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Lichen species co-occurrence patterns on five trees species of the montane rainforest of Gran Piedra, Santiago de Cuba

Dania Rosabal¹, Ana Rosa Burgaz² and Orlando J. Reyes³

Abstract: Rosabal, D.; Burgaz, A. R. & Reyes, O. J. 2014. Lichen species co-occurrence patterns on five trees species of the montane rainforest of Gran Piedra, Santiago de Cuba. *Bot. Complut.* 38: 97-104.

This study aims to determine lichens co-occurrence patterns on five phorophyte species in the montane rainforest of Gran Piedra, Santiago de Cuba. In each plot, all trees of these five species: *Gomidesia lindeniana*, *Coccoloba wrightii*, *Clusia tetrastigma*, *Dendropanax arboreus* and *Brunellia comocladifolia* were surveyed. On the 51 sampled phorophyte trees, 53 lichen species were found. Only *Gomidesia lindeniana* and *Coccoloba wrightii* exhibited probabilities for the C-score and CHECKER indices significantly higher than expected by chance; consequently, lichens co-occurrence are non-random on these phorophytes. For *Dendropanax arboreus*, *Clusia tetrastigma* and *Brunellia comocladifolia* the null hypothesis for these indices was not rejected. The enhanced of frequency of lichen species, increase the number of species pairs forming a checkerboard distribution. In conclusion, lichen species co-occurred less often than expected by chance, although this pattern was not similar for all phorophytes species.

Key words: lichens co-occurrence, co-occurrence index, competitive interactions.

Resumen: Rosabal, D.; Burgaz, A. R. & Reyes, O. J. 2014. Patrones de co-ocurrencia de líquenes corticícolas sobre cinco especies de árboles en la pluvisilva montana de la Gran Piedra, Santiago de Cuba. *Bot. Complut.* 38: 97-104.

El presente trabajo tiene como objetivo determinar los patrones de co-ocurrencia de líquenes corticícolas sobre cinco especies de forófitos en la pluvisilva montana de la Gran Piedra, Santiago de Cuba. En cada parcela se muestrearon todos los árboles de *Gomidesia lindeniana*, *Coccoloba wrightii*, *Clusia tetrastigma*, *Dendropanax arboreus* y *Brunellia comocladifolia*. Se encontraron 53 especies de líquenes, sobre 51 árboles muestreados. Solo *Gomidesia lindeniana* y *Coccoloba wrightii* exhibieron probabilidades estadísticamente significativas para los índices C-score y CHECKER; por tanto, la co-ocurrencia de líquenes fue no aleatoria sobre estos forófitos. Para *Dendropanax arboreus*, *Clusia tetrastigma* y *Brunellia comocladifolia* la hipótesis nula para estos índices no fue rechazada. La frecuencia de líquenes estuvo positivamente correlacionada con el aumento del número de pareja con distribuciones tablero. En conclusión, las especies de líquenes co-ocurrieron menos frecuentemente que lo esperado por azar, aunque este patrón no fue similar para todas las especies de forófitos.

Palabras claves: co-ocurrencia de líquenes, índices de co-ocurrencia, interacciones competitivas.

INTRODUCTION

The assemblage rules posit by Diamond (1975), emphasize the importance of interspecific interaction in determining the species composition of a community. One of them proposes that competitive interactions among species lead to non-random co-occurrence patterns. The competition is one of the most important mechanisms in structuring a community and its diversity (Armstrong & Welch 2007). Keddy (2001) defines it as the negative effect of an organism on another for the consumption or

the access control to a resource that is limited in its availability.

A null model is a generator of patterns based on the randomization of the ecological data of a random sampling, from a well-known distribution to a completely at random. Certain elements of the data remain constant and others vary stochastically to create new patterns in the one it assembles. The randomization creates a pattern that could be expected in absence of a particular ecological mechanism. These analyses reveal patterns of the community that are outstanding to prove ecological theories.

