

# Little Giants: Lichens in Tropical Dry Forests

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## Abstract

Lichens, complex symbiotic associations between fungi and photosynthetic partners, are widespread in terrestrial ecosystems but remain poorly studied in tropical dry forests (TDFs). This review synthesizes current knowledge on the diversity, ecological roles, adaptive traits, and ethnobotanical uses of lichens in TDFs, with a focus on the Neotropics. As most lichens discussed here are crustose species that inhabit tree bark, this paper also provides a thoughtful review of the origin, distribution, and highly heterogeneous floristic composition of TDFs, which directly shape lichen habitats. It discusses how lichens have evolved to cope with seasonal water stress, emphasizing desiccation tolerance as a key feature of the symbiosis. This review also explores lichen community composition, interactions with host trees, microclimatic conditions, herbivory, and soil crust formation. Despite evidence of high species richness, functional diversity, and ecological importance, lichens in TDFs are largely overlooked in conservation strategies. Moreover, several regions remain vastly understudied, and many species likely remain undescribed. Ethnolichenological practices, though scarce, underscore the cultural and medicinal value of these organisms. Given the high rates of habitat loss and endemism in TDFs, there is a pressing need to expand research on lichen diversity and to investigate the evolutionary origins of their survival strategies. The conservation of these lichens is inseparable from the conservation of TDFs themselves. Understanding how lichens adapt to the harsh and variable conditions of TDFs is essential for integrating them into biodiversity conservation and ecosystem restoration frameworks.



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## 1. Introduction

Lichens are a unique symbiosis between fungi and photosynthetic organisms representing eukaryotic algae or prokaryotic cyanobacteria, traditionally named “blue-green algae”, plus a diverse fungal and bacterial microbiome [1–4]. Lichens represent one of several mutualistic lifestyles that have evolved among fungi, with other important ones being ecto- and endomycorrhizal fungi or fungi living in symbiosis with ants or termites [5–9]. The biology of the lichen symbiosis has recently undergone a shift in its understanding, from a primarily nutritional symbiosis, with the carbohydrates of the photobiont being used for the growth of the fungal component, to a symbiosis fostering desiccation tolerance, i.e., with the fungus using part or most of the carbohydrates to protect cell structures against cellular desiccation [4].

Lichens are found in nearly all terrestrial ecosystems, being absent only from large, continental sandy deserts, such as the Sahara, and permanently ice-covered regions [10–12]. Some lichens are also aquatic in freshwater or live partially submerged in marine coastal environments. At the landscape level, lichens exhibit comparably high diversity both in temperate and tropical regions, but at the level of individual ecosystems, their highest diversity is found in the tropics, especially in tropical rainforests [13]. Tropical dry forests (TDFs) also harbor a considerable diversity, especially of crustose lichens [14–17] but these ecosystems have not been well studied in terms of their lichen biota.

Here, we provide an overview of the existing knowledge on lichens in TDFs, focusing on neotropical regions where these ecosystems are most diverse and cover larger areas than in other tropical regions [18,19]. We emphasize the diversity, biology, and ecology of tropical dry forest lichens, as well as aspects of their potential uses and applications, and conservation issues in this highly threatened ecosystem. Because understanding lichens requires understanding the ecological and floristic context in which they occur, we also provide a review of tropical dry forests themselves.

## 2. Tropical Dry Forests: Definition, Evolution, Current Distribution, Conservation Status, and Similar Biomes

Initially, TDFs were described based on climate characteristics [18,20–23]. More recently, functional traits have also been included to define TDF plant communities [24,25]. Based on various definitions of TDFs by different authors (Table 1), a summary definition could be as follows: forest occurring in tropical and frost-free regions with a seasonal climate, including a dry period of 3 to 7 months with low precipitation (<100 mm per month), annual rainfall between (250–)500 and 2000 mm, a mean annual temperature of  $\geq 25$  °C; at least half of trees being drought deciduous and >10 m tall, an intermediate shade-tolerant tree layer being present, occasional herbaceous plants in the understory (C3 grasses, no C4 grass layer); occurring predominantly on fertile soils with good retention of nutrients (low lixiviation), and forming a litter layer floor.

### 2.1. Evolution and Paleoclimatic Fluctuation of TDFs in the Neotropics

Regarding their origin, the Eocene fossil record of South America shows the occurrence of TDF floristic elements, for example, *Pterocarpus* Jacq. (*Fabaceae* Lindl.), as well as *Bombacoideae* Burnett. (*Malvaceae*) and *Euphorbiaceae* Juss., in central Colombia [34] and deciduous genera such as *Cordia* L. (*Boraginaceae* Juss.), *Hura* L. (*Euphorbiaceae*), and *Dalbergia* L.f. (*Fabaceae*) in Perú [35]. During the Eocene–Oligocene transition, there was a long and slow drop in temperature c. 34 Ma after a period of increased temperatures and CO<sub>2</sub> during the Early Eocene Climate Optimum. In contrast, later in the Neogene, tropical savannas and xerophytic forests developed, probably in areas occupied by tropical rainforest; the reasons behind this event are still debated [36].

More recently, for Southern South America, phytosociological analyses of seasonal woodlands show a pattern that suggests that in the past (18,000–12,000 BP), there was a “dry diagonal” in what is today’s Chaco, Cerrado, and Caatinga regions, coinciding with the contraction of humid forests [37], and with more than 100 species having repeated distribution patterns, suggesting a past widespread existence of TDFs, possibly in the drier and cooler periods of the Pleistocene [38].

**Table 1.** Different definitions of tropical dry forests (TDFs) since 1968.

| Author(s)                                                                             | Annual Average Temperature (°C) | Annual Precipitation (mm) | Dry Season (Months) | Vegetation Type                                                                                                | Soil                     | Altitude (Masl) |
|---------------------------------------------------------------------------------------|---------------------------------|---------------------------|---------------------|----------------------------------------------------------------------------------------------------------------|--------------------------|-----------------|
| Holdridge (1967) [20]                                                                 | 17                              | (400-)700–2000            |                     | >50% of trees are deciduous                                                                                    | -                        | -               |
| Murphy and Lugo (1986) [26], Miles et al. (2006) [18]                                 | frost free                      | (250-)500–2000            | 4 to 7              |                                                                                                                | -                        | -               |
| Menaut et al. (1995) [27], Mayaux et al. (2005) [28], Meir and Pennington (2011) [23] | >17                             | 250–2000                  | at least 3          | Upper stratum trees deciduous, no dominant species                                                             | -                        | -               |
| FAO (2012) [29]                                                                       |                                 | 500–1500                  | 5 to 8              |                                                                                                                | -                        | -               |
| Sánchez-Azofeifa et al. (2005) [22]                                                   | 25                              | 700–2000                  | at least 3          | At least 50% of trees are drought deciduous                                                                    | -                        | -               |
| Ratnam et al. (2011) [30], Charles-Dominique et al. (2015) [31]                       |                                 |                           |                     | Woody, >10 m tall vegetation, intermediate shade-tolerant tree layer and grass, occasional patches of C3 grass | litter layer             | -               |
| Gentry (1995) [21]                                                                    |                                 | >1600                     | 5 to 6              | -                                                                                                              | -                        | -               |
| Trejo and Dirzo (2000) [32]                                                           | 22–26                           | 400–1300                  | 6 to 8              | -                                                                                                              | -                        | up to 2000      |
| González-M (2018) [33]                                                                | 26                              |                           | 3 to 5              | -                                                                                                              | fertile, low lixiviation | up to 1200      |

Because of the different definitions of TDFs (i.e., seasonally, deciduous, semideciduous, caducifolious, mesophilous, and broadleaf dry forests), including their vernacular regional names (“caatinga”, “cuabal”), comparative analyses are complex, including floristics, ecology, and distribution.

