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Richness of Lichens Consumed by *Constrictotermes cyphergaster* in the Semi-arid Region of Brazil

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Abstract

The consumption of lichens by *Constrictotermes cyphergaster* termites is suggested in the literature, but not yet demonstrated with concrete evidence. We examined the use and richness of lichens consumed by *C. cyphergaster* during both the dry and rainy seasons in a semiarid environment in northeastern Brazil by monitoring the foraging of five termite colonies for ten consecutive days during each period. Twenty-nine species of corticolous lichens were consumed by *C. cyphergaster*, with seasonal variations in the richness of their ingestion. *Chrysothrix xanthine*, *Pertusaria flavens*, and *Dirinaria confluens* were the lichen species most consumed. TLC analyzes of termite gut contents revealed twelve secondary lichen compounds ingested in both seasons, while staining showed fragments of fungal hyphae, green algae, and typical lichen spores. This study represents the first systematic survey of the abundances of lichens that compose the diet of *C. cyphergaster* and indicates the seasonal selectivity of that resource related to the chemical compositions of the lichen stalks.

Introduction

Termites are eusocial insects and the most important decomposers in tropical forest, savanna, and desert ecosystems (Lo & Eggleton, 2011). In a remarkable display of adaptive radiation of feeding habits, termite diets include, among different species, necromasses in different stages of decomposition, herbaceous plants, litter, fungi, termite nests or mound materials, animal excrement, carcasses, soil organic material (humus), and lichens (Lee & Wood, 1971; Wood, 1978; Edwards & Mill, 1986; Bignell & Eggleton, 2000; Donovan et al., 2001).

Lichens have been reported being used as food resources by *Hospitalitermes*, *Grallatotermes*, *Longipeditermes*, and *Lacessitermes* termites (Roisin & Pasteels, 1996; Miura &

Matsumoto, 1997, 1998; Martius et al., 2000), and one of the six described species of the genus *Constrictotermes* (Bourguignon et al., 2011). According Miura and Matsumoto (1997), lichens can provide 10 to 60 times more nitrogen to those insects than wood (their main food source). Except for the energy roles of lichens in termite diets, little is known about interactions between those organisms, their foraging strategies, or the species richness of lichens that make up their diet.

Lichens are stable, self-sustaining unions between fungi (the mycobiont) and photoautotrophic algae or cyanobacteria (the photobiont), and represent a significant portion of the earth's biological diversity (Honda, 2012). Among other ecosystem services provided by lichens is the production of a variety of antiherbivory compounds that can be tolerated by some animals (Gerson & Seaward, 1977;



Richardson & Young, 1977) and used for their own benefit (Hesbacher et al., 1995).

The termite *Constrictotermes cyphergaster* (Termitidae), found in the Caatinga and Cerrado biomes in Brazil, has been described as a potential lichen consumer (Bordereau & Pasteels, 2011; Mathews, 1977), but there is no firm evidence to date of that behavior. Moura and Vasconcellos (2006) observed that the termite *C. cyphergaster* maintained contact with lichens during foraging, but those authors were unable to conclude if the lichens were actually being consumed. Furthermore, Bezerra-Gusmão (pers. comm.) observed termite individuals foraging extensively on lichens and assumed they were used as food resources.

In order to demonstrate the consumption of lichens by *C. cyphergaster*, we surveyed the diversity of lichen species ingested by that termite in an area of Caatinga vegetation in the semiarid region of northeastern Brazil and tested the hypothesis that this consumption would be influenced by seasonal factors.

Materials and Methods

Study area

Field observations were conducted at the São João do Cariri Experimental Station (EESJC) (7°20'34"S, 36°31'50"W) belonging to Federal University of Paraíba (UFPB) in northeastern Brazil. The station area covers 381 ha, at elevations ranging from 400 to 700 m a.s.l. The region has an average annual precipitation rate of 386 mm, 50% humidity, and mean monthly temperatures ranging from 28 to 35 °C (Paraíba State Government, 1985). The regional climate is hot and dry, with irregular distributions of short periods of rainfall, with a prolonged dry season.