¹ Departamento de Biología, Universidad de Oriente, Patricio Lumumba s.n., Santiago de Cuba, C. P. 90500, Cuba (corresponding author: drl@cnt.uo.edu.cu)

² Departamento de Biología Vegetal I, Facultad de Biología, Universidad Complutense de Madrid, E-28040 Madrid, Spain

³ Centro Oriental de Ecosistemas y Biodiversidad, Santiago de Cuba.

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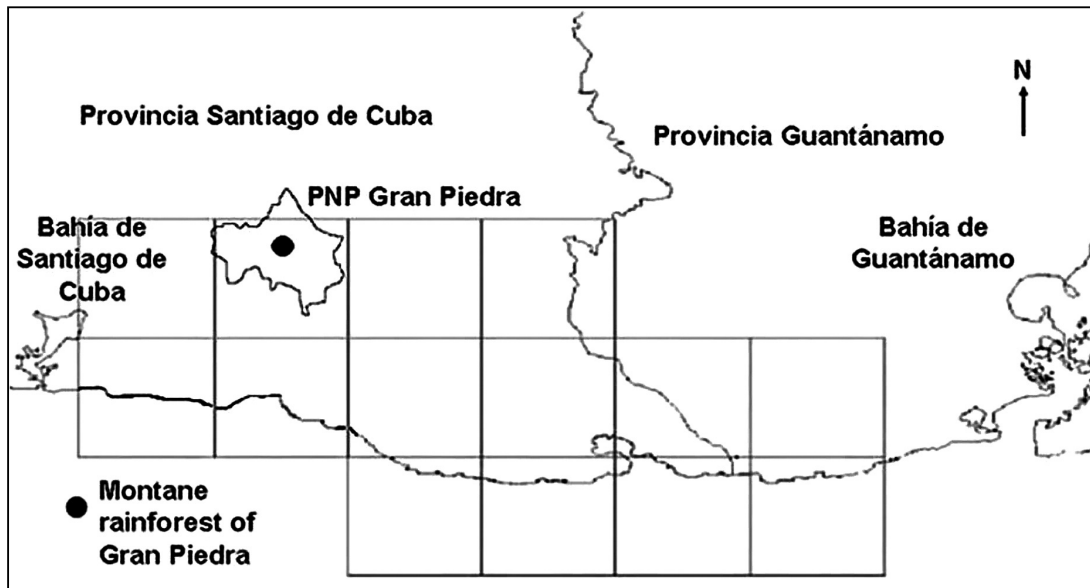


Fig. 1– Map of the protected area of Gran Piedra in Santiago de Cuba.

Null models have been a useful tool for evaluating pattern in presence-absence matrices (Gotelli & Graves 1996).

The montane rainforest of Gran Piedra shows a high floristic diversity and is considered a low forest by its physiognomy (Reyes *et al.* 2005). This forest belongs to the protected area “Paisaje Natural Protegido Gran Piedra”, with low disturbs level. The stress-gradient hypothesis (Bertness & Callaway 1994) postulates that facilitation is dominant in harsh conditions whereas competition is more important in benign environments. Therefore, we hypothesized that corticolous lichens would co-occur less often than expected by chance in the montane rainforest of Gran Piedra. This study aims to determine lichens species co-occurrence patterns on five phorophyte species in this forest.

MATERIALS AND METHODS

Study area. Field studies were carried out between March (2008) to May (2009) in the montane rainforest of Gran Piedra, Eastern Cuba, at about 1200 m above sea level (Fig. 1). This forest occupies a continuous area with an extension of 600 ha. The climate is typically tropical, with a mean annual rainfall of 1664 mm and mean annual temperature of 18.4°C. Relative humidity is nearly 90% mainly due to rainfall and fog, being the last one an important source of humidity with an average of 238 days/year (Montenegro 1991). The average number of days with rain is 130 and the average insolation is five to seven hours/day (Montenegro 1991).