## 2.2. Current Distribution and Patterns of Plant Diversity

In the early 1980s, almost half of all tropical forests were considered dry forests [39]. More recently, Miles et al. [18] estimated a total area of 105 billion ha of TDFs across the tropics, distributed as follows: 54% in South America, 12.5% in North and Central America, 13.1% in Africa, 16.4% in Eurasia, and 3.8% in Australasia and insular Southeast Asia. According to the Intergovernmental Panel on Climate Change (IPCC 2023), there are 784 million ha of TDFs left, i.e., 0.7% of the original estimated cover [40]. The current distribution of TDFs, made from the data set of the Terrestrial Ecoregions of the World, is presented in Figure 1. This data set was based on Holdridge’s definition of TDFs [41]. Latin American TDFs experienced a 12% reduction between 1980 and 2000 [18]. Given the prevalence of TDFs in the Neotropics, we will focus on this region in our review.

In the present day, these forests remain as scattered fragments from México to Costa Rica (along the Pacific coast and Yucatán Peninsula), the Caribbean, Northern South América (Caribbean region of Colombia and Venezuela), coastal Ecuador and Northern Perú, the inter-Andean dry valleys in Colombia, Ecuador, Perú and Bolivia, Central Brazil, and in fertile soil areas in the Cerrado biome, which is their southern distribution in the limited temperate zone [19,42–45].

As mentioned before, there are broad climatic parameters to define TDFs (length of dry season or precipitation), resulting on a variety of plant physiognomy, for example, taller forests if there is relatively more moisture, or bark totally covered by mostly white, crustose lichens, which is presumably the reason why the Tupi people gave the name Caatinga (“white forest”) to the Brazilian northeastern TDF [46,47]. Nonetheless, because of their ecological, structural, and floristic similarities, neotropical seasonally dry tropical forests should be considered together in biogeographic analyses, although in the present,

they occur in widely disjunct areas [38]. Additionally, TDFs can be found mixed or within other biomes, such as the Brazilian Cerrado, the Chacom or the savannas of the Orinoco in Colombia and Venezuela. As mentioned, the neotropical dry forests in South America have a plethora of names, from “caatinga” in Northeast Brazil, to “bosque tropical caducifolio” or “selva baja caducifolia” in Mexico, and “cuabal” in Cuba, which in part hinders comparisons [22]. The variety of names used for these forests gives the impression of different origins and dynamics, in addition to their high beta diversity, making scientific discussions about them difficult. However, in the past decades, new or renovated efforts to study dry ecosystems have produced a clearer image this important biome.

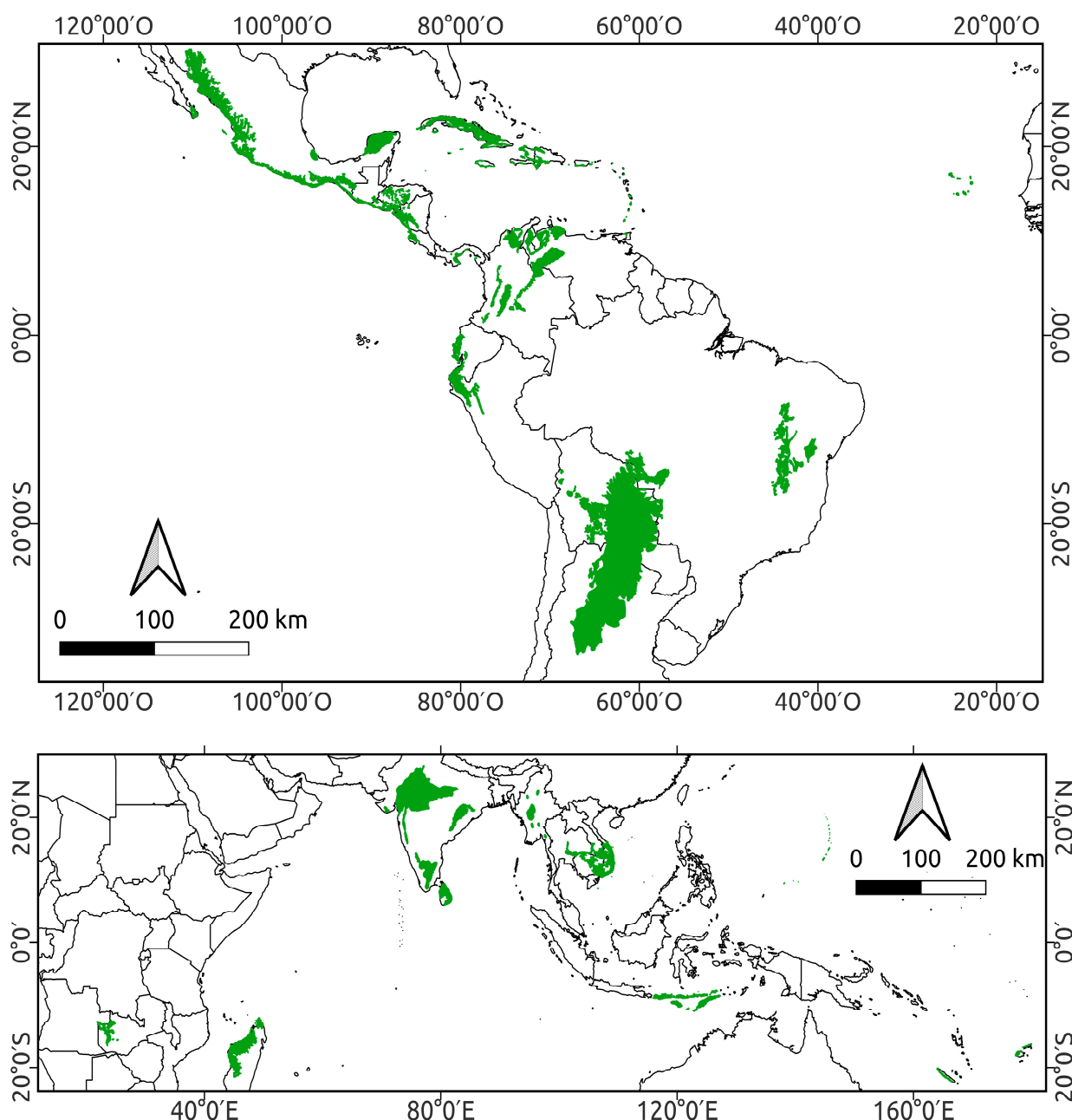


**Figure 1.** Current distribution of TDFs according to the Ecoregions map of the World Wildlife Foundation: America (**above**), Africa, and Asia (**below**).

Banda et al. [19] looked at patterns of floristic diversity in Neotropical dry forests (based on 835 inventories and 4660 species of woody plants) from Mexico and the Caribbean to Argentina and Paraguay. Using clustering analysis, twelve floristic groups were

identified (Mexico, Antilles, Central America–Northern South America, the Northern inter-Andean valleys, the Central inter-Andean valleys, Central Andes coast, Tarapoto–Quillabamba, Apurimac–Mantaro, Piedmont, Misiones, Central Brazil, and Caatinga). Interestingly, the two groups with higher floristic diversity are not at the equator but are in the opposite direction: México and Caatinga, according to the “reverse latitudinal gradient” described by Gentry [21]. Additionally, Mexico stands out having a very similar number of species to Caatinga (1072 vs. 1112) but in one-third of the land area. The methodology used by DRYFLOR et al. [19] allows a proxy for endemism, showing the highest percentages in Mexico (73%) and the Caribbean (65%), and the lowest in Central Brazil, partially due to the high number of species shared with other floristic groups.

