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Associations between tree snails and corticolous lichens in a secondary forest in eastern Cuba

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Abstract: Snail-lichen interactions have received little attention in tropical ecosystems. Here, we studied the species richness of corticolous lichens with snail grazing traces on host trees inhabited by the Cuban tree snails, *Polymita venusta*, *Liguus fasciatus* and *Hemitrochus lucipeta* at La Rinconada, eastern Cuba. We sampled lichen specimens from ground level to 2 m, on the trunks of 15 host trees of eight species, in a 6 000 m^2 forest patch, in April 2012. In addition, we sampled snail feces from the three snail species. Most of the tree snail and lichen species were associated with a tree species usually with smooth bark, *Senna atomaria*. We found 30 lichen species, of which 19 were identified to species, three to genus, and eight remain undetermined. Non-metric multidimensional scaling and χ^2 tests showed that the three snail species had different associations with lichen species. *Liguus fasciatus* is associated with *Physcia sorediosa* and *P. aipolia*; *H. lucipeta* is associated with *Platythecium grammitis* and an unknown lichen, and *P. venusta* is associated with *Buellia spuria* and *Chrysothrix candelaris*. Evidence from snail grazing damage on lichen species, together with ingested spores from six species, suggested that *L. fasciatus* and *P. venusta* are generalist herbivores.

Keywords: herbivory, lichen-animal interaction, Gastropoda, Stylommatophora.

Resumen: Asociaciones entre moluscos arborícolas y líquenes cortícolas en un bosque secundario de Cuba oriental. En los ecosistemas tropicales las interacciones moluscos-líquenes han recibido escasa atención. En el presente trabajo se estudió la riqueza específica de líquenes cortícolas con huellas de herbivoría de los moluscos arborícolas cubanos, *Polymita venusta*, *Liguus fasciatus* and *Hemitrochus lucipeta*, en La Rinconada, Cuba oriental. En abril 2012, en un transecto de bosque secundario de 6 000 m^2, se recolectaron muestras de líquenes hasta 2 m de altura sobre el suelo, en troncos de 15 árboles de 8 especies. Además, se recolectaron heces de las tres especies de moluscos. La mayoría de los moluscos y líquenes utilizaron como substrato árboles de *Senna atomaria*, generalmente con corteza lisa. Se recolectaron 30 especies de líquenes, 19 identificadas hasta especie, 3 hasta género y 8 permanecen sin identificación. El Escalamiento Multidimensional no Paramétrico y las pruebas χ^2 mostraron que las tres especies de moluscos se asocian de manera diferencial con especies de líquenes. *Liguus fasciatus* estuvo asociado con *Physcia sorediosa* y *P. aipolia*, *H. lucipeta* con *Platythecium grammitis* y una especie indeterminada, mientras *P. venusta* se asoció con *Buellia spuria* y *Chrysothrix candelaris*. La evidencia de las huellas de herbivoría de los moluscos a los líquenes, conjuntamente con la presencia en las heces de esporas de seis especies de líquenes, sugiere que *L. fasciatus* y *P. venusta* son especies herbívoras generalistas.

Palabras Clave: Gastropoda, herbivoría, interacción liquen-animal, Stylommatophora.

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Introduction

Snails are key components of terrestrial communities due to their role as detritivores and herbivores (Rollo, 1988; Baur *et al.*, 1992, 1994, 2000; Curry, 1994; Hatziioannou *et al.*, 1994; Cameron, 2016; Price *et al.*, 2016). They are known to exert selective pressures affecting the phenology, morphology and defensive systems of various tree species and their epiphytes, including lichens (Lücking and Bernecker-Lücking, 2000; Speiser, 2001; Asplund and Gauslaa, 2008; Asplund *et al.*, 2010; Boch *et al.*, 2016).

Land snails that feed on lichen are often generalists and their snail grazing traces on lichens have been frequently reported (Coker, 1967; Peake and James, 1967; Shachak *et al.*, 1987; Fröberg *et al.*, 1993; Baur *et al.*, 1995, 2000; Lücking and Bernecker-Lücking, 2000; Vatne *et al.*, 2010; Boch *et al.*, 2015; Asplund *et al.*, 2016, 2018). Although there is a growing interest in snail-lichen associations (Lawrey, 1983; Fröberg *et al.*, 2006, 2011; Asplund *et al.*, 2010; Asplund and Wardle, 2013, 2017), most of the focus has been mainly onnon-tropical regions despite the remarkable lichen species richness occurring in the tropics (Lücking *et al.*, 2014; Hawksworth and Lücking, 2017). In Cuba, this gap is noteworthy given not only the high diversity of Cuban lichens (Pluntke, 1984; Minter *et al.*, 2001, 2002; Rosabal *et al.*, 2016) but also of Cuban land snails (Hernández-Quinta *et al.*, 2017).