The regional vegetation is open, tree-shrub caatinga, dominated by the plants *Cenostigma pyramidale* Tul., *Croton blanchetianus* Müll. Arg., *Combretum leprosum* Mart., *Jatropha mollissima* (Pohl) Baill., *Aspidosperma pyrifolium* Mart., and *Tacinga palmadora* (Britton and Rose) N.P. Taylor and Stuppy (Barbosa et al., 2007). The soils are classified as Chromic/VerticLuvisols (Alfisols - USDA) in lowland areas, with Litholic Neosols associated with rock outcrops in an undulating landscape at higher elevations (Chaves et al., 2000).

Sampling Procedures

Five nests of *C. cyphergaster* spaced at least 50 m one from another were monitored during foraging activities in both the dry (November of 2012) and rainy (March of 2013) seasons. Observations were made over ten consecutive days for each climatic period (focusing always on the same nests), from 18:00h to 06:00h. All established foraging columns were monitored from the time the termites first left their nests to the farthest points of their foraging routes (about 18 m).

All of the lichen thalli explored were marked to determine termite visitation frequencies (= No. of times). The study did not take into account trails in the vegetation canopy, limiting its focus to the lower portions of the vegetation (up to ca. 2 m). At the end of the ten days of monitoring, the lichens visited were collected for identification and chemical analyses.

Lichen identifications were made using thalli characteristics such as shape, ascoma type, and ascospore color, size, and septation. Transversal sections of the thalli and ascoma were treated with iodine (I) and/or potassium hydroxide (KOH). The species were identified by consulting Cáceres (2007), Lücking and Rivas-Plata (2008), and Marbach (2000).

Lichen Intake

In order to evaluate lichen intake by termites, 20 workers from each nest population were captured after leaving a lichen thallus and placed in distilled water. A portion of the gut (crop) of each worker was dissected and its contents extracted. That material was stained with neutral red, phenol red, or 10% toluidine blue to detect the presence of lichen structures.

Lichen Chemical Analysis

The presence of lichenic compounds in *C. cyphergaster* guts was evaluated in 100 workers from each nest that were collected directly in the field while foraging on lichens. The workers were dissected, their digestive guts removed, and extracts were prepared using cold acetone. The lichen patches visited by *C. cyphergaster* were scraped with a steel blade and 10 mg of the biomass of each species was also extracted with acetone (1ml) to obtain their secondary metabolic compounds.

The extracts were subjected to thin layer chromatography (TLC) on F₂₅₄₊₃₆₆ Merck silica gel plates that were run in solvent system A (toluene/dioxane/acetic acid 180: 45: 5, v/v/v) (Culberson, 1972). After solvent evaporation, the plates were developed under long and short UV light, sprayed with 20% sulfuric acid, and subsequently heated on a hot plate at 50 °C until the bands became visible.

The compounds were identified based on their R_f and band colors, which were compared to standards of atranorin, divaricatic, usnic, norstictic, parietin, estictic, tamnolic, and didimic acids, compounds frequently encountered in lichens. Literature reviews on lichen biochemistry were consulted, and the descriptions of Rambold et al. (2001) were used to identify bands not comparable to the standards used.

Data Analysis

The relative frequencies of termite visits to the lichens were determined by the numbers of times each species was visited during the survey. Differences in termite visitation frequencies to lichens between the dry and rainy seasons were evaluated using the Kruskal-Wallis test. Lichen community

similarities between the two seasons were evaluated using non-metric multidimensional scaling (NMDS), and the structures of lichen clusters were compared through similarity analysis (ANOSIM), at a significance level of 5%. The analyzes were performed using Primer 6.1.1 software.