Looking at a single country, a comprehensive study of 537 TDF fragments in Colombia [33] explored the environmental conditions and floristic composition of six regions (Caribbean, Cauca Valley, Magdalena Valley, North Andean, Orinoquia, and Patía), concluding that 13% of the variation in plant species composition is explained by environmental and soil factors. Colombia’s TDFs cannot be defined based only on total annual precipitation and annual mean temperature, and there are three distinctive separate groups (the Caribbean, the inter-Andean valleys, and Orinoquia), with a high species turnover among and within regions, and high levels of regional endemism.

### 2.3. Conservation of TDFs

As previously noted, most remnants of TDFs are fragmented patches, and a tiny proportion of them has some conservation status at the national level (Colombia, 5%, Costa Rica, 0.4%, México, 0.18% [43,48]). In Colombia, the TDFs in the Caribbean region are one of the ten most threatened, categorized in critical condition and near collapse [49].

Tropical dry forests can thus be considered neglected. Comparatively speaking, TDFs have received less attention than tropical humid forests, including conservation policies at the international level [50,51] and, given the high fragmentation of remaining forests, some conservation policies do not apply [52]. As pointed out by Rodríguez [53], a hectare of pastures has a higher economic value than a hectare of forest, an economic phenomenon that comes from colonial times.

In contrast, TDF ecosystems have been heavily used by communities around the world (about one third of the total human population lives in these ecosystems), benefiting from its fuel, timber, medicines, and food (corn, banana, beans, yams, and fodder), precisely because TDF soils are more fertile and their climate more benevolent to humans [54]. The main drivers of biodiversity loss in TDFs are agriculture, cattle, and infrastructure [33].

TDFs exhibit lower alpha diversity when compared with other ecosystems, but they are remarkable for their beta diversity. For example, in Colombia, when comparing the flora composition of each of their fragments, the average number of repeated species is 27 out of 100 [33]. This is very important because conservation efforts need to go beyond the protection of a few fragments and need to aim to preserve most of its heterogeneity, especially due to a high amount of endemism. For instance, Colombian TDFs have at least 2600 species of plants, 230 birds, 60 mammals, and 82 amphibians [48].

Some TDFs have been identified within biodiversity hotspots (areas with more than 1500 endemic plants that have lost 70% or more of their original known area). This has been considered an important concept since 43% of mammals, reptiles, and birds, as well as more than half of plant endemic species, occur within the 36 declared hotspots, which in turn represent 2.5% of Earth’s land surface. This concept was born with the objective of conserving as many species as possible at the least cost [55]. Within those current 36 biodiversity hotspots, Gillespie et al. [56] examined the least protected forests in biodiversity hotspots, combining the existence of protected areas within the hotspots and forest

cover. Figure 2 shows 10 TDFs that were classified in the quartile with the smallest forest cover. Surprisingly, two of them, the Cauca Valley and the Patía Valley in Colombia, do not have a protected area.

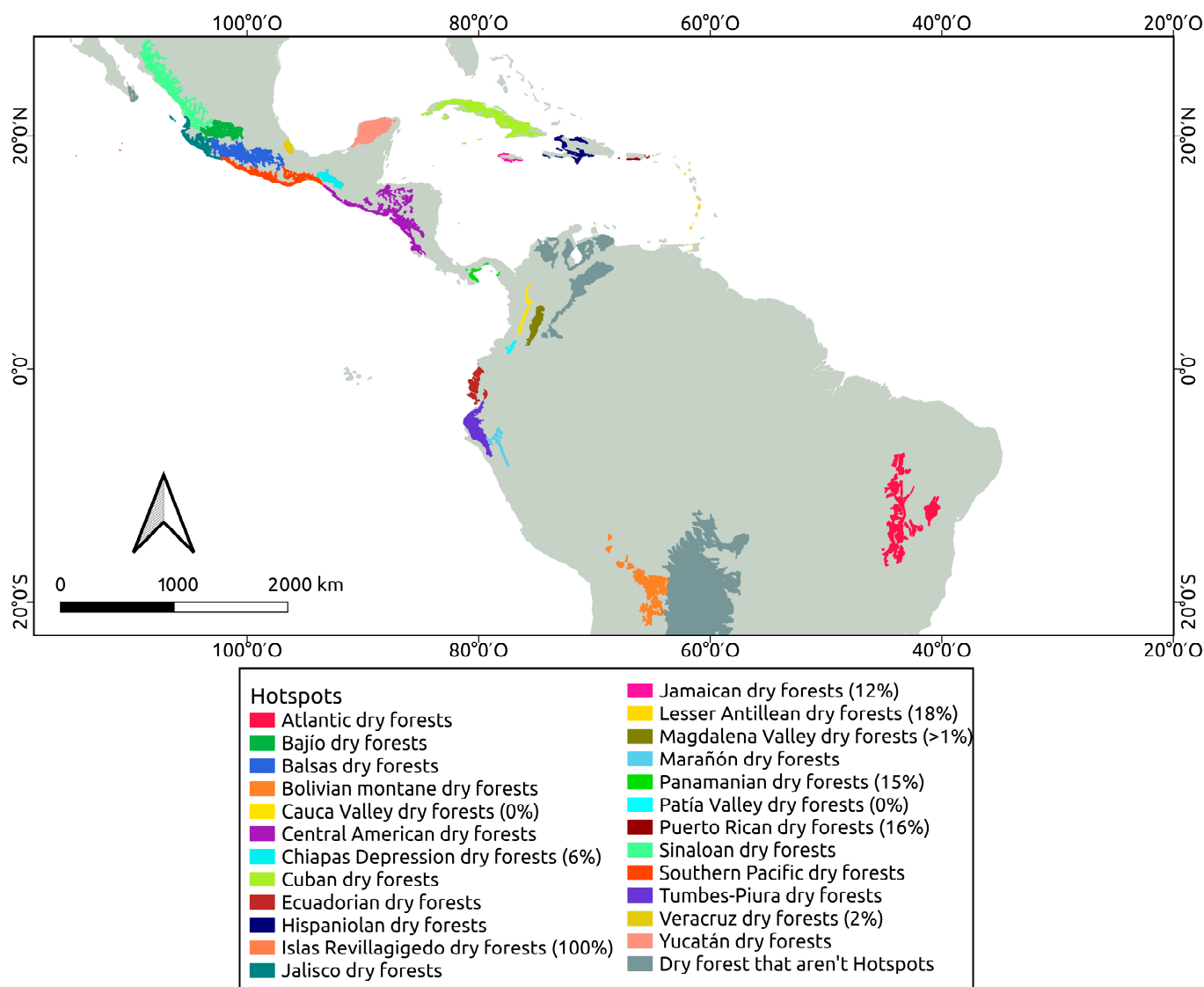


**Figure 2.** Rare forest ecoregions within biodiversity hotspots based on the first quartile of forest cover in protected areas. Modified from Gillespie et al. [56]. TDFs within the rarest hotspots and their percentage of protected areas: Jamaican (12%), Lesser Antilles (18%), Puerto Rican (16%), Chiapas (6%), I. Rivillagigedo (100%), Panamanian (15%), Veracruz (2%), Cauca (0%), Magdalena (<1%), and Patía (0%).

Although the biodiversity hotspot concept has helped in prioritizing and even channeling financial aid to ecosystem conservation (until 2003, USD 70 million were invested [55]); other conservation strategies need to be placed and focused, for example, on high endemism of other organisms (like lichens and insects, among others) or ecosystem services.