The montane rainforest of Gran Piedra shows a high floristic diversity. The vegetation is composed of one arboreal stratum of 12–18 m high and emerging trees up to 25 m. The understory is 5 m high and the herbaceous stratum covers about 25–50% of the ground. Epiphytes as bromeliads, bryophytes and lichens are conspicuous (Reyes *et al.* 2005).

The species *Gomidesia lindeniana* O. Berg (Myrtaceae), *Coccoloba wrightii* Lindau (Polygonaceae), *Clusia tetrastigma* Vesque (Clusiaceae), *Dendropanax arboreus* (L.) Decne. et Planch. (Araliaceae) and *Brunellia comocladifolia* Bonpl. (Brunelliaceae) are some of the most frequent and characteristic trees in the montane rainforest of Gran Piedra (Reyes *et al.* 2005). *Coccoloba wrightii* and *Clusia tetrastigma* are multi-districal endemics of eastern Cuba, reaching 18 m in the Sierra Maestra massif (Bisse 1989, López *et al.* 1994). *Gomidesia lindeniana* is a small tree about 10 m high, distributed in the Antilles. *Dendropanax arboreus* and *Brunellia comocladifolia* reach the canopy of the forest with 15 m high; they are distributed in the Antilles and Central America.

Sampling design. Nine square plots of 625 m² were sampled; separated at least 50 m. In each plot, all trees of these five species: *Gomidesia lindeniana*, *Coccoloba wrightii*, *Clusia tetrastigma*, *Dendropanax arboreus* and *Brunellia comocladifolia* were surveyed (Table 1). Each tree was sampled from the ground to 2 m height.

Lichens were identified following the criteria of Sierk (1964), Wirth & Hale (1978), Hale (1987), Moberg (1990), Brako (1991), Galloway (1994), Lumbsch *et al.* (1999), Brodo *et al.* (2001), Aptroot *et al.* (2008, 2009). The nomenclature used was according to Kirk (2008), Mangold *et al.* (2008) and Rivas-Plata *et al.* (2010). A Novel XSZ-N207 Biological Microscope and a Novel NTB-2B Stereoscope were used in the identification

Table 1
List of the phorophyte species and number
of the sampled trees

Families	Species	N° of sampled trees
<i>Araliaceae</i>	<i>Dendropanax arboreus</i>	10
<i>Brunelliaceae</i>	<i>Brunellia comocladifolia</i>	9
<i>Clusiaceae</i>	<i>Clusia tetrastigma</i>	10
<i>Myrtaceae</i>	<i>Gomidesia lindeniana</i>	10
<i>Polygonaceae</i>	<i>Coccoloba wightii</i>	12

process. The vouchers were deposited in the Charles Ramsdem Herbarium of Universidad de Oriente, Santiago de Cuba, section of the BSC. Species frequency was determined by the number of trees on which a species occurred.

Data analysis. We constructed matrices of presence-absence where the presence of each lichen species (row) on each tree of the phorophyte species (columns) was represented. In order to detect the co-occurrence patterns of lichens community on the five phorophyte species, three indices were estimated: the C-score, the number of checkerboard species pairs (CHECKER) and the number of the species combinations (COMBO) (Gotelli 2000).

The C-score was calculated for each pair of species as $(r_i - S)(r_j - S) / (r_i r_j - S^2)$ where r_i and r_j are the matrix row totals for species i and j , while S is the number of squares where both species occur. This score was then averaged for all possible pairs of species in the matrix. This index gives an idea of species segregation (less species co-occurrence) or aggregation (more species co-occurrence), which allow distinguish between competition and facilitation; as well it is insensitive to noise in the data. The second index was calculated by counting the number of unique pairs of species that never co-occurred. The number of species combinations (COMBO) was counted by checking the columns of each matrix for specific combinations. COMBO may reflect the existence of forbidden species combinations. In a competitively structured community, there should be a higher C-score, more checkerboard species pairs and a lower number of species combinations than expected by chance (Gotelli 2000).

