

Research Article



## Phorophyte Preference of *Manglicolous lichens* in Davao City, Philippines

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### ABSTRACT

Mangrove phorophytes offer a vital biological substrate for cryptogamic variety, especially to lichens. The identification of these distinct substrates, which contain crucial biological forces controlling epiphytic assembly, is still lacking. Despite the well-known zonation pattern of vascular plants, little is known about how host architectural features and forest management status affect lichens in tropical ecology. In this study, the selected extensive mangrove forests of Davao City, Philippines, the species composition and phorophyte specificity of lichen species were identified. Principal Coordinate Analysis (PCoA) and non-parametric Analysis of Similarities (ANOSIM) tests were used to assess community turnover in the 13 main phorophyte species. The results showed that the phorophyte species was the primary factor influencing diversity. *Sonneratia alba* is a rugose-barked species that supports the highest richness (14 species) and has a substantial reservoir of generalist species. The conventional rugosity idea was undermined by the smooth-barked *Bruguiera cylindrica*, which sustained an exceptionally high variety of 11 species, indicating cortical lenticels as crucial microhabitats for specialized graphid guilds. Furthermore, a monospecific connection with the halotolerant *Psilolechia lucida* was supported by the saline bark of *Avicennia marina* acting as a tight environmental filter. Statistical analysis showed that cryptogamic recovery lagged behind vascular reforestation, making restored and industrial sites compositionally similar. In contrast, the protected site maintained a distinct host-supported population. These results highlight how crucial it is to preserve a range of phorophyte assemblages to support specific epiphytic roles in mangrove conservation.



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## 1. Introduction

Mangrove phorophytes are physiologically distinctive and challenging habitats for epiphytic establishment. They create a transition zone between terrestrial and marine environments with high hypersalinity, tidal flooding, and strong sunlight. The association between the halophytic mangrove trees and "manglicolous" lichens is an international hotspot for substrate ecology. The most important environmental filters that could account for the presence of a particular cryptogamic assemblage on such a substrate are the physicochemical

properties of mangrove bark, especially pH, roughness, and water-holding capacity (Nash III 2008). Lichens are poikilohydric plants that lack cuticular protection and, therefore, in contrast to vascular epiphytes, depend directly on their phorophyte for physical support, water retention, and micronutrient accumulation (Brodo *et al.* 2001). Despite their apparent lack of epiphyte species diversity, the mangrove ecosystem supports distinctive lichen communities with physiological adaptations to withstand salt spray and drying conditions (Lücking *et al.* 2008).

Moreover, host specificity, or the strength of the preference of lichens for a certain tree, is one of the most significant topics in lichenology. In the Neotropical

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region, a study was carried out by Cáceres *et al.* (2007). This study showed that different characteristics of the phorophyte are significant factors in determining the composition of crustose lichens, even if microclimatic factors do have a certain effect. Studies on mangroves in Asia support that mangroves are not randomly distributed. The lichen communities of *Rhizophora* and *Lumnitzera* species in Thailand were found to be non-random by Mongkolsuk *et al.* (2011), suggesting variation in bark fissures. Likewise, quantitative survey research in India has found that phorophytes with rough bark, such as *Avicennia* sp., always support greater lichen diversity and density than those with smooth bark (Logesh *et al.* 2012; Panda *et al.* 2017). These findings demonstrate that phorophytes play an important role in shaping epiphytic biodiversity in mangroves.

In the Philippines, the focus of lichenological studies has been on mountain and dipterocarp forests, and significant diversity analyses have been conducted in the Cordillera Region, Bukidnon's Mount Musuan, and even in Metro Manila. New records of species and better knowledge of corticolous and manglicolous lichens have been made possible by recent surveys that have expanded to include understudied habitats such as mangrove forests in Calabarzon and protected coastal areas in Pangasinan (Lucban and Paguirigan 2019; Fajardo 2024; Weenalei & Anthony 2025). Based on the revised checklists, there are over 1,200 lichen taxa that can be found in various habitats in the Philippines. This shows that the research is no longer limited to the usual types of forests but also includes secondary forests and even urban areas (Paguirigan 2020; Taer *et al.* 2023).

Locally, Davao City has a unique study environment that exemplifies both fast development and mangrove remnants. *Rhizophora*, *Avicennia*, and *Sonneratia* are the most abundant mangrove species found in the Davao Gulf (Melana *et al.* 2000), although they are increasingly being threatened by human encroachment. Despite the well-known vascular flora in the region, the epiphytic lichen fauna associated with the wetlands has yet to be assessed. Ecological niche theory, which defines the role of a species within its environment in terms of resource use and biological associations, is used in this research (Khatibi & Sheikholeslami 2016).

One of the important elements of this research is the concept of niche differentiation, which plays a significant role in understanding how species can survive by exploiting different microhabitats (Slagsvold & Wiebe 2007). The current research aims to determine if manglicolous lichens in Davao City have a strong host

preference and the patterns of association between lichen communities and mangrove phorophytes. Relationships between lichens and phorophytes are believed to be non-random, with certain mangrove species supporting a greater variety of lichens due to microhabitat conditions specific to that species.

It is simpler to comprehend how habitat layout influences cryptogamic diversity in coastal forests when ecological niche theory is applied to the relationship between hosts and lichens. This study is related to Sustainable Development Goal (SDG) 15: "Life on Land" (United Nations DESA 2018). By assessing the structural suitability of various mangrove phorophytes, this work establishes a scientific foundation for the conservation of compositionally diverse mangrove assemblages. In coasts that are progressively becoming more urbanized, this strategy is thought to be essential for preserving linked species and boosting ecological resilience.