#### 2.4. Delimitation Towards Other Seasonally Dry Areas/Other Tropical Dry Ecosystems

Dry forests and savannas occur in regions with often similar climatic conditions, but savannas are generally not classified as dry forests in a strict sense. In general, soil parameters determine the formation of savannas, in particular the nutrient content, acidity, and the concentration of heavy metals. Additionally, fire also plays a role in the formation of these ecosystems [54]. A good example is the Brazilian Caatinga vs. the Brazilian

Cerrado: the first is a dry forest ecosystem and the second is a savanna ecosystem, with its trees exhibiting a very different physiognomy, including, for example, very thick bark and often small, leathery leaves. These features then also influence the composition of lichen communities.

The Chaco semi-arid forests and woodlands of the plains of N Argentina, W Paraguay, SE Bolivia, and W Mato Grosso do Sul in Brazil experience regular annual frosts and are considered a subtropical extension of temperate vegetation formations [54], although they have been included in floristic studies of TDFs, taking into account their high canopy and density of trees [21]; however, considering their soil composition (saline, alkaline) and extreme temperatures (winter frosts to 49 °C in summer), their vegetation is not floristically or ecologically related to TDFs but more with Monte and Andean prepuna formations [57]. This confusion is evident in vernacular names, where genuine dry forests in Mato Grosso do Sul, which do not experience frosts, are also called “chaco” [58].

The Cerrado biome is located in Central Brazil and has an extension of approx. 2 million square kilometers. *Sensu lato* is a savanna woodland subjected to natural fires, on well-drained, low calcium and magnesium soils along gradients of fertility, giving rise to different vegetation types. The flora is characterized by species of the families *Fabaceae*, *Malpighiaceae* Juss., *Myrtaceae* Juss., *Melastomataceae* Juss., and *Rubiaceae* Juss. [57] which are adapted to fire (corky bark, and xylopodia), making this biome floristically distinct. However, in areas with fertile soils, dry forests occur [59].

### 3. Lichens: Definition, Diversity, and Biology

As mentioned, lichens are one of three dominant forms of symbioses between fungi and photosynthetic organisms, the other two being ectomycorrhiza, mostly found in the Basidiomycota Whittaker ex R.T. Moore and a few Ascomycota Caval.-Sm. forming mushrooms, and arbuscular endomycorrhiza, characteristic of the Glomeromycota C. Walker & A. Schüßler [5–9]. Most lichen fungi (99%) are found in the Ascomycota, and only a few are in the Basidiomycota. To date, about 20,000 species of fungi are known to form lichens; three-quarters of them are concentrated in a single class of Ascomycota, the Lecanoromycetes O.E. Erikss. & Winka [60]. The origin of lichen symbiosis is not known, but evidence points towards multiple and independent lichenization events, including at the base of Lecanoromycetes, several independent cases within Eurotiomycetes O.E. Erikss. & Winka, Sordariomycetes O.E. Erikss. & Winka, Dothideomycetes O.E. Erikss. & Winka, Arthoniomycetes O.E. Erikss. & Winka, and Lichinomycetes Reeb, Lutzoni & Cl. Roux in Ascomycota, as well as three independent cases within Agaricomycetes Doweld in Basidiomycota [61,62]. Interestingly, important fungi such as the mold genera *Aspergillus* P. Micheli ex Haller and *Penicillium* Link belong to Eurotiomycetes, although the class does not derive from a lichenized ancestor; it not only includes lichens, but it is sister to Lecanoromycetes, an important viewpoint when assessing the biochemical potential of lichens [62–64], given that both classes share phylogenetically related Polyketide synthase (PKS) genes involved in the production of secondary compounds [65].

In tropical climates with high temperatures, the dominant growth forms include crustose and squamulose lichens, as these have advantages in covering larger areas with low biomass, hence balancing either water stress or low light conditions [66].

Lichen fungi differ from other fungi in three key aspects: they form a highly elaborate, three-dimensional architecture distinct from undifferentiated fungal mycelia, they are desiccation-tolerant at the cellular level, and they grow extremely slowly [4,66–68]. Three-dimensional architecture and desiccation tolerance allow lichen fungi to occupy habitats that other fungi cannot colonize and to form superficial, permanent vegetative structures. The slow growth of lichens compared to other fungi or plants—lichens on

average grow in a year what other fungi and plants may achieve in a day—has puzzled researchers, but insight into the physiology of the metabolite transfer between algae or cyanobacteria and fungi and the mechanisms of desiccation tolerance has shed light on this phenomenon. To be able to desiccate at the cellular level without damage to the cellular apparatus, enzymes and other proteins and DNA are protected by a layer of sugar alcohols (polyols), in a process called vitrification [69]. Upon rehydration, cell metabolism starts almost immediately, but the protective polyols are washed out. Given that these polyols come from the photobiont as carbon-based currency, these carbohydrates are no longer available for growth. Consequently, the more frequently and the longer a lichen gets desiccated, and then rehydrated, fewer carbohydrates are available for growth, and the slower the lichen growth. Indeed, macrolichens with larger biomass and faster growth rates are found in environments with reduced water stress [4]. Desiccation tolerance of lichens is thus of particular interest in tropical dry forests, where water stress, especially during the dry season, may be severe.

## 4. The Tropical Dry Forest as a Habitat for Lichens

### 4.1. Ecophysiological Challenges

As mentioned, the lichen symbiosis is no longer considered a purely nutritional symbiosis but rather a symbiosis that fosters desiccation tolerance of the involved fungi. Tropical dry forests are of particular interest in this respect as they provide very specific conditions for the lichens occurring there. Similar to what happens in other ecosystems [70], lichens in TDFs undergo a daily wetting and drying cycle; however, there are marked physiological responses that differ between the rainy and dry seasons. During the rainy season, the climatic conditions are comparable to those of a rain forest, that is, a closed luxurious canopy that limits the amount of light in the understory, high relative humidity, and high temperature, but instead of frequent rain days, TDFs typically have rains that are sporadic, intense, short, and intercalated with dry periods of several days [71]. In theory, these conditions allow the lichens to be metabolically active for long periods of time, but currently, the ecophysiological responses of lichens in TDFs have not been studied. Longer metabolically active periods could provide more opportunities to photosynthesize, but also higher respiration rates during warm and humid nights, which translate to negative growth if the carbon lost to respiration exceeds the carbon gained by photosynthesis [66]. The negative rate between respiration and photosynthesis could be further exacerbated by the closed canopy, which limits light during the day, and by the canicular periods, which are the warm and dry periods during the rainy season. Due to these climatic conditions and the rate of respiration and photosynthesis, the dominant growth forms of lichens in TDFs are crustose and microfoliose.

During the long, dry season, lichens can be metabolically active as well and obtain water from the air humidity or the morning dew [17]. As mentioned before, TDFs are highly variable, and those that are closer to the coast tend to have higher levels of relative humidity throughout the year. For instance, the Chamela forest in the Pacific coast of Mexico has a strong oceanic influence that results in mean monthly values of relative humidity above 75% year-round [71], with dew formation for around 100 days per year [72]. As a result, the Chamela forest currently has the highest recorded value of lichen biomass per hectare for a tropical ecosystem, even though most of its lichens are crustose forms [17]. Most TDFs have a strong oceanic influence (Figure 1), but inland areas of this ecosystem are expected to have lower relative humidity in the dry season. In this situation, lichens could undergo longer periods without the necessary conditions to be metabolically active, and consequently, their biomass per hectare of forest will be much lower.