Results

Twenty-nine crustose lichen species distributed among 17 genera were found to be associated with the diet of *C. cyphergaster* (Table 1). The richness of lichen species consumed by termites was dissimilar between seasons (Fig 1). The dissimilarity observed using NMDS was confirmed by ANOSIM (Global test: $R = 0.192$; $p = 0.04$). Eleven lichen species were ingested only in the rainy season, ten only in the dry season, while eight were consumed during both climatic periods (Table 1).

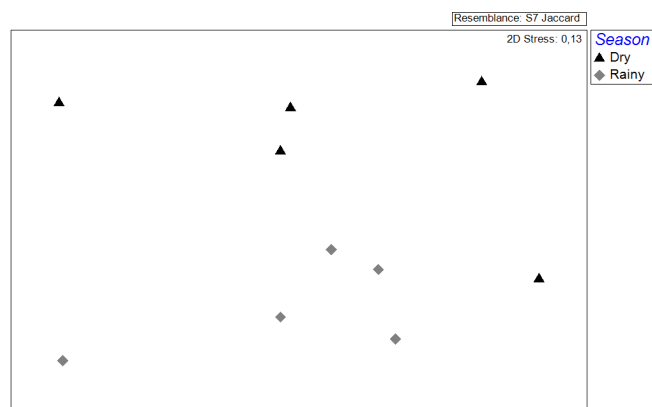


Fig 1. Non-metric multi-dimensional scaling ordination of similarity of lichen diversity ingested by *Constrictotermes cyphergaster* in the dry (2012) and rainy (2013) seasons in the Semiarid Region of Northeastern Brazil.

Table 1. Lichens consumed by *Constrictotermes cyphergaster*, relative frequency (%) of visits to the lichen thalli and secondary compounds observed in a semiarid region, NE Brazil. Legend: DS – dry season; RS – rain Season.

| Lichens Consumed | Relative Frequency (%) | | Secondary compounds |
|--|------------------------|------|---|
| | DS | RS | |
| Dry season | | | |
| <i>Anisomeridium subprostans</i> (Nyl.) R.C. Harris | 4.2 | 0 | Unidentified substance |
| <i>Anisomeridium tamarindi</i> (Fée) R.C. Harris | 4.2 | 0 | No substance detected |
| <i>Graphis submarginata</i> Lücking | 2 | 0 | Norstictic acid |
| <i>Graphis</i> sp. Adans | 2 | 0 | Norstictic acid |
| <i>Lecanora achroa</i> Nyl. | 8.3 | 0 | Norstictic acid; 2'-O-methylperlatolic acid |
| <i>Lecanora helva</i> Stizenb. | 4.2 | 0 | 2'-O-methylperlatolic acid |
| <i>Opegrapha</i> cf. <i>arengae</i> Vain | 2.1 | 0 | 2'-O-methylperlatolic acid |
| <i>Pertusaria quassiae</i> (Fée) Nyl. | 2.1 | 0 | Stictic acid |
| <i>Pertusaria</i> sp. DC. | 2.1 | 0 | Unidentified substance |
| <i>Polymeridium proponens</i> (Nyl.) R.C. Harris | 2.1 | 0 | No substance detected |
| Rainy season | | | |
| <i>Anisomeridium albisedum</i> (Nyl.) RC Harris | 0 | 1.2 | No substance detected |
| <i>Arthonia</i> sp. Ach. | 0 | 7.4 | Unidentified substance |
| <i>Coniocarpon cinnabarinum</i> DC. | 0 | 1.2 | No substance detected |
| <i>Canoparmelia</i> sp. Elix & Hale | 0 | 1.2 | Stictic acid |
| <i>Clandestinotrema</i> sp. Rivas Plata, Lücking & Lumbsch | 0 | 2.5 | No substance detected |
| <i>Graphis cincta</i> (Pers.) Aptroot | 0 | 4.9 | Tamnolic acid |
| <i>Mycoporum eschweileri</i> (Müll. Arg.) R.C. Harris | 0 | 1.2 | No substance detected |
| <i>Lecanora leprosa</i> Fée | 0 | 8.6 | Stictic acid |
| <i>Polymeridium albocinereum</i> (Kremp.) R.C. Harris | 0 | 1.2 | No substance detected |
| <i>Polymeridium amyloideum</i> R.C. Harris | 0 | 2.5 | Lichexanthone |
| <i>Polymeridium subcinereum</i> (Nyl.) R.C. Harris | 0 | 1.2 | No substance detected |
| Lichens consumed in both periods | | | Rainy Dry |
| <i>Chrysothrix xanthina</i> (Vainio) Kalb | 18.7 | 6.2 | Vulpinic acid Vulpinic acid |
| <i>Arthopyrenia cinchonae</i> (Ach.) Müll. Arg. | 8.3 | 6.2 | No substance detected No substance detected |
| <i>Dirinaria confluens</i> (Fr.) D. D. Awasthi | 12.5 | 10.2 | Divaricatic acid; Terpenes Divaricatic acid; Triterpenes |
| <i>Dirinaria leopoldii</i> (Stein) D.D. Awasthi | 4.2 | 1.2 | Divaricatic acid Triterpenes |
| <i>Glyphis scyphulifera</i> (Ach.) Staiger | 4.2 | 11.1 | No substance detected No substance detected |
| <i>Leucodecton occultum</i> (Eschw.) Frisch | 4.2 | 7.4 | Stictic acid Norstictic acid; Stictic acid |
| <i>Pertusaria flaven</i> Nyl. | 10.4 | 23.4 | Didymic acid Unidentified substance |
| <i>Pyrenula anomala</i> (Ach.) Vain. | 4.2 | 1.2 | Unidentified substance No substance detected |