Torre (1950) remarked that the Cuban snails, *Polymita* spp., feed exclusively on lichens and fungi growing epiphytically on their host trees. Díaz-Piferrer (1961) confirmed Torre's approach through an analysis of the stomach content in *Polymita muscarum* (Lea, 1834). This snail species was associated with host trees having a high abundance of epiphyte fungi (Bidart, 1997). Likewise, the most common host tree species of *Polymita venusta* (Gmelin, 1792) also supported the most lichen genera (Reyes-Tur and González-Rodríguez, 2003). *Liguus fasciatus* (Müller, 1774), a tree snail often co-occurring with *Polymita* spp. seems to display similar feeding preferences for corticolous lichens (*i.e.*, bark-growing), fungi and algae (Pilsbry, 1946; González-Guillén, 2014; González-Guillén *et al.*, 2018). Yet, for the rest of Cuban tree snails, information is scattered, insufficient or missing.

Here, our purpose was to identify the lichen species with grazing traces growing on host trees of the tree snails *P. venusta*, *L. fasciatus* and *Hemitrochus lucipeta* (Poey, 1854) in hills located at La Rinconada, Jiguaní municipality, Granma province, Cuba. We also evaluated the association of the three tree snails with corticolous lichen species, including evidence from snail feces.

Materials and Methods

Study area

The studied forest was located at La Rinconada locality, 10 km Southeast of Jiguaní municipality in Granma province, eastern Cuba (Fig. 1). The stand was a secondary forest, as defined by the criteria of Capote and Berazaín (1984). Dominant plant species included *Acacia* sp.; *Bromelia pinguin*, L.; *Comocladia dentata*, Jacq.; *Croton lucidus*, L.; *Cupania* sp.; *Eugenia* sp.; *Lantana* sp.; *Lysiloma* sp.; *Senna atomaria* (L.) Irwin & Barneby, and *Smilax havanensis*, Jacq. The maximum height of these trees and shrubs ranged between 5 and 12 m and they formed a closed canopy with a 50 m^2 total area of harvested-related gaps.

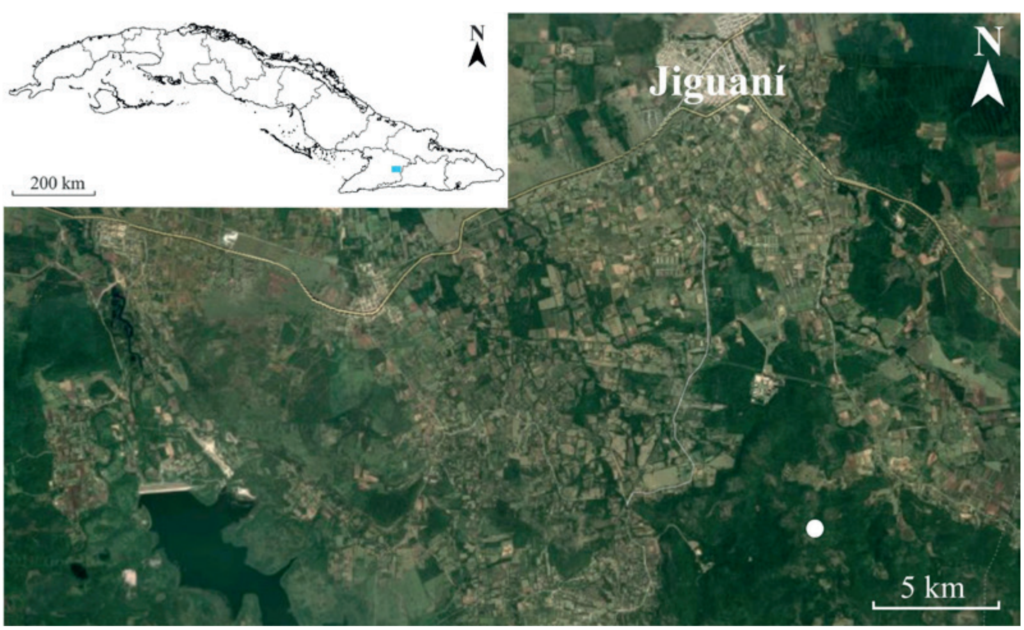

Figure 1. Geographical location of study site in Jiguaní municipality, on eastern Cuba.
Figura 1. Posición geográfica de la localidad de estudio en el municipio Jiguaní, Cuba Oriental.