We used for the comparison fixed-equiprobable null model, which is recommended for a sample list (Gotelli 2000). In this model, only the frequency of each species was fixed while the total number of species supported by a single tree was reshuffled randomly, allowing any number of species, from zero to the total number of species recorded. This method assume that trees are similar in quality and size, therefore it permits vary the number of species.

In order to make the results comparable, we calculated the standardized effect size (SES) for each indices as $(I_{obs} - I_{sim}) / SD_{sim}$, where I_{obs} is the observed value for a given index of the lichen community structure, while I_{sim} and SD_{sim} are

the mean and standard deviation of the 5000 indices calculated from the simulated communities, it reflects the pattern expected in the absence of species interactions (Maestre *et al.* 2010). The SES quantifies the number of standard deviations that the observed index is above or below the mean index of the simulated matrices. The null hypothesis is that the average standardized effect size is zero (Gotelli & McCabe 2002). The SES measured from C-score index indicates segregation ($SES \geq 0$) and agregation ($SES \leq 0$) (Maestre *et al.* 2008). A single sample t-test was used to assess the null hypothesis that the mean SES measured from C-score index did not differ from zero (Belinchón *et al.* 2012); for this procedure, STATISTICA V. 6.0 program was used. The co-occurrence analysis was conducted using Ecosim 7.0 (Gotelli & Entsminger 2006).

Using STATISTICA V. 6.0, the Spearman rank correlation ($p < 0.05$) was applied to find a relationship between richness and frequency of lichens and the observed values of the three indices.

RESULTS

On the 51 sampled phorophyte trees, 53 lichen species were found. The family with the higher number of species was *Graphidaceae* (17); *Herpothallon rubrocinctum* was the most frequent species (Table 2). The highest species richness and frequency were found on *Dendropanax arboreus*, *Clusia tetrastigma* and *Brunellia comocladifolia* (Table 3).

The C-score and the number of checkerboard species (CHECKER) indices showed higher values for the observed matrices than the mean of the simulated indices for all phorophyte species, except for *Dendropanax arboreus*. However, only *Gomidesia lindeniana* and *Coccoloba wrightii* exhibited probabilities for these observations significantly higher than expected by chance; consequently, lichens co-occurrence are non-random on these phorophytes (Table 4). On the other hand, for *Dendropanax arboreus*, *Clusia tetrastigma* and *Brunellia comocladifolia* the null hypothesis for these indices was not rejected; therefore, lichens co-occurrence on these trees is random. The SES values from both indices were higher than zero in all phorophyte species except for *Dendropanax arboreus*. Nevertheless, these values did not differ significantly from zero ($t = 1.19, p = 0.3$). The number of combinations (COMBO) was lower than the mean of the simulated indices and the SES was lower than zero, but these values did not were statistically significant (Table 4). The Spearman rank correlation analysis was only significant for CHECKER and frequency of lichens ($r_s = 0.9, p = 0.037$). Thus, the enhanced of frequency of lichen species, increase the number of species pairs forming a checkerboard distribution.

Table 2
Families and species of lichenized fungi on five phorophytes species in Gran Piedra montane rainforest.
Numbers correspond to lichen species frequencies. **Gl:** *Gomidesia lindeniana*, **Cw:** *Coccoloba wrightii*,
Ct: *Clusia tetragymna*, **Da:** *Dendropanax arboreus* and **Bc:** *Brunellia comocladifolia*