Termite visitation frequencies to the lichens did not differ significantly between the two seasons ($P = 0.69$; $df = 1$; $H = 0.15$). The lichens *Chrysothrix xanthina*, *Dirinaria confluens* and *Pertusaria flavens* and *Lecanora achroa* were the most visited ones.

TLC analyses revealed twelve secondary lichen compounds ingested in both seasons (Table 1; Figs 2 and 3). In the dry season, six TLC bands were observed in the acetone extracts of termite crop samples. Bands with $R_f = 0.82$ and 0.42 were identified as atranorin and divaricatic acid respectively (Fig 2).

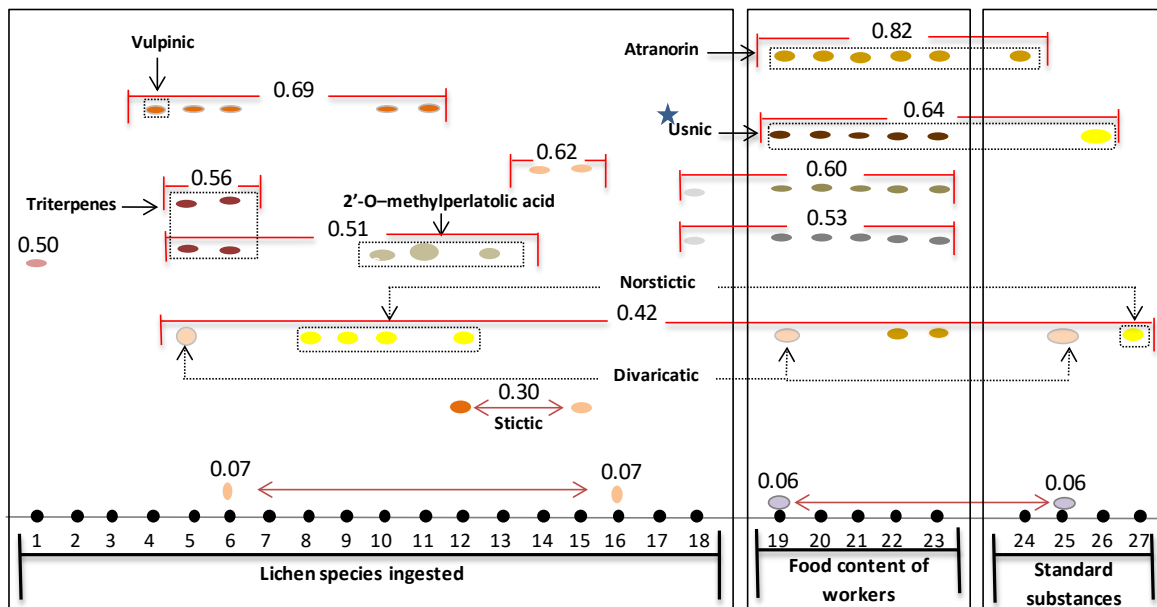


Fig 2. Thin layer chromatography of lichens organic extracts ingested by *Constrictotermes cyphergaster* and crop food content of workers during foraging in dry season (2012) in a semiarid region of northeastern Brazil. Chromatography points: 1-18: (Lichens): 1- *Anisomeridium subprostans*; 2- *A. tamarindi*; 3- *Arthopyrenia cinchonae*; 4- *Chrysothrix xanthina*; 5- *Dirinaria confluens*; 6- *D. leopoldii*; 7- *Glyphis scyphulifera*; 8- *Graphis submarginata*; 9- *Graphis* sp.; 10- *Lecanora achroa*; 11- *L. helva*; 12- *Leucodecton occultum*; 13- *Opegrapha* cf. *arengae*; 14- *Pertusaria flavens*; 15- *P. quassiae*; 16- *Pertusaria* sp.; 17- *Polymeridium proponens*; 18- *Pyrenula anomala*. 19 to 23: (Craw food content of workers who ate lichens): 19- Nest Population 1; 20 - Nest Population 2; 21- Nest Population 3; 22- Nest Population 4; 23- Nest Population 5. 24-27: (Standard substances): 24- Atranorin; 25- Divaricatic acid; 26- Usnic acid; 27- Nortistic acid.