## 2. Materials and Methods

### 2.1. Research Design

A quantitative ecological assessment was used in this study to illustrate the substrates and habitat characteristics of mangrove phorophytes. This study examined the relationship between cryptogamic richness and abundance as markers of tree habitat quality, based on the community ecology concepts described by Magurran (2004). Although this work was observational and depended on in situ assessment rather than experimental manipulations, these objectives can be satisfied to establish host specificity.

### 2.2. Study Area and Site Characterization

In Figure 1, three mangrove areas that represent a gradient of anthropogenic disturbance and management regimes were the focus of field evaluations conducted in Davao City's coastal zones in September and October of 2025. These extensive mangrove forests were determined by the Department of Environment and Natural Resources (DENR) Region XI. Particularly, the Aboitiz Cleanergy Park, located in Matina Aplaya (7°01'41.28' N, 125°34'31.99' E), is an eight-hectare Marine Protected Area with strong structural integrity and continuous ecological recovery. It also serves as a rigorously protected urban sanctuary. On the other hand, the mangrove ecosystem at Purok 18-A Pax, Panacan (7°09'24.84' N, 125°39'24.84' E) is fragmented and under industrial stress, with little natural regrowth and human

# Study Area: Sampling Sites

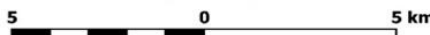
Sources:  
Basemap © OpenStreetMap (OSM)  
NAMRIA & OCHA PHL Admin, 2024  
Bing Maps Satellite Imagery, © Microsoft

## LEGEND

-  Sampling Site
-  National Highway
-  Secondary Highway
-  Tertiary Highway



Scale 1:150,000  
EPSG: 4326  
WORLD GEODETIC SYSTEM 1984  
(WGS 84)



The Study Area is situated in Davao City, within the province of Davao del Sur which is part of the Mindanao island group in the Philippines.

Davao City is highlighted (red) on the Mindanao island group map

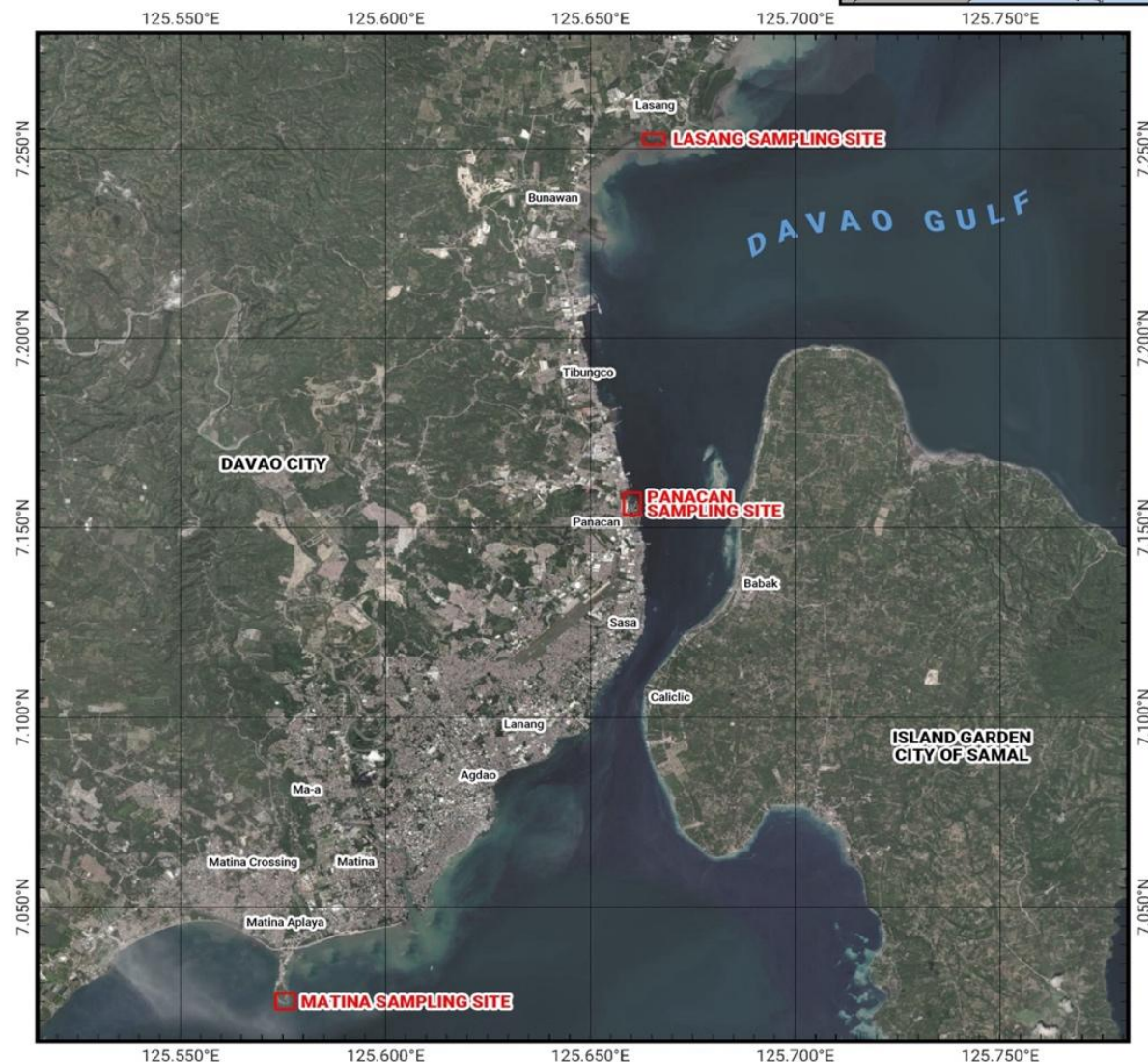
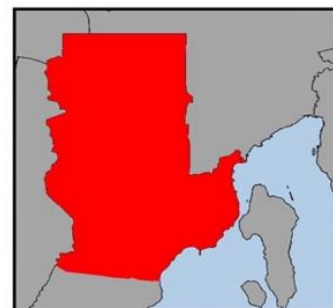


Figure 1. Map of the study area. Location of the three sampling stations (Matina, Panacan, Lasang) along the coast of Davao City, Philippines

encroachment. The Tambongon Fisherfolks Association (TAMFIAS) oversees the third site, which is situated in Sitio Tambongon, Lasang (7°15'27' N, 125°39'51' E). With a varied mangrove assemblage and a roughly twofold increase in mangrove cover over the previous ten years, it exemplifies successful community-based restoration.