Families	Species	Gl	Cw	Ct	Da	Bc	Total
<i>Arthoniaceae</i>	<i>Cryptothecia striata</i> Thor	0	0	0	0	1	1
	<i>Herpothallon rubrocinctum</i> Aptroot et al.	3	2	4	1	4	14
<i>Bacidiaceae</i>	<i>Phyllopsora buettneri</i> (Müll. Arg.) Zahlbr.	1	0	2	2	3	8
	<i>Phyllopsora confusa</i> Swinscow & Krog	0	1	0	1	0	2
	<i>Phyllopsora corallina</i> (Eschw.) Müll. Arg.	0	2	3	0	0	5
	<i>Phyllopsora isidiotyla</i> (Vain.) Riddle	0	0	0	1	0	1
	<i>Phyllopsora parvifolia</i> (Pers.) Müll. Arg.	0	2	2	4	0	8
<i>Coccocarpiaceae</i>	<i>Coccocarpia palmicola</i> (Spreng.) Arv. & D.J. Galloway	0	1	0	0	0	1
<i>Coenogoniaceae</i>	<i>Coenogonium disjunctum</i> Nyl.	0	0	0	2	0	2
	<i>Coenogonium interplexum</i> Nyl.	0	0	0	1	0	1
	<i>Coenogonium interpositum</i> Nyl.	0	1	0	0	0	1
	<i>Coenogonium leprieurii</i> (Mont.) Nyl.	0	0	2	0	0	2
	<i>Coenogonium linkii</i> Ehrenb.	0	1	0	0	0	1
	<i>Coenogonium pusillum</i> (Mont.) Lücking et al.	0	0	1	2	1	4
<i>Collemaaceae</i>	<i>Leptogium austroamericanum</i> (Malme) C.W. Dodge	0	2	2	1	0	5
	<i>Leptogium azureum</i> (Sw. ex Ach.) Mont.	0	0	0	1	0	1
	<i>Leptogium cyanescens</i> (Pers.) Körb.	0	0	1	0	0	1
<i>Crocyniaceae</i>	<i>Crocynia pyxinoidea</i> Nyl.	1	3	3	1	4	12
<i>Graphidaceae</i>	<i>Chapsa neei</i> (Hale) Mangol & Lücking	0	0	0	0	2	2
	<i>Glyphis cicatricosa</i> Ach.	1	0	0	0	0	1
	<i>Graphis adpressa</i> Vain.	1	0	0	3	0	4
	<i>Graphis elegans</i> (Borrer ex Sm.) Ach.	0	0	0	1	1	2
	<i>Graphis triticea</i> Nyl.	0	0	0	1	0	1
	<i>Graphis rustica</i> Kremp.	0	0	1	1	1	3
	<i>Myriotrema costaricensis</i> (Müll. Arg.) Hale	2	0	0	0	0	2
	<i>Ocellularia antillensis</i> Hale	0	1	1	1	1	4
	<i>Ocellularia crocea</i> (Kremp.) Overeem & D. Overeem	1	0	0	0	1	2
	<i>Ocellularia dolichotata</i> (Nyl.) Zahlbr.	0	0	1	0	1	2
	<i>Ocellularia perforata</i> (Leight.) Müll. Arg.	0	0	0	2	1	2
	<i>Ocellularia praestans</i> (Müll. Arg.) Hale	1	4	1	2	3	11
	<i>Ocellularia subpraestans</i> (Hale) Hale	1	0	0	0	0	1
	<i>Ocellularia terebrata</i> (Ach.) Müll. Arg.	0	0	0	0	2	2
	<i>Thelotrema adjectum</i> Nyl.	0	1	0	0	0	1
	<i>Thelotrema lepadinum</i> (Ach.) Ach.	0	1	0	0	0	1
<i>Thelotrema porinoides</i> Mont. & Bosch	0	0	0	1	0	1	
<i>Lobariaceae</i>	<i>Sticta weigelii</i> Isert	0	1	0	1	0	2

Table 2 (cont.)