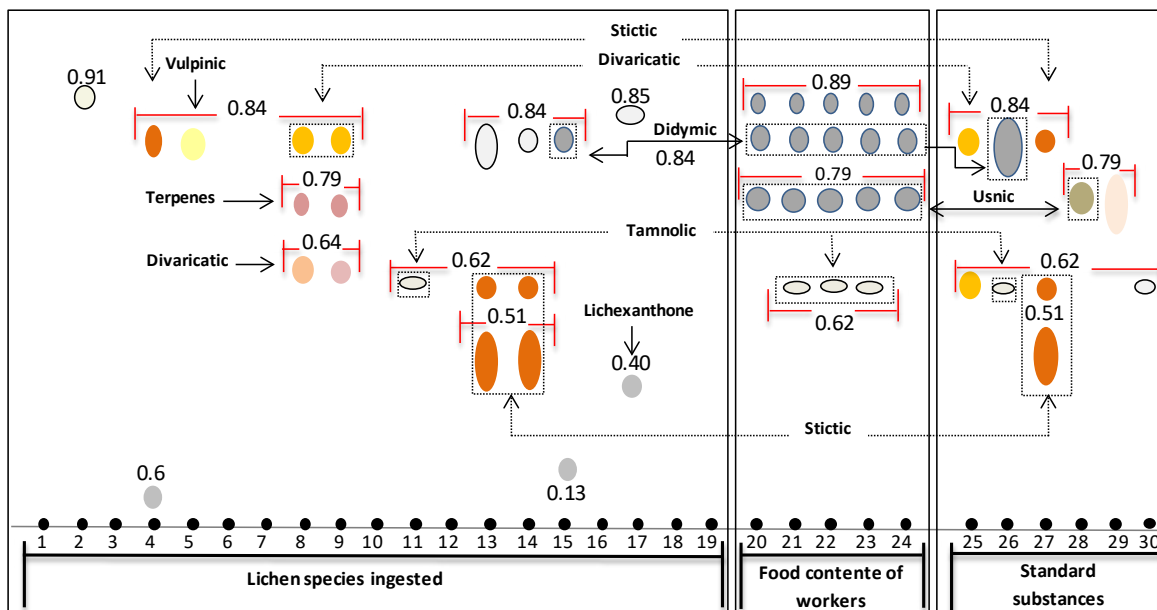


Fig 3. Thin layer chromatography of lichens organic extracts ingested by *Constrictotermes cyphergaster* and crop food content of workers during foraging in wet season (2013) in a semiarid region of northeastern Brazil. Chromatography points: 1-19: (Lichens): 1- *Anisomeridium albisedum*; 2- *Arthonia* sp.; 3- *Arthopyrenia cinchonae*; 4- *Canoparmelia* sp.; 5- *Chrysothrix xanthina*; 6- *Clandestinotrema* sp.; 7- *Coniocarponcin nabarinum*; 8- *Dirinaria confluens*; 9- *D. leopoldii*; 10- *Glyphis scyphulifera*; 11- *Graphis cincta*; 12- *Mycoporumes chweiler*; 13- *Lecanora leprosa*; 14- *Leucodecton occultum*; 15- *Pertusaria flavens*; 16- *Polymeridium albocinereum*; 17- *P. amyloideum*; 18- *P. subcinereum*; 19- *Pyrenula anomala*. 20 to 24: (Food contents of the workers who ate lichens): 20- Nest Population 1; 21 - Nest Population 2; 22- Nest Population 3; 23- Nest Population 4; 24- Nest Population 5. 25-30: (Standards substances): 25- Divaricatic acid; 26- Tamnolic acid and didymic; 27- Stictic acid; 28- Usnic acid; 29- Atranorin; 30- Parietin.