### 2.3. Administrative Compliance and Ethical Considerations

To ensure that the study is compliant with regulations and that the environment is protected, all necessary administrative and ethical approvals were secured before data gathering. A gratuitous permit was issued by the DENR Region XI, while locational clearances were secured from the park administrators and local government units. The research design was conducted using non-invasive sampling methods to ensure the health of the phorophyte. The University Research Ethics Board of Davao Oriental State University formally supervised the research to ensure that it met all the necessary standards of ecological research.

### 2.4. Sampling Design and Phorophyte Selection

To examine lichen distribution patterns across phorophyte species, an opportunistic sampling approach was employed, constrained by field accessibility and the presence of mature mangrove trees suitable for lichen colonization. However, to reduce sampling bias, a standardized sampling effort was implemented by selecting 30 phorophyte individuals per sampling station, with trees spaced at least ten meters apart to ensure independence and minimize spatial autocorrelation. These used as regional keys for identifying trees during field observations, based on the published observations of Primavera (2009) and Leбата-Ramos (2013).

Tree selection prioritized mature individuals with stable and accessible trunks, as these provide more suitable microhabitats for lichen establishment compared to younger trees (Reynolds *et al.* 2017). While phorophyte species were sampled based on their availability within each site, the relative abundance of host species was documented and considered during data interpretation to account for potential sampling bias.

Consequently, the observed patterns of lichen richness and distribution are interpreted in relation to host availability, and are indicative of host association rather than absolute host preference.

### 2.5. Specimen Collection and Preservation

To protect the phorophyte, the samples were taken using conventional non-destructive techniques. In corticolous species, only the bark sections bearing thalli were removed using a flat-edged chisel to prevent vascular cambium damage (Nayaka 2014). A colorless nail polish was applied right once to stop bacteria from penetrating the exposed bark tissue. To enable repeated morpho-anatomical and chemical investigations, a minimum collection of two thalli per morphospecies was collected. To prevent deterioration, such as fungal growth or thallus curling, the specimens were placed in labeled polythene bags and squashed between newspaper blotters after a clear-field collection (Fajardo & Bawingan 2019).

### 2.6. Characterization of Phorophyte-Associated Epiphytic Communities

The identification of lichen specimens in this study were identified using an integrative taxonomic approach combining morphological, anatomical, and chemical analyses. Initial identification was conducted through morphological examination of thallus characteristics, including growth form, color, surface texture, and reproductive structures (e.g., apothecia and lirellae), using a stereomicroscope at 40× magnification. Detailed anatomical features were further examined using a compound microscope at 400× magnification. Diagnostic structures such as the ascus, ascospores, hymenium, epihymenium, and subhymenium were analyzed to support species-level identification (Joshi *et al.* 2018; Fajardo & Bawingan 2019).

Chemical characterization was performed using standard spot tests, including potassium hydroxide (K), sodium hypochlorite (C), para-phenylenediamine (P), and iodine (I), to detect the presence of secondary metabolites such as depsides, depsidones, and amyloid compounds. These tests were used to confirm morphological interpretations and distinguish closely related taxa. Taxonomic identification was guided by standard lichenological references, including Awasthi (1991) and Purvis *et al.* (1992), supplemented by genus-specific keys for *Bacidia* (Ekman 2001; Lee & Hur 2022), *Graphis* (Lücking *et al.* 2009), and *Lecanora* (Santos *et al.* 2023). Specimens that could not be confidently resolved to species level were assigned to morphospecies or indicated using “cf.” notation, following standard taxonomic practice. Species reported

at the species level in this study are based on validated identifications from Tadena and Dedal (2026), where diagnostic reproductive structures (e.g., apothecia) were examined microscopically.

### 2.7. Phorophyte Identification

Using Primavera's (2009) Philippine Mangroves field guide, which was updated and supported by other authors (Barcelete *et al.* 2016; Pototan *et al.* 2017), mangrove species at each site were identified to estimate their extent at each location. Leбата-Ramos (2013) also referenced the Field Guide on Mangrove Species and Structure Analysis in this study.

### 2.8. Classification of Phorophyte Functional Types

To determine the effect of substrate texture on lichen communities, the species of phorophyte were categorized into functional groups based on texture using the standardized description of mangrove bark texture as described in Primavera *et al.* (2004) and Polidoro *et al.* (2010). The two host tree types were "Rugose/Fissured" and "Smooth/Flaking." This category of classification enables the assessment of structural host specificity without the requirement for observation of microclimatic conditions in situ by serving as a proxy for microhabitat complexity.

### 2.9. Statistical Analysis of Host Specificity

The effect of species of phorophyte on the composition of lichen assemblages was examined by multivariate analysis using the Paleontological Statistics (PAST) software package (Hammer *et al.* 2001). Because this type of ordination is efficient for visualizing binary data in low-dimensional space, and does not require the minimization of stress, as in Non-metric Multidimensional Scaling, Principal Coordinate Analysis (PCoA) with the Jaccard dissimilarity index was employed to display differences in composition among host trees (Gower 1966; Legendre & Legendre 2012). One-way Analysis of Similarities (ANOSIM) was carried out with the same distance measure to confirm the patterns identified in the PCoA. This provided a global R value to assess the level of separation between the groups of phorophyte, with significance tested at  $p < 0.05$  (Clarke 1993).