#### 4.2. Lichens in Soils: Biocrusts

Lichens are an important part of biological soil crusts (biocrusts), especially in dry climates. Biocrusts provide important ecosystem services (i.e., increase soil organic carbon, modify nutrient dynamics and soil respiration, counterbalance disturbance-induced soil degradation, promote forest regeneration, etc.) [73]. Biocrusts are composed of cyanobacteria, mosses, lichens, bacteria, and microfungi. The biocrust composition in TDFs has been largely neglected, but studies from the Brazilian Caatinga demonstrate their importance. In one study [74], the Caatinga biocrust was composed of more than 50 taxa, seven of which were lichens: *Buellia* sp. De Not., *Cladonia foliacea* (Huds.) Willd., *C. verticillaris* (Raddi) Mont., *Heppia conchiloba* Zahlbr., *Lecidia* sp. Ach., *Peltula michoacanensis* (B. de Lesd.) Wetmore, and *Bibbya* cf. *albomarginata* (H. Kilius & Gotth. Schneid.) Kistenich, Timdal, Bendiksby & S. Ekman. The authors discussed that the area studied was degraded by goats and other human activities that prevent a higher diversity of lichens (present on biocrusts that are less disturbed, but there is also a constraint to lichen growth given by rainfall, sandy soils, or the presence of vascular plants).

The genus and species *Sulzbacheromyces caatingae* (Sulzbacher & Lücking) Hodkinson & Lücking [75,76] were described from the Brazilian Caatinga and represent one of the few species in the completely lichenized order Lepidostromatales Hodkinson & Lücking, a rare case in Basidiomycota. Although the species is now known from other ecosystems [77] and the genus currently has a neotropical distribution, the studies of the Caatinga biocrust were pivotal to understanding the evolution of the order Lepidostromatales. Clearly, the biocrust component of TDFs is in great need to be included in future studies and has great potential to facilitate new discoveries.

#### 4.3. Lichen Biodiversity in TDFs

Compared to tropical rainforest lichens, tropical dry forests are generally understudied in terms of their lichen communities. Compared to the 12 major regions of neotropical dry forests [19], only a few have been studied in more detail regarding their lichens. At the forefront is the Caatinga in northeastern Brazil, with a number of inventories from different sites and including analysis on macroecology, phylogenetic metacommunity structure, and conservation [14,77,78]. Central American and Northern South American dry forests (Nicaragua through Venezuela and Ecuador) have also been the subject of several local inventories [16,79–82]. Recently, Mexican dry forests have been the subject of model studies in the Chamela region and in Central Mexico, including taxonomic and ecological aspects, as well as functional traits [17,83–86]. However, the remaining nine regions remain understudied, including Central Brazil, Misiones, and the Piedmont in Bolivia and Argentina, but also the Central Andes Coast and Interandine Valleys and the Antilles [19]. Some studies have also been conducted on paleotropical TDF lichen communities [87].

In several studies predicting the global diversity of important components of tropical lichen communities, such as *Graphidaceae* Dumort., *Pyrenulaceae* Rabenh., and *Trypetheliaceae* Eschw. [88–90], the authors showed that most of the species occur in wet tropical forests, but certain elements are characteristic of TDFs, often lacking studies. Thus, *Trypetheliaceae* is the second largest family of corticolous lichens after *Graphidaceae*, and there is an estimate of about 800 total species of this family, of which only 421 have been described [88], and many of which are characteristic of TDFs [91].

Trees in dry forests generally contain high lichen cover and diversity, dominated by crustose growth forms and generally displaying white or bright colors, which are related to sunlight exposure [92]. For example, in Puerto Rico, TDFs are the lowland ecosystems with the highest lichen diversity [93]. It is rather common to find trees almost completely

covered with lichens in dry forests; Miranda-González and McCune [17] calculated that crustose lichen biomass represents 61% of the foliar biomass, that is, 1340–1988 kg/ha, demonstrating the importance of these organisms in the ecological relationships of dry forests. The name of the Brazilian Caatinga (“white forest”) is supposedly derived from the white bark of the trees visible during the dry season, caused by a cover of white, crustose lichens [46].

Lichen diversity in TDFs corresponds with the high heterogeneity displayed by its vegetation. In the same sense, knowledge about lichens in this ecosystem is also lower than that about tropical humid forests, meaning that there is a deep need to conduct basic research to document their diversity and ecological importance. For example, one study in Atlántico—a small department in Colombia’s Caribbean region—increased the number of lichens known from Atlántico from 84 to 135, including 19 possible new species [80].

#### 4.4. Lichen Communities in TDFs Compared to Other Tropical Habitats

Lichen communities in tropical dry forests have a characteristic composition in terms of the predominant taxa, differentiating them from other tropical ecosystems, such as lowland and montane rain forest, but also edaphic vegetation types, such as the Brazilian Cerrado. While multiple inventories of lichens in these different habitats across the entire Neotropics reveal these patterns, only a few studies have used quantitative approaches to evidence the level of composition differentiation between these habitat types in terms of their lichen communities. A study in Brazil using multivariate community analysis found a clear differentiation between the Caatinga dry forest, the Atlantic rain forest, and the so-called Brejos de Altitude—isolated montane rain forest remnants emerging from within the Caatinga region [14]. According to that study, indicator taxa for the Caatinga include *Caliciaceae* Chevall. (e.g., *Baculifera* Marbach & Kalb, *Dirinaria* (Tuck.) Clem.), species of *Pertusaria* DC. with xantheses, the red-fruited *Haematomma persoonii* (Fée) A. Massal., and *Ramboldia haematites* (Fée) Kalb, Lumbsch & Elix, as well as *Neoprotoparmelia multifera* (Nyl.) Garima Singh, Lumbsch & I. Schmitt. The latter was recently identified as a species complex, and the species in its strict sense appears to be restricted to dry valleys in the Colombian Andes [94].

Two studies using the approach of phylogenetic community structure, one in Mexico, focusing on *Parmeliaceae* Bercht. & J. Presl [95], and one in Brazil, including all lichens [78], came to remarkably similar results when comparing tropical dry and rain forests. In both regions, lichen communities in tropical dry forests exhibited phylogenetic clustering with regard to the Net Relatedness Index (NRI), i.e., a filtering effect resulting in predominance of certain lineages. In contrast, the tropical rain forest showed phylogenetic overdispersion, meaning that the phylogenetic diversity was higher than expected by chance. In the case of Brazil, comparing the Caatinga with the Amazon and the Atlantic rain forests, this effect was particularly strong. Notably, in both cases, the Nearest Taxon Index (NTI) behaved similarly in both the dry forest and the rain forest areas, indicating slight (over-)dispersion, meaning that the most closely related taxon was not necessarily predominant in the same habitat. For Mexican *Parmeliaceae*, the dominant genera in tropical dry forests were revealed to be *Parmotrema* A. Massal. and *Xanthoparmelia* (Vain.) Hale. In the case of Brazil, the Caatinga was overproportionally rich in Arthoniomycetes at the class level, with Arthoniales Henssen ex D. Hawksw. & O.E. Erikss., Pyrenulales Fink ex D. Hawksw. & O.E. Erikss., and Caliciales Bessey at order level, and *Arthoniaceae* Rchb., *Pyrenulaceae*, *Graphidaceae*, and *Caliciaceae* at family level. This agrees with findings of other lichens in Mexico [84] and with the multivariate community studies previously conducted in Brazil [14].