The $R_f = 0.64$ band was apparently equivalent to usnic acid, but the staining reaction did not correspond well to that standard (possibly due to its low concentration in the gut contents of the termites). Other compounds with $R_f = 0.60$, 0.53 , and 0.42 did not coincide with any of the standards used and could not be identified (Fig 2).

Four bands were observed in the gut contents of termites in the rainy season, and three of them coincided with the standards for didimic ($R_f = 0.84$), usnic ($R_f = 0.79$), and tamnolic acid ($R_f = 0.62$). An additional band was observed at $R_f = 0.89$ that did not correspond to any of the chemical standards utilized in this analysis (Fig 3).

Color analyses of the solid material collected from *C. cyphergaster* worker crops revealed algal cells, different spore types, and fungal hyphae (Fig 4).

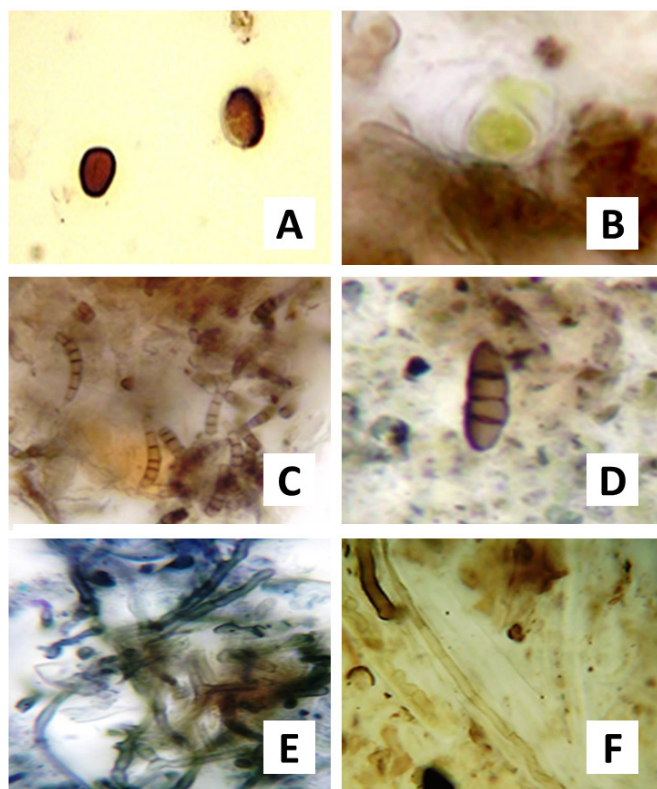


Fig 4. Lichen structures observed in the solid substrate of the crops of the workers of *Constrictotermes cyphergaster* after consuming lichens in the Semiarid Region of northeastern Brazil. Algae Cells (A and B); Fungal Cells (C and D); Fungal hyphae (E and F).