## 3. Results

### 3.1. Classification of Phorophyte Functional Types

The 13 dominant mangrove species in Davao City can be categorized into two distinct functional texture groups: "Rugose/Fissured" and "Smooth/Flaking," depending upon the description of the bark morphology. Table 1 shows the results of the classification.

*Rhizophora* species (*R. apiculata*, *R. mucronata*, *R. stylosa*), *Sonneratia alba*, *Lumnitzera racemosa*, and *Bruguiera gymnorrhiza* are included in the "Rugose/Fissured" group. These species are characterized by vertical or horizontal fissures and tessellated surfaces. On the other hand, *Aegiceras floridum*, *Ceriops tagal*, *Excoecaria agallocha*, and *Avicennia* species (*A. marina*, *A. lanata*) belong to the "Smooth/Flaking" group. *Bruguiera* showed notable intra-generic diversity, whereas *Bruguiera gymnorrhiza* is rugose, *Bruguiera cylindrica* is categorized as "Smooth/Flaking" because of its corky lenticels, which resemble mosaics and lack substantial cracks. Furthermore, it was observed that *Sonneratia caseolaris* changed from being smooth and waxy in its juvenile phases to being cracked and flaky as it matured.

### 3.2. Phorophyte Species Composition and Availability

Phorophyte species composition varied among the three sampling stations, according to the floristic assessment (Figure 2). Across all sites, *Sonneratia alba* was found to be the most prevalent host ( $n = 7$  per sampling area).

*Rhizophora stylosa* ( $n = 8$ ) and *Aegiceras floridum* ( $n = 5$ ) dominated the species composition at the Matina station. *Ceriops tagal* ( $n = 3$ ) and *A. floridum* were only found at Matina. On the other hand, *Avicennia marina* and *Rhizophora apiculata* shared codominance in the Panacan (Industrial) and Lasang (Restored) stations. Being the sole location to host mid-zone vegetation like *Bruguiera gymnorrhiza*, *Bruguiera cylindrica*, and *Lumnitzera racemosa*, the Lasang station had the highest total phorophyte diversity. At the Panacan location, a high frequency of *Avicennia marina* was noted.

Table 1. Functional textural classification of mangrove phorophyte species based on bark morphology descriptions

Genus	Species	Bark Description (Primavera <i>et al.</i> 2004)	Functional textural group
<i>Aegiceras</i>	<i>A. floridum</i>	Smooth to slightly creviced; dark gray/brown with small lenticels	Smooth/Flaking
<i>Avicennia</i>	<i>A. lanata</i> (syn. <i>A. rumphiana</i> )	Smooth to mottled; often with peeling or flaking patches	Smooth/Flaking
<i>Avicennia</i>	<i>A. marina</i>	Smooth, mottled green/gray; peeling in flakes	Smooth/Flaking
<i>Bruguiera</i>	<i>B. cylindrica</i>	Smooth to grayish with mosaic-like corky lenticels	Smooth/Flaking
<i>Bruguiera</i>	<i>B. gymnorhiza</i>	Rough, deeply fissured, or grid-cracked	Rugose/Fissured
<i>Ceriops</i>	<i>C. tagal</i>	Flaking; reddish-brown, often peeling in parchment-like strips	Smooth/Flaking
<i>Excoecaria</i>	<i>E. agallocha</i>	Smooth; gray with prominent lenticels, becoming slightly fissured with age	Smooth/Flaking
<i>Lumnitzera</i>	<i>L. racemosa</i>	Fissured, dark brown, and rough	Rugose/Fissured
<i>Rhizophora</i>	<i>R. apiculata</i>	Rugose; vertically fissured, gray to dark gray	Rugose/Fissured
<i>Rhizophora</i>	<i>R. mucronata</i>	Rugose; rough and horizontally fissured	Rugose/Fissured
<i>Rhizophora</i>	<i>R. stylosa</i>	Rugose; rough, fissured to grid-cracked (tessellated)	Rugose/Fissured
<i>Sonneratia</i>	<i>S. alba</i>	Rough, fissured, and creamy to brown	Rugose/Fissured
<i>Sonneratia</i>	<i>S. caseolaris</i>	Smooth and waxy (young) to cracked/flaky (mature); often less rugose than <i>S. alba</i> but functionally textured compared to <i>Avicennia</i>	Rugose/Fissured