A study compared the community composition of lichens between Caatinga and Brejos de Altitude (forest enclaves in the semiarid NE of Brazil) [96], finding that lichen

communities are clearly different and that lichens can be used as indicators of ecosystems in dry forests. Similarly, a preliminary study in Mexico [97] found a marked differentiation in the species composition of the genus *Graphis* Adans. across three tropical ecosystems: tropical dry forests, tropical rain forests, and cloud forests. Lichen diversity is known to increase with altitude and its associated climatic gradient in many ecosystems [98], but to our knowledge, there are no studies regarding this for TDFs. In mountain ranges, tree composition is strongly related to lichen communities [99]. Is this “prediction power” a result of the amount of research conducted in humid forests?

One climate change study on forest plots in Africa found that one of the effects of drought on dry forests is a stronger decline in phylogenetic diversity, explained by the influence of water stress deficiency, but also nutrient content, acidity, and texture of soil [100].

#### 4.5. Regional Differences of Lichen Communities in Neotropical TDFs

Certain lichens have been reported as characteristic of tropical dry forest across a broad geographic range, at least throughout the Neotropics, such as *Helminthocarpon leprevostii* Fée or *Pyrenula ochraceoflava* (Nyl.) Willey. However, molecular studies have shown that such presumably widespread species often represent species complexes, with a strong biogeographic signal, as shown in *P. ochraceoflava* s. lat. [101]. This is not surprising given that tropical dry forests vary markedly in their abiotic parameters, tree composition, physiognomy, and evolutionary history [19]. It is therefore expected that lichen communities will vary in a similar way, at least to some extent. For instance, the presumably widespread *Neoprotoparmelia multifera*, a characteristic element of tropical dry forests, originally described from Colombia, was demonstrated to represent multiple species [94]. Recent inventories of areas of tropical dry forest in Mexico, Colombia, and Brazil have revealed many species new to science and apparently only occurring in these regions, especially in the Arthoniales and Graphidales Bessey [16,80,84,102], but also in better-known groups of macrolichens [101,103], suggesting an undescribed diversity across different taxonomic groups. However, to date, no quantitative analysis has been conducted on the differentiation of lichen metacommunities in Neotropical dry forests.

Even within a given region of tropical dry forest, particularly those defined by Banda et al. [19], there appears to be considerable heterogeneity in lichen community composition at the landscape level, i.e., between different sites. For instance, a comparison of four TDF remnants within the department of Atlántico in the Colombian Caribbean revealed high between-site beta diversity values, since only 6.7% of 135 species were found on all four forests, and one of them had 38 unique species [80]. The reason for such variation is not immediately clear. It could be related to the relative location of the forest with respect to the coastline (salinity gradient), the variation in tree composition between these sites, or to the individual disturbance history of each site, or all of the above, as the latter may also affect tree species composition and demography. In the Atlantic rain forest of Brazil, which exhibits a similar level of reduction and fragmentation as in the tropical dry forest, it has been shown that individual remnants often harbor unique lichens, attributed to fragmentation and extinction of populations elsewhere [104], and similar patterns are to be expected for dry forest fragments. Preliminary data from Mexico [105] also showed that, regardless of the distance between regions, conserved areas of TDFs have a much larger beta diversity than the one found between secondary forests.

#### 4.6. Phorophyte and Microclimatic Differentiation

Zooming in further, within a given site of tropical dry forest, the lichen community structure is expected to depend largely on phorophyte features and microclimatic condi-

tions, as was found for other tropical ecosystems, such as tropical rain forests and montane forests [106,107]. Few such studies have been conducted in tropical dry forests, however. In a study in Ecuador [15], the highest richness of lichens (Graphidaceae, *Stirtonia* A.L. Sm., *Syncesia* Taylor) was found on trees with a higher diameter at breast height (DBH) and smooth bark (*Bursera graveolens* Triana & Planch., *Cochlospermum vitifolium* (Willd.) Spreng. and *Cynophalla mollis* J.Presl), although there were some genera (*Bathelium* Ach., *Caloplaca* Th. Fr., *Cresponea* Egea & Torrente, *Opegrapha* Ach., *Physcia* (Schreb.) Michx., and *Trypethelium* Spreng.) growing on trees with rough bark (*Cynophalla mollis* and *Tabebuia billbergii*). Interestingly, studies in Mexico found a decrease in both species richness and lichen abundance on trees with a higher DBH [17] and no conclusive correlation between lichen communities and phorophyte species [97,105]. These findings remark the importance of the microclimatic conditions offered by TDFs, which, at the same time, have a high beta diversity.

In a semi-deciduous forest in Cuba, the epiphytic lichen communities at the edge and in the interior of the semi-deciduous forest of Monte Barranca differ markedly in their composition [108]. The edge of the forest is more diverse in corticolous lichens and included species such as *Glyphis cicatricose* Ach., *Coniocarpon cinnabarinum* DC., *Physcia solediosa* (Vain.) Lynge, *Trypethelium eluteriae* Spreng., *Chrysothrix candelaris* (L.) J.R. Laundon, *Graphis leptocarpa* Fée, and *Bacidia circumspecta* (Norrl. & Nyl.) Malme, all of which are considered tolerant of high light [92]. *Porina distans* Vězda & Vivant is a dominant species in both the interior and along the edge of this forest, suggesting that this species may have a broad physiological tolerance, unlike typical *Porinaceae* Rchb., a family considered to be more characteristic of undisturbed and old-growth secondary forests [109]. These differences are best explained by changes in light conditions, and the pattern is congruent with that observed in different tropical and boreal forests [110–112].

A particular feature of tropical dry forests is the marked difference between the wet and the dry season. During the wet season, the closed canopy of the fully leafed trees renders the forest quite similar to a tropical rain forest, especially in the shaded understory. During the dry season, however, the understory is fully exposed, with increased water stress at the ecosystem level [83]. Thus, the microhabitat differences that occur in the wet season between the shaded understory, the semi-exposed light gaps, and the exposed canopy branches may disappear entirely in the dry season, and it is unclear which of the two seasons has more influence on community formation.

#### 4.7. Competition

At yet another level, lichen community structure is also determined by competition and other biotic interactions. In tropical dry forests, bryophytes are generally rare, and so lichens compete mostly with other lichens, including the same species, for space [66,113]. That this competition is fierce is shown by the often completely covered tree barks, especially on smooth-barked trees. Long-term studies are needed to understand the development of lichen communities and how inter- and intraspecific competition may play out over time.

#### 4.8. Lichenivory in TDFs

Lichen herbivory in dry forests is poorly known. Miranda-González [83] used photographs to calculate the amount of herbivory during four years in 19 microplots at the Biosphere Reserve Chamela-Cuixmala, finding that the annual amount of herbivory on lichens is remarkably similar to that of leaves and that the lichen biomass annual consumption per hectare of forest represents 28.5% of the biomass lost to total herbivory when considering leaf folivory (chewing) and lichenivory together [83]. One substantial difference is that in TDFs, lichen availability is permanent, whereas leaves are present for consumption only during the wet season.

Animals that feed from lichens have been intensely documented in many ecosystems [114], with TDFs being the exception. For TDFs, we found only three reports concerning one bird and two insects consuming at least one species of lichen. Large ground finches from the Galapagos consume *Rocella gracilis* Bory, a fruticose lichen growing on *Bursera graveolens* in Daphne Major island [115]. A *Psychidae* caterpillar in Mexico [85] consumed species of *Dirinaria* and *Parmotrema* (see below), and *Constrictotermes cyphergaster*, a termite from a TDFs in Southeastern Brazil, consumed at least 29 species of lichens, with the most consumed being *Chrysothrix xanthina* (Vain.) Kalb, *Pertusaria flavens* Nyl., and *Dirinaria confluens* (Fr.) D.D. Awasthi. [116]. Of those 29 lichen species, 10 were part of their diet exclusively during the dry season, and about 40% of the algae survived the digestive process, suggesting the dispersal of these lichens via endozoochory [116]. This ecological aspect of lichens needs to be studied, but preliminary data [83] confirms that several species of invertebrates in TDFs have a diet based on lichens.