Discussion

The presence of lichen structures and compounds in the digestive tract of *C. cyphergaster* confirms their consumption by that termite. Information about cost/benefit ratios between those two organisms are relatively scarce, and there are many more questions than conclusive answers available concerning their interactions.

Crustose lichens are common in the diets of *Hospitalitermes* termites, as confirmed by the presence of spores of *Phaeotrema* sp., *Phaeographis* sp., and *Melaspilea*

sp. in their digestive tracts (Collins, 1979). The consumption of *Pertusaria* spp. and *Lecanora* spp. by snails and lepidopterans was previously observed (Plitt, 1934; Bailey, 1970; Boch et al., 2015). Those lichens were among the most visited by termites in the present study, and their thalli were the most frequent along the foraging trails of *C. cyphergaster*. Boch et al. (2015) reported that snails appear to prefer the lichens that are most frequent in their habitat, and they avoid less common species through their recognition of secondary compounds – supporting the idea that consumers adapt more readily to the most abundant foods.

Some lichenivorous invertebrates are considered potential dispersers of photobionts and mycobionts through their feces (Nash, 2008; Fröberg et al., 2001; Boch et al., 2011), and it is possible that *C. cyphergaster* makes up part of that group. Many of the green algae and spores found in that termite's digestive tract were apparently viable, and could form new lichens. Tests of the viability of those structures are currently being undertaken to clarify that hypothesis (Barbosa-Silva et al., in preparation).

According to Lawrey (1980), lichen-derived compounds can show direct toxicity to the intestinal microflora of invertebrates that consume them. Bezerra-Gusmão et al. (2015) were able to inhibit the growth of eight bacterial symbiont morphotypes in the guts of *C. cyphergaster* with usnic acid. Other compounds, such as norsictic and divarictic acids, and atranorin and parietin present in the lichens consumed by *C. cyphergaster*, also have antifungal and/or antibiotic effects (Bustinza, 1950; Ribeiro et al., 2002; Tay et al., 2004; Manojlovic et al., 2005). However, the roles of those compounds in termite diets still need to be investigated.

The seasonal differences observed in the species of lichens exploited by *C. cyphergaster* may reflect physicochemical variations in lichen steles (Dixon & Paiva, 1995; Giordani & Incert, 2007) as seasonality can promote changes in the activities of antioxidant enzymes, flavonoids, anthocyanins, and phenolic compounds found in lichens (Ghorbanli et al., 2012) that presumably alter the palatability of lichen stems (Gauslaa et al., 2013). Thus, knowing that the caatinga domain experiences extreme seasonal abiotic conditions (Sampaio, 1995; Silva et al., 2009), we accept the hypothesis that those variations can promote a seasonal selectivity of lichens by the termites.

The overall diversity of lichens ingested by *C. cyphergaster* is almost certainly greater than that documented in the present study, as it was impossible to investigate their foraging trails in the canopy – limiting our observations to the lower vegetation levels (up to 2 m). The list of lichen species that constitute the diet of *C. cyphergaster* will almost certainly be extended by future studies in other areas where it occurs.

In conclusion, the lichen species recorded in the present study are common in Caatinga environments (Cáceres, 2007; Cáceres et al., 2008; Menezes et al., 2011), and *C. cyphergaster* consumed 29 lichen species (with seasonal variations). This

report represents the first systematic examination of lichen intake by those termites and raises the following questions: (1) What is the cost/benefit balance of interactions between termites and lichens? (2) What evolutionary advantage(s) does feeding on lichens offer? and, (3) Which lichen compounds play important roles in termite diets?

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