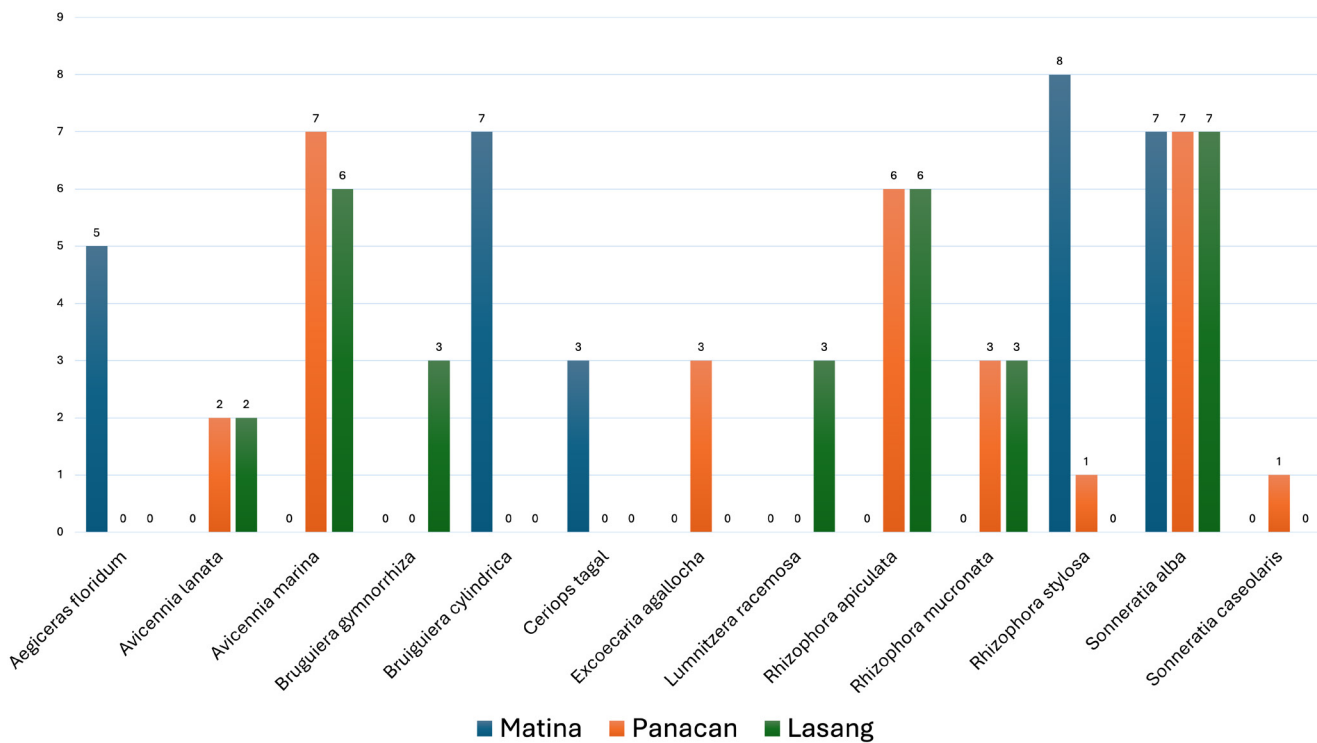


Figure 2. Species composition and abundance of mangrove phorophytes. Distribution of mangrove tree species sampled across the three selected mangrove forests in Davao City, Philippines. The chart illustrates the variation in host availability, with *Sonneratia alba* appearing as a dominant species across sites

### 3.3. Phorophyte Suitability and Cryptogamic Assemblage Patterns

A hierarchy in substrate compatibility was found in the quantitative evaluation of epiphytes on 13 mangrove species (Table 2). With 14 lichen species, including foliose taxa (*Pyxine* sp.) and crustose taxa (*Bacidia* sp., *Pyrenula* sp., *Lepraria* sp.), *Sonneratia alba* (Rugose/Fissured) (Figure 3D) supported the highest specific richness.

On the other hand, just one species (*Graphis cincta*) was maintained by *Sonneratia caseolaris*. Nine lichen species, mostly *Psilolechia lucida* and members of the Graphidaceae family (e.g., *Graphis* species), were supported by *Rhizophora* species, especially *Rhizophora mucronata* and *Rhizophora stylosa* (Figure 3A). *Bruguiera cylindrica* showed exceptionally high richness among the "Smooth/Flaking" group,

Table 2. Mangrove phorophyte preference and frequency of occurrence of manglicolous lichens in Davao City

Mangrove phorophyte species	Lichen species	Frequency	No. of manglicolous lichen species
<i>Aegiceras floridum</i>	<i>Arthothelium</i> sp.	5	3
	<i>Opegrapha</i> cf. <i>astraea</i>	5	
	<i>Opegrapha</i> cf. <i>dimidiata</i>	5	
<i>Avicennia lanata</i>	<i>Lepraria</i> sp. 1	4	3
	<i>Chrysothrix xanthina</i> (Vain.) Kalb	2	
	<i>Lepraria</i> sp. 3	2	
<i>Avicennia marina</i>	<i>Psilolechia lucida</i> (Ach.) M. Choisy	13	1
	<i>Diorygma pruinatum</i>	5	
	<i>Arthothelium</i> sp.	2	
	<i>Graphis immersicans</i> A.w. Archer	2	
	<i>Graphis modesta</i> Zahlbr.	2	
	<i>Graphis nuda</i> (H. Magn.) Staiger	2	
<i>Bruguiera cylindrica</i>	<i>Opegrapha</i> cf. <i>astraea</i>	2	11
	<i>Opegrapha</i> cf. <i>dimidiata</i>	2	
	<i>Dirinaria</i> cf. <i>minuta</i>	1	
	<i>Graphis</i> cf. <i>kelungana</i>	1	
	<i>Allographa fujianensis</i>	1	
	<i>Heterodermia</i> sp.	1	
	<i>Cryptothecia</i> sp. 2	3	
	<i>Candelariella</i> sp.	1	
	<i>Arthothelium</i> sp.	2	
<i>Bruguiera gymnorhiza</i>	<i>Diorygma pruinatum</i>	2	2
	<i>Opegrapha</i> cf. <i>astraea</i>	2	
	<i>Opegrapha</i> cf. <i>dimidiata</i>	1	
	<i>Dirinaria</i> cf. <i>minuta</i>	1	
	<i>Allographa fujianensis</i>	1	
	<i>Heterodermia</i> sp.	1	
	<i>Psilolechia lucida</i> (Ach.) M. Choisy	1	
<i>Ceriops tagal</i>	<i>Cryptothecia</i> sp. 2	2	8
	<i>Lepraria</i> sp. 1	2	
	<i>Arthothelium</i> sp.	2	
	<i>Diorygma pruinatum</i>	2	
	<i>Opegrapha</i> cf. <i>astraea</i>	1	
	<i>Opegrapha</i> cf. <i>dimidiata</i>	1	
<i>Excoecaria agallocha</i>	<i>Dirinaria</i> cf. <i>minuta</i>	1	2
	<i>Allographa fujianensis</i>	1	
	<i>Heterodermia</i> sp.	1	
<i>Lumnitzera racemosa</i>	<i>Psilolechia lucida</i> (Ach.) M. Choisy	3	1
	<i>Candelariella</i> sp.	1	
<i>Rhizophora apiculata</i>	<i>Cryptothecia</i> sp. 2	2	2
	<i>Lepraria</i> sp. 1	2	
<i>Rhizophora mucronata</i>	<i>Phaeographis</i> sp.	3	9
	<i>Candelariella</i> sp.	11	
	<i>Chrysothrix xanthina</i> (Vain.) Kalb	1	
	<i>Psilolechia lucida</i> (Ach.) M. Choisy	4	
	<i>Candelariella</i> sp.	1	
	<i>Dirinaria</i> cf. <i>minuta</i>	1	
	<i>Graphis modesta</i> Zahlbr.	1	
	<i>Lecanora helva</i> Stizenb.	1	
	<i>Lepra corallina</i>	1	
	<i>Lepra corallina</i> var. <i>minor</i>	1	
<i>Rhizophora stylosa</i>	<i>Lepraria</i> sp. 1	1	9
	<i>Pyxine</i> sp. 2	1	
	<i>Diorygma pruinatum</i>	6	
	<i>Graphis immersicans</i> A.w. Archer	6	
	<i>Graphis modesta</i> Zahlbr.	6	
	<i>Graphis nuda</i> (H. Magn.) Staiger	6	
	<i>Lepraria</i> sp. 1	2	
	<i>Graphis</i> cf. <i>kelungana</i>	1	
	<i>Heterodermia</i> cf. <i>tremulans</i>	1	
	<i>Lepra corallina</i>	1	
	<i>Psilolechia lucida</i> (Ach.) M. Choisy	1	