#### 4.9. Lichens and Camouflage

The decoration behavior of a caterpillar of the moth family *Psychidae*, using lichens as camouflage, has been studied in a dry forest in Mexico [85]. Molecular studies of the caterpillar bags revealed that *Dirinaria consimilis* s. lat. (Stirt.) D.D. Awasthi is the most common species, but also taxa from the genera *Chrysothrix* Mont., *Parmotrema*, and *Pertusaria*, and the recently described *Phyiscia ornamentalis* R. Miranda, Campos-Cerda, and Herrera-Camp. [103], and one in an unknown genus in the order Arthoniales. The results also suggest that the caterpillars prefer *D. consimilis* and *D. leopoldii* (Stein) D.D. Awasthi, both containing sekikaic acid (instead of divaricatic acid present in the other *Dirinaria* species in the study area). In addition to protecting the insect from predation, it is possible that lichen bags provide extra protection by regulating the microclimatic conditions and the microbiome associated with the caterpillar [117].

#### 4.10. Ethnolichenology

Ethnolichenology is the study of the relationship between lichens and human cultural practices, including their medicinal, ceremonial, ornamental, and practical applications. Given the preference of humans to settle where TDFs exist (with more favorable climatic conditions and fertility than humid forests) and its consequential dismay, there are very few ethnolichenological studies on TDFs, including countries with original long extensions of these forests, such as México and Brazil. Therefore, we present a summary of cultural uses of lichens from other similar dry ecosystems.

One of the main uses that these communities give to lichens is as herbal remedies for different health problems. For example, the Chácobo indigenous people from the Bolivian Gran Chaco use at least six species of lichens as natural treatments to relieve chest pain, appendix problems, headaches, liver disorders, and rheumatism. Among those six lichen species, two remain unidentified; one is the macrolichen *Parmotrema zollingeri* (Hepp) Hale, and very importantly, three species are microlichens (*Chiodecton* sp. Ach., *Eschatogonia* sp. Trevis and *Laurera purpurina* (Nyl. ex Leight.) Zahlbr. now *Marcelaria purpurina* (Nyl. ex Leight.) Aptroot, Nelsen & Parnmen) [118]. The use of microlichens in ethnolichenology is rarely reported; perhaps there is a bias against their small size by both the local communities and ethnolichenologists.

In the semi-arid Caatinga of northeastern Brazil, the Pankararu community calls certain lichens “flor-de-pedra” (stone flower) and uses them traditionally as medicine. Specifically, a mixture of *Parmelinella salacinifera* (Hale) Marcelli & Benatti, *Heterodermia galactophylla* (Tuck.) W.L. Culb., and *Parmotrema wrightii* L.I. Ferraro & Elix is prepared as a water infusion to relieve digestive problems such as diarrhea and vomiting. This preparation is

also used in traditional treatments for epilepsy and “culturally caused” illnesses (possibly curses) by burning it as incense. Pankararu healers also know about restrictions: for example, *H. galactophylla* and *P. salacinifera* should not be given to children or pregnant women because of their adverse effects [119,120].

In Mexico, both indigenous and mestizo communities have included lichens in their traditional pharmacopoeia; however, to date, there are no specific studies documenting the use of lichens from tropical dry forests (TDFs) in the country. Bautista-González [121] reported that the Yuman peoples, settled in xerophytic scrublands of Baja California, use at least six species of the genus *Xanthoparmelia* for therapeutic purposes, mainly to treat heart, urinary, and digestive conditions. Additionally, the Tarahumara people from the Sierra Madre in northwestern Mexico, although living in a more temperate region dominated by dry coniferous forests, are culturally connected to the use of desert plants. They use lichens like *Usnea hirta* (L.) F.H. Wigg. (formerly known as *Usnea variolosa* Motyka) to prepare remedies and tonics. Pennington reported that the Tarahumara incorporated different species of this genus in the fermentation of traditional alcoholic beverages and also used them to produce medicinal dyes, possibly aiming for both healing and nutritional effects in their ceremonial preparations [122]. Although these examples come from ecosystems different from TDFs, they highlight the ethnolichenological knowledge associated with arid and semi-arid landscapes in Mexico, suggesting that similar practices may exist but remain undocumented in tropical dry forests.

In the inter-Andean valley and other regions of South America, there are additional reports of the medicinal use of lichens involving species from families that also include taxa found in tropical dry forests (TDFs). For example, in indigenous markets in Peru, species from the family Roccellaceae Chevall. were historically sold for therapeutic purposes. One species, possibly belonging to the genus *Roccella* DC., was used to treat cough and another to reduce fever, both as part of the traditional Andean pharmacopoeia. Although the species were not taxonomically identified, recent studies confirm the presence of *Roccella* species, such as *R. gracilis* and *R. ramitumidula* R. Miranda, G. Epitacio, Tehler, N. Sánchez & Herrera-Camp., in tropical dry forests of Mexico [123]. This suggests a potential biogeographical and cultural link that warrants further study. Similarly to other indigenous cultures around the world, it is believed that indigenous populations of the Eastern Chaco in Argentina collected lichens for use in handicrafts and ritual ceremonies, as well as for food, natural dyes, and raw materials for folk remedies, especially for the treatment of respiratory conditions. Today, lichen thalli are routinely sold in Córdoba’s herbalist shops for the preparation of medicinal infusions [124,125].

Beyond their medicinal applications, lichens have also been documented as decorative materials, due to the wide variety of forms and colors they display. In the markets of Veracruz (Mexico), for instance, people collect entire branches covered with lichens to decorate homes and public spaces [126]. Tropical dry forests host a high diversity of lichens, with various morphotypes and striking colors, providing local communities with abundant natural material potentially suitable for dry arrangements and ornamental elements. However, no specific decorative uses of lichens have been documented in this ecosystem to date.

Regarding practical uses, that is, material applications of lichens, the most notable are natural dyes obtained from different species and their use in crafts. The use of lichen-based dyes has a long history worldwide, and it was also important in Central and South America. During the late pre-Hispanic and colonial periods, large amounts of *Roccella* spp. lichens were harvested along the arid Pacific coasts to produce the purple dye known as “orchil,” which was highly valued in the European textile industry. Although this activity was promoted mainly by colonizers (especially in Peru, Chile, and Baja California, Mexico), it is

likely that local peoples had empirical knowledge of the purple color change produced by fermenting these lichens in ammonia (urine), possibly using them on a small scale to dye traditional textiles [127].

In ethnographic records from the Andean region of Peru, lichens from the genus *Ramalina* Ach., collected from dry hills (and possibly also present in tropical dry forests), were used to dye wool fibers yellow. Antúnez de Mayolo (1989) documented at least one species of *Ramalina*, known as q'olle by weavers, which produces a beige-yellow dye, used with traditional dye plants [128].

In Colombia, the Guane people (Santander) use the lichen known as “barbas de piedra” (possibly *Usnea amblyoclada* (Müll. Arg.) Zahlbr., formerly treated as a variety of *U. barbata* (L.) F.H. Wigg.) as a pigment to dye natural fibers [129,130]. Similarly, in various Andean regions, lichens have been traditionally employed as sources of natural dyes. Species from the genera *Parmelia* Ach. and *Xanthoria* (Fr.) Th. Fr., locally known in Quechua as *rumi-unku*, as well as lichens of the genus *Ramalina*, referred to as *inti-sunkha*, have been used to obtain reddish hues [131]. This practice demonstrates ancestral knowledge of the dyeing properties of these symbiotic organisms.

Finally, although ethnolichenological studies in tropical dry forests (TDFs) remain scarce, available evidence reveals that local communities in other areas have long relied on lichens for traditional medicine. In arid regions of Mexico, Nahua peoples harvest *Usnea* to prepare home remedies for fever, digestive troubles, minor burns, and colds [132]; in Sinaloa, *Roccella babingtonii* Mont. (now *R. gracilis*) is infused to alleviate asthma and fever [133]; and in Brazil's Caatinga, *Cladonia sanguinea* Eschw. (now *C. miniata* G. Mey.) is applied to treat childhood mouth ulcers [120]. These species are recorded in floristic surveys of TDFs along Colombia's Caribbean coast and Mexico's Pacific dry forests, confirming their ecological presence and underscoring the importance of lichens in treating wounds, skin ailments, and respiratory or digestive disorders within traditional health systems, despite the limited formal documentation to date.

#### 4.11. Chemical Compounds and Bioactive Properties of Lichens

Lichens synthesize diverse secondary metabolites, including dibenzofurans, depsides, depsidones, anthraquinones, lactones, and others, which contribute to both traditional uses and pharmacological potential. Molnár and Farkas compiled over 1050 lichen-derived compounds, many exhibiting antiviral, antitumor, antimicrobial, antioxidant, and allelopathic activities [134].

Usnic acid is among the most studied lichen compounds. Present in genera found in TDFs, such as *Usnea*, and certain species of *Cladonia* P. Browne, *Evernia* Ach., *Ramalina*, and *Parmotrema* [135–140], it is typically identified by thin-layer chromatography, although in some cases it has been confirmed by high-performance liquid chromatography or mass spectrometry. Pharmacological studies have confirmed that lichen extracts containing usnic acid can exhibit a variety of biological activities, including antibacterial, antifungal, antiviral, antioxidant, anti-inflammatory, and anticancer effects [141]. It shows inhibitory effects against *Staphylococcus aureus*, antiviral action against SARS-CoV-2, and pro-inflammatory activity in tumor cells, although potential hepatotoxicity has also been reported [142–144].

Other dibenzofurans include didymic acid, the first aromatic dibenzofuran reported from lichens, found in Neotropical *Cladonia* species. Its analogues, condidymic and subdidymic acids, exhibit antimicrobial and phytotoxic effects [136,145]. In fact, didymic and condidymic acids show potent antibacterial activity against *S. aureus*, comparable to that of usnic acid [146]. Another dibenzofuran, schizopeltic acid, was recently tentatively identified in *Helminthocarpon leprevostii*, a crustose lichen characteristic of Colombia's Caribbean

dry forests. Crude extracts of this lichen, dominated by schizopeltic acid and an unknown nitrogen-containing dibenzofuran, display significant antifungal activity [147].

Depsidides are another important class of metabolites. Atranorin, widely reported to be found in various lichen genera, exhibits antioxidant, antimicrobial, and cytotoxic properties [148–151]. Lecanoric acid, abundant in *Parmotrema andinum* (Müll. Arg.) Hale, has antimicrobial and antiproliferative effects [152,153]. Among the most bioactive depsidides is diffractaic acid, detected in *U. strigosa* (Ach.) Pers. has shown analgesic and antiviral activity against dengue, Zika, and Chikungunya viruses, with no apparent cytotoxicity [154]. More recently, gyrophoric acid has been reported to exert antidepressant and anxiolytic activity in vivo in Wistar rats, promoting hippocampal neurogenesis, reducing oxidative stress, and producing anxiolytic-like behavioral responses, suggesting its potential as a neuroactive compound [155]. Other depsidides, such as umbilicaric, hiascic, perlatolic, and stenosporic acids, although poorly studied, have demonstrated antioxidant and anti-inflammatory properties [153].

In addition, several lichens from TDFs in neotropical countries have also been reported as sources of bioactive anthraquinones, particularly emodin, 7-chloroemodin, and parietin. These compounds, found in genera such as *Pyrenula* Ach., *Caloplaca*, *Xanthoria*, and *Teloschistes* Norman, are responsible for the intense orange to red pigmentation in lichens and play ecological roles in photoprotection [102,156,157]. Moreover, they exhibit diverse biological activities: emodin and its chlorinated derivatives show antimicrobial, antioxidant, antiviral (partially inactivating HSV-1), and selective cytotoxic effects against tumor cells, while parietin displays photoprotective, antifungal, and antiangiogenic properties [158–161]. These findings highlight the pharmacological potential of lichen-derived anthraquinones in the underexplored context of neotropical TDFs.

Among the most relevant metabolites produced by lichens, depsidones stand out due to their structural diversity and notable pharmacological potential, and they have been widely documented in species inhabiting arid ecosystems. In particular, the *Graphidaceae* family, which is common in remnants of TDFs, produces these substances that, in addition to their biological interest, are often used as taxonomic diagnostic characters [162,163]. Stictic acid, for instance, detected in *Graphis* species from dry areas, has shown selective cytotoxic effects against cancer cells, preferentially inhibiting the growth of HT-29 human colon carcinoma cells over non-malignant cells (IC<sub>50</sub> ~29 µM), suggesting a selective anticancer effect [164]. Likewise, norstictic acid has demonstrated strong antiproliferative activity against triple-negative breast cancer cells. Both in vitro and in vivo studies have shown that it suppresses cell proliferation, migration, and invasion, and significantly reduces tumor size in a murine xenograft model. It has potential as a lead compound for targeted breast cancer therapy [165]. Fumaprotocetraric acid has also been associated with antioxidant, expectorant, and neuroprotective effects due to its capacity to modulate redox balance, suggesting potential anti-inflammatory activity and beneficial effects on the respiratory system [166,167]. Other common depsidones, such as salazinic acid, have been extensively studied for their potent antioxidant and photoprotective properties, protecting against damage caused by UV radiation [168].

Another important chemical group found in lichens corresponds to lactones, which include macrolactones, sesquiterpenic lactones, “depsilactones,” and aromatic lactones, among others. In tropical dry forests, key species such as *Candelaria concolor* (Dicks.) Arnold, an indicator of severe degradation in remnants of the Chaco dry forest, and *Chrysothrix xanthina* exhibit chemical compositions rich in pinastric acid and pulvinic acid-type lactones [124,169].

Among these compounds, vulpinic acid exhibits significant antimicrobial activity and protects human skin cells from oxidative stress caused by UVB radiation, demon-

strating both antioxidant and anti-inflammatory properties [170,171]. Other notable examples include the macrolactone (+)-aspicilin, identified as a potent antibiotic, and (+)-protolichesterinic acid, a sesquiterpenic lactone, which has shown anticancer activity by inducing apoptosis in tumor cells [172,173].

## 5. Conclusions

Our understanding of the lichens of TDFs has increased significantly in recent years, with studies ranging from the systematics of the lichens themselves to their ecological, human, and applied roles. It is evident, however, that the great heterogeneity of TDFs is replicated in their lichens, with several endemic species, contrasting environments, and different neighboring ecosystems at the landscape level; thus, a one-fit approach to study the TDFs of the world is not ideal.

It has been demonstrated multiple times that species that are considered widely distributed are, in many cases, species complexes that are highly endemic. A first step towards better understanding the lichens of this ecosystem is to include a genetic component in studies that require the correct identification of the species. This way, an objective comparison between areas of TDFs will be possible.

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## Abbreviations

The following abbreviations are used in this manuscript:

TDF Tropical Dry Forest

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