Families	Species	Gl	Cw	Ct	Da	Bc	Total
Parmeliaceae	<i>Hypotrachyna livida</i> (Taylor) Hale	0	0	0	0	1	1
	<i>Parmotrema tinctorum</i> (Despr. ex Nyl.) Hale	0	0	0	0	1	1
Pertusariaceae	<i>Pertusaria azulensis</i> B. de Lesd	0	0	0	1	0	1
	<i>Pertusaria velata</i> (Turner) Nyl.	2	0	0	0	0	2
Physciaceae	<i>Heterodermia leucomela</i>	0	2	2	1	1	6
Porinaceae	<i>Porina distans</i> Vězda & Vivant	2	2	3	3	2	12
	<i>Porina mastoidea</i> Fée	1	3	2	1	2	8
	<i>Porina nucula</i> Ach.	0	0	2	0	0	2
Pyrenulaceae	<i>Pyrenula andina</i> Aptroot	0	0	0	0	1	1
	<i>Pyrenula cubana</i> (Müll. Arg.) R.C. Harris	0	0		1	0	1
	<i>Pyrenula duplicans</i> (Nyl.) Aptroot	0	0	1	0	0	1
	<i>Pyrenula macrocarpa</i> A. Massal.	0	0	1	1	0	2
	<i>Pyrenula santesis</i> (Nyl.) Müll. Arg.	0	0	1	0	1	2
	<i>Pyrenula subcongruens</i> Müll. Arg.	0	0	0	1	0	1
	<i>Pyrenula mamillana</i> (Ach.) Trevis.	0	0	2	0	0	2
Trypetheliaceae	<i>Pseudopyrenula subnudata</i> Müll. Arg.	0	1	1	3	0	5
	<i>Trypethelium subcatervarium</i> Malme	0	0	0	0	1	1

Table 3
Species richness and frequency values for each
phorophyte species

Phorophytes	Richness	Frequency
<i>Gomidesia lindeniana</i>	12	17
<i>Coccoloba wrightii</i>	18	31
<i>Clusia tetrastigma</i>	22	39
<i>Dendropanax arboreus</i>	28	42
<i>Brunellia comocladifolia</i>	22	36

DISCUSSION

Lichen assemblages on *Gomidesia lindeniana* and *Coccoloba wrightii* co-occurred less often than expected by chance in the montane rainforest of Gran Piedra. Lichens on these phorophytes were organized into checkerboard distributions, which agreed with the basic predictions of Diamond (1975) assembly rules model.

Gomidesia lindeniana and *Coccoloba wrightii* show a small area of the trunk, compared to the other three phorophytes. This feature could imply a decrease of the suitable microsites on the bark, restraining the colonization of lichens with different ecological niches. Also, this characteristic of the trunk reduces the surface exposed to diaspores that could potentially originate new thallus. According to Maestre *et al.* (2008), lichens species co-occurrence is determined by habitat conditions, dispersion and forms of growth. Rosabal *et al.* (2012, 2013) found that lichens with crustose biotype and sexual reproduction are the most frequent strategies in the montane rainforest of Gran Piedra. As well, Rosabal *et al.* (2010) describe the microclimatic conditions as suitable for the establishment of lichens in the understory of this forest. Thus, the limiting resource on these phorophytes is the size of the habitat. The patterns observed related to the lichens co-occurrence coincides with the phenomenon of segregation of niches, where the lichens similar in biotype and dispersion forms are separated by their habitat requirements, diminishing the competition. According to Jaksic & Marone (2007),

Table 4

Summary of the indices values for each phorophyte species. Significant p-values are in bold. **Obs**: values of the indices in observed matrices, **Sim**: simulated matrices, **CHECKER**: number of species pairs forming a checkerboard distribution, **COMBO**: number of species combinations, **SES**: standardized effect size