The abbreviation "sp." indicates identification to the genus level, while "cf." (confer) denotes a provisional identification that requires further verification. Values represent the frequency of occurrence of lichen species on the respective mangrove phorophytes. Species-level identifications presented in this table follow Tadena and Dedal (2026), where diagnostic morphological, anatomical, and chemical characters—including apothecia and ascospore features—were examined. The present study utilizes these validated identifications for ecological analysis

Table 2. Continued

Mangrove phorophyte species	Lichen species	Frequency	No. of manglicolous lichen species
<i>Sonneratia alba</i>	<i>Phaeographis</i> sp.	8	
	<i>Allographa fujianensis</i>	6	
	<i>Bacidia</i> cf. <i>arceutina</i>	5	
	<i>Biatora</i> sp.	5	
	<i>Chrysothrix xanthina</i> (Vain.) Kalb	5	
	<i>Lepraria</i> sp. 2	5	
	<i>Pertusaria</i> sp.	5	14
	<i>Pyrenula</i> sp.	5	
	<i>Pyxine</i> sp. 1	5	
	<i>Psilolechia lucida</i> (Ach.) M. Choisy	4	
	<i>Cryptothecia</i> sp. 1	3	
	<i>Cryptothecia</i> sp. 2	1	
<i>Sonneratia caseolaris</i>	<i>Lepra</i> cf. <i>albopunctata</i>	1	
	<i>Lepraria</i> sp. 1	1	
	<i>Graphis cincta</i>	1	1

The abbreviation "sp." indicates identification to the genus level, while "cf." (confer) denotes a provisional identification that requires further verification. Values represent the frequency of occurrence of lichen species on the respective mangrove phorophytes. Species-level identifications presented in this table follow Tadena and Dedal (2026), where diagnostic morphological, anatomical, and chemical characters—including apothecia and ascospore features—were examined. The present study utilizes these validated identifications for ecological analysis

supporting 11 species. The Graphidaceae family, which includes *Graphis immersicans*, *Graphis modesta*, *Graphis nuda*, and *Opegrapha* spp., dominated the assemblage. A combination of crustose (*Arthothelium* sp.) and foliose (*Heterodermia* sp.) species were found in *Ceriops tagal*, which supported an intermediate richness of eight species.

*Avicennia* species showed the lowest richness. A monospecific association consisting only of *Psilolechia lucida* (n = 13) was found in *Avicennia marina* (Figure 3C). Three species were found in *Avicennia lanata* (Figure 3B), with "dust lichens" like *Lepraria* spp. predominating, as well as *Chrysothrix* sp.

### 3.4. Spatial Turnover and Community Similarity (Beta Diversity)

An analysis of similarities (ANOSIM) revealed minimal but substantial spatial structure in the composition of lichen communities (Global R = 0.172, p < 0.001) (Table 3). Matina's community structure was considerably different from that of Lasang (R = 0.288, p < 0.001) and Panacan (R = 0.217, p < 0.001), according to pairwise comparisons. Nevertheless, there was no statistically significant difference between the lichen communities in Lasang (Restored) and Panacan (Industrial) (R = 0.014, p = 1.000), suggesting homogeneous populations across these two locations.

### 3.5. Ordination of Lichen Communities (PCoA)

Jaccard dissimilarity-based Principal Coordinates Analysis (PCoA) explained 31.9% of the total

variation in lichen assemblages (PCoA 1: 18.4%; PCoA 2: 13.5%) (Figure 4). The Matina site formed a distinct and compact cluster, largely separated from the other stations along the positive axes of PCoA 1 and PCoA 2. In contrast, the Panacan (Industrial) and Lasang (Restored) sites exhibited substantial overlap in ordination space, primarily within the negative to central range of PCoA 1. Although the Lasang group displayed a broader convex hull area, indicating greater compositional dispersion, its overlap with Panacan suggests similarities in community structure.

However, the relatively low proportion of explained variation indicates that a large fraction of the variability in lichen community composition is not captured by the first two axes. This suggests that additional factors, beyond those represented in the ordination, contribute to community structure. Microenvironmental variables such as bark pH, moisture availability, light exposure, and fine-scale substrate heterogeneity may influence species distribution at the local level. Furthermore, stochastic processes, including dispersal limitation and random colonization events, may also play a significant role in shaping lichen assemblages in these dynamic mangrove ecosystems.

## 4. Discussion

### 4.1. Functional Traits and Substrate Stability

Underpinning the hypothesis that bark rugosity is a key mechanical filter facilitating lichen colonization, the classification of phorophytes is a critical variable in the evaluation of epiphytic assemblage distribution.



Figure 3. Mangrove tree trunks containing manglicolous lichens. The images depict the bark surface morphology of dominant phorophytes: (A) *Rhizophora stylosa* (Rugose/Fissured), (B) *Avicennia lanata* (Smooth/Flaking), (C) *Avicennia marina* (Smooth/Flaking), (D) *Sonneratia alba* (Rugose/Fissured). Note the deep fissures in (A) and (D) compared to the smooth, peeling texture in (B) and (C)

Table 3. Pairwise analysis of similarities (ANOSIM) of lichen community composition between mangrove sites based on the Jaccard similarity index

Comparison	R Statistic	p-value (Bonferroni)	Significance
Global Test	0.1719	< 0.001	***
Matina vs. Lasang	0.2876	< 0.001	***
Matina vs. Panacan	0.2174	< 0.001	***
Panacan vs. Lasang	0.0140	1.000	ns

In a drying mangrove ecosystem, the presence of deep bark fissures not only serves to maximize the surface area and duration of hydration for poikilohydric lichens (Mongkolsuk *et al.* 2011), but also facilitates "propagule trapping," whereby microscopic diaspores are locked against frictional forces through fissured bark, such as that of *Bruguiera gymnorhiza* (Cáceres *et al.* 2007).

The low richness of lichens on *Sonneratia caseolaris* highlights the restricted role of ontogenetic variations, especially the waxy nature characteristic of its juvenile phase (Primavera *et al.* 2004), even though the stability and texture of species such as *Sonneratia alba* render them highly sensitive phorophytes (Aragón *et al.* 2025).

#### 4.2. Host Specificity and Niche Differentiation

A notable exception from the conventional "roughness-diversity" rule was noted in *Bruguiera cylindrica*. It performed better than a few tough hosts despite being included in the "Smooth/Flaking" group. Given that "script lichens" (Graphidaceae) predominate on this host, deep fissures may be detrimental to this guild and are superfluous. The most ideal microtopography is likely provided by the unique feature of *Bruguiera cylindrica*'s

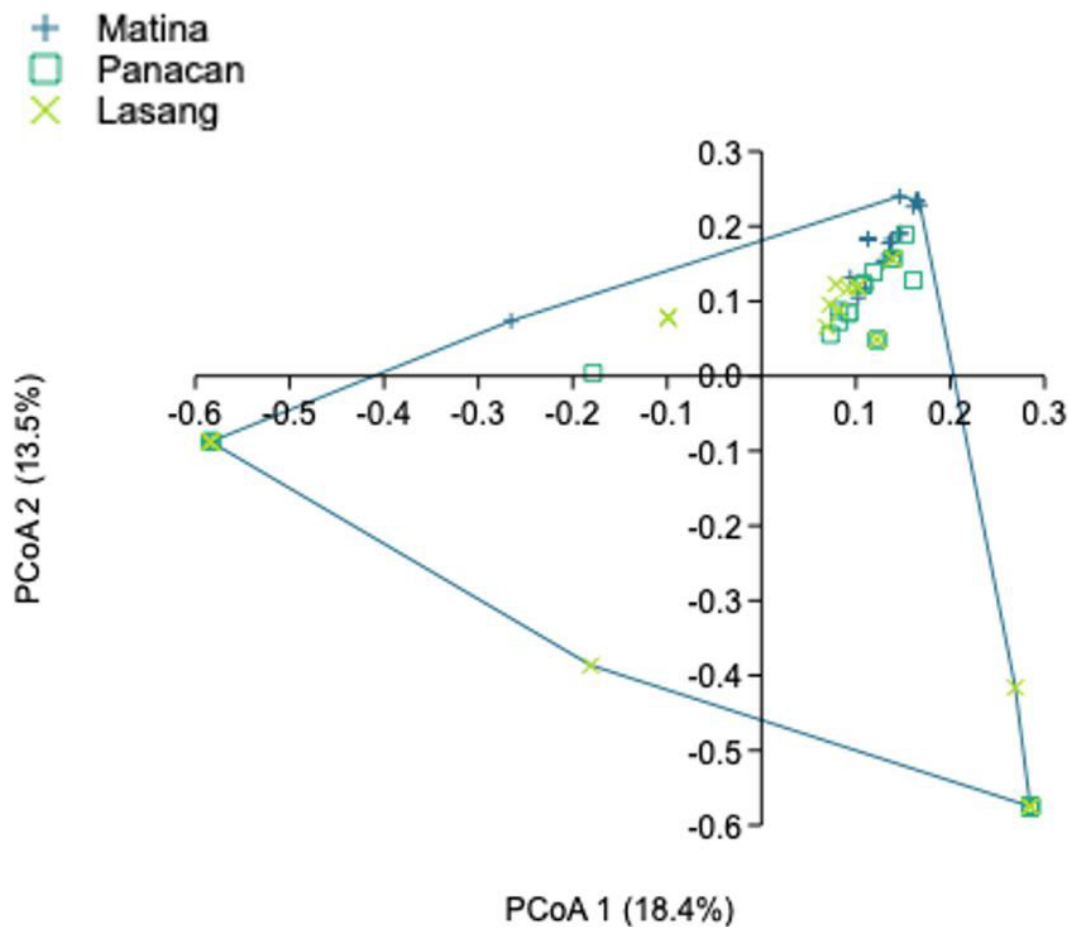


Figure 4. Principal coordinates analysis (PCoA) ordination of lichen communities. The ordination plot visualizes the variation in lichen assemblages on mangrove phorophytes across three study sites (Matina, Panacan, Lasang). The plot is based on Jaccard dissimilarities of presence-absence data. Convex hulls delineate the ecological composition space occupied by each site. The first two principal coordinates explain 31.9% of the total variation (PCoA 1: 18.4%; PCoA 2: 13.5%). Points represent individual trees; points closer together indicate greater similarity in lichen species composition

"mosaic-like corky lenticels," which are smooth enough to for lirellae to develop laterally without interference but rough enough to catch spores (Lücking *et al.* 2008). This indicates that *Bruguiera cylindrica* is an excellent host for guilds of graphids.

*Avicennia* species are an example of the "Smooth/Flaking" bark group, which often offers a physiologically difficult substrate for lichen colonization because of decreased rugosity and substrate instability. While flaking results in an unstable surface that prevents secure attachment, smooth bark promotes water runoff and reduces the moisture retention required for lichen development. Research on *Avicennia marina* subsp. *australasica*, reports comparatively reduced lichen species richness; in some areas, only seven species have been identified, suggesting less ideal conditions for lichens on this genus. In contrast, mangroves with rougher bark,

such as *Rhizophora* species, have more lichen variety and offer more stable and moisture-retentive substrates. These findings support the hypothesis that the *Avicennia flaking* and smooth bark reduces lichen growth by creating a less favorable microenvironment (Reynolds *et al.* 2017; Lucban and Paguirigan 2019). The monospecific dominance of *Psilolechia lucida* on *Avicennia marina* indicates a harsh filter; salt-sensitive species are likely to be excluded from the hypersaline bark surface (Logesh *et al.* 2012). This stress-tolerant niche seems to be occupied by *Psilolechia lucida*, a halotolerant specialist.

*Ceriops tagal* was found to be of intermediate suitability. It can produce damp micro-pockets around overlapping bark scales, which can result in the formation of foliose species like *Heterodermia* sp., which favor wet circumstances, even though its peeling bark prevents established reinitiation (Cáceres *et al.* 2007).

### 4.3. Drivers of Community Turnover and Spatial Divergence

The persistence of a "core" assemblage linked to widely spread hosts like *Sonneratia alba* is suggested by the low Global R-value (0.172), which shows a significant degree of overlap in species composition. On the other hand, pairwise shows that sites emphasize host drives as a cause of local divergence. The unique variety of host trees present in the PCoA, especially the absence of *Avicennia* species and the presence of *Cerriops tagal* and *Aegiceras floridum*, are what cause the "Matina Divergence" seen there. According to Cáceres *et al.* (2007), the distinct lichen association (such as the lack of *Psilolechia lucida*) demonstrates that the particular host tree assembly plays a crucial role in regulating geographical turnover.

The co-dominance of *Rhizophora apiculata* and *Avicennia marina* in both locations accounts for the unexpected statistical resemblance ( $R = 0.014$ ) between the restored Lasang site and the industrial Panacan site. A homogenization impact results from this typical lichen-host relationship (Clarke 1993). Furthermore, as seen in cyanolichen communities in newly created forest patches, lichen colonization in restored environments frequently suffers from a considerable lag, with the complete return of species richness perhaps requiring several decades to more than a century. Less established lichen communities that are not yet statistically different from disturbed or industrial sites are usually found in early successional or pioneer habitats, like those dominated by *Lumnitzera* sp. Dispersal capacity, habitat structure, and geographical scale are factors that affect colonization; smaller disturbances and closeness to mature forests encourage quicker recolonization and diversity recovery (Nascimbene *et al.* 2009; Bartemucci *et al.* 2022; Gjerde *et al.* 2025).

### 4.4. Conclusion on Ecological Assembly and Future Research

In conclusion, mangrove phorophytes act as specialized biological filters. The assembly is shaped by a tradeoff between chemical stress (supporting specialists on *Avicennia marina*), micro-topographic heterogeneity (supporting Graphids on *Bruguiera cylindrica*), and enhanced stability (supporting high richness on *Sonneratia alba*). The remaining unexplained variation in the PCoA (approx 68%) suggests that pioneer lichen vegetation in these dynamic environments is also controlled at the micro-level, such as by pH of individual tree bark, light gradients, or random settlement.

Moreover, the use of opportunistic sampling may influence the observed distribution of lichens across

phorophytes, particularly where host species vary in abundance. Therefore, the patterns reported here should be interpreted as indicative of host association within the sampled communities rather than definitive measures of host preference.

For future researchers, to better understand how particular environmental filters like salinity determine the distribution of specialized guilds, they should examine the biochemical characteristics of mangrove bark, such as pH levels and secondary metabolite concentrations. Furthermore, to determine the exact period of the "colonization lag" and identify the pioneering lichen species that could serve as a bio-indicator for a successful cryptogamic colonization, longitudinal monitoring is also required. Future studies incorporating direct measurements of microclimatic variables and bark physicochemical properties are recommended to better resolve the drivers of lichen community variation. Finally, a better understanding of the relationship between host architecture and forest management and lichen community assembly may be achieved by extending this research to include microclimatic variables such as light intensity and humidity at different heights in the canopy.

### Conflict of Interest

The author declares that there is no conflict of interest.

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