Field sampling and laboratory analysis

Field work was done April 14th-15th, 2012 in a 6 000 m^2 transect (2 000 m length x 3 m width). We selected 15 living trees of 8 species on which we found evidence for presence of the tree snails *P. venusta*, *L. fasciatus* and *H. lucipeta*. Distance to closest sampled tree was minimum 40 m. Each studied host tree was identified to species. We recorded host tree total height (in m), snail species present, number of snail individuals, and lichen species richness up to 2 m height of the trunk. Each tree was investigated by two researchers for 1 h, the total area sampled was between 1 000 and 2 000 cm^2.

Corticolous lichens bearing evidence of snail herbivory were sampled for identification in the laboratory. In addition, a sample of snails was captured and housed individually in plastic containers. Their fecal matter was sampled after 20 min and then they were released to their original host trees. Fecal samples were kept in plastic bags at room temperature, between 7-15 days prior to examination with a stereomicroscope in the laboratory. Grazing traces on lichens were ascribed to these gastropods through direct observations and examination of grazed damage by photography of the traces by snail radulae (Fig. 2).

Lichens were identified using specialized keys (Wirth and Hale, 1978; Moberg, 1990; Brodo *et al.*, 2001; Aptroot *et al.*, 2008) and viewing through two Novel microscopes: XSZ-N207 and NTB-2B. Nomenclature followed Mycobank (Crous *et al.*, 2004; Robert *et al.*, 2005, 2013).

Data analysis

The occurrence frequency of each lichen species was estimated as the percentage of host trees with presence records of each lichen species of the total number of studied trees. A Sørensen similarity matrix was computed from the presence-absence matrix of tree snail and lichen species in sampled host trees. This similarity matrix including both, snails and lichens, was used to conduct a Non-metric multidimensional scaling (NMDS) for the visualization of multivariate patterns. This scaling was accomplished with 25 permutations, establishing as significant interaction criteria the stress values over or equal to 0.1 (Jongman *et al.*, 2001; Quinn and Keough, 2002). To validate the NMDS results, we used the χ^2 (Chi-square) test to compare the observed frequencies of co-ocurrence between the tree snail and lichen species, and the expected frequencies if such co-ocurrence was just random. Statistical routines were performed using STATISTICA v. 6.1 (StatSoft, 2003) and PRIMER v. 6.0 (Clarke and Gorley, 2006).

Results

Tree snails associated with host trees

Liguus fasciatus was the most frequent snail (n = 38 snail specimens, 73 % of the trees), followed by *P. venusta* (n = 21, 60 %) and *H. lucipeta* (n = 29, 20 %, restricted to *Lysiloma* sp.), with a total of 88 snails over all three species. Over all

FIGURE 2. Different patterns of grazing traces on lichens caused by the radulae of tree snails, A. Large grazing traces and B. Small grazing traces.

FIGURA 2. Diferentes patrones de huellas de herbivoría causadas por las rádulas de moluscos arborícolas a los líquenes, A. Huellas de talla grande y B. Huellas de talla pequeña.

species, abundance of snails per host tree ranged from one to 18 individuals. Grazing traces of tree snails on lichens were recorded for 93 % of the host trees. Most of the trees had smooth bark (53 %) and heights ranged from 2 to 9 m. Tree snails were detected on 8 tree species, with higher frequencies on *Senna atomaria* (40 %) and *Lysiloma* sp. (20 %); these two species commonly had smooth barks and varied in height between 3 and 6 m. Host species with only one occurrence of a tree snail were *Melicoccus bijugatus* Jacq., *Acacia* sp., *Eugenia* sp., *Harrisia eriophora* (Pfeiff.) Britton, *Oxandra laceolata* (Sw.) Baill., and one unidentified tree species without leaves and flowers; however, only the first species had smooth bark.

Tree snail-corticolous lichen associations

The corticolous lichen species collected in the studied locality are given in Table 1. There were 30 lichen species belonging to at least 17 genera and 12 families; 19 were identified to species; three to genus, and eight were not determined because they were