Phorophytes	C-score				CHECKER				COMBO			
	Obs	Sim	p	SES	Obs	Sim	p	SES	Obs	Sim	p	SES
<i>Gomidesia lindeniana</i>	1,74	1,51	0,002	2,07	59	53	0,007	1,85	9	9,1	0,7	-0,14
<i>Coccoloba wrightii</i>	2,37	2,16	0,002	2,06	128	118	0,002	2,10	11	11,7	0,2	-1,50
<i>Clusia tetrastigma</i>	2,18	2,12	0,310	0,58	166	164	0,460	0,28	10	9,9	1,0	0,09
<i>Dendropanax arboreus</i>	1,52	1,61	0,930	-1,64	281	298	0,970	-2,23	10	9,9	1,0	0,06
<i>Brunellia comocladifolia</i>	1,14	1,06	0,160	0,98	86	80	0,070	1,23	5	4,9	1,0	0,03

while more similar species are in the use of the resource, more segregated should be the niches to avoid the competitive exclusion; prediction reflected in the obtained results.

Rosabal *et al.* (2013) found that lichen species diversity on these five phorophytes varied in relation to diameter of the trunk, roughness, pH and phenol concentration of the bark. Also, this lichens diversity was correlated with *Clusia tetrastigma*, *Dendropanax arboreus* and *Brunellia comocladifolia*, suggesting suitable habitat conditions for growth of lichens. We did not find a pattern, statistically significant that indicates that the co-occurrence of species is lesser than expected by chance on these three phorophytes compared with *Gomidesia lindeniana* and *Coccoloba wrightii*. Therefore, *Clusia tetrastigma*, *Dendropanax arboreus* and *Brunellia comocladifolia* favor establishment and co-occurrence of lichens. Jaksic & Marone (2007) settled that if the niche of a species is included inside the niche of a second species and both are dominant in different levels of the resource, the first one will cause the decrease of the frequency of the non-dominant species in that level of the resource, allowing the co-existence.

According to Pitta *et al.* (2012), significant pairwise co-occurrence patterns are not the rule in the majority of biotic communities. Only a few matrices exhibit significant deviations from random patterns and a large part of the discussion on species co-occurrence had originally been based on a few exceptional data sets that are not indicative of general patterns. In the montane rainforest of Gran Piedra, we cannot generalize that lichens assembly co-occurred less often than expected by chance, because co-occurrence patterns vary depending on the habitat conditions.

Consistent with Maestre *et al.* (2008), the SES higher or lower than zero indicates species segregation or aggre-

gation, respectively. We did not could demonstrate statistically lichen species segregation, in a broad view. However, the SES values of *Gomidesia lindeniana* and *Coccoloba wrightii* were very higher than zero; hence, we consider that lichen species segregation is occurring at least on these two phorophytes. Belinchón *et al.* (2012) did not find that SES values were significantly higher than zero with fixed-equiproable null model, in agreement with our results.

The magnitude of the species co-occurrence was not affected by the species richness, but it was influenced by species frequency. Lichen species with high frequency could displace to others by colonization of the available microsite. Also, some species show low frequency and high space dispersion, which adds a stochastic component to the probability of finding these species in the area. The combination of these two strategies could enhance of the number of species pairs forming a checkerboard distribution. According to Halffter *et al.* (2005), a strong replacement of species and a high number of rare species are characteristic of tropical forests, even without any change in the environment. This occurs as consequence of the high diversity of habitats and niches to occupy for the species. Belinchón *et al.* (2012) did not find relationship between the co-occurrence of species and the total number of co-existing species, the coverage of dominant species nor the coverage of bryophytes. They did not evaluate the effect of frequency on the co-occurrence of species; therefore our results coincide partially with those of these authors.

In conclusion, lichen species co-occurred less often than expected by chance, although this pattern was not similar for all phorophytes species. Lichen species co-occurred less in *Gomidesia lindeniana* and *Coccoloba wrightii* than *Clusia tetrastigma*, *Dendropanax arboreus* and *Brunellia comocladifolia*. Probably, because the last

three show characteristic that favor species coexistence. Lichens on *Gomidesia lindeniana* and *Coccoloba wrightii* showed species segregation, possibly as result of competitive interaction by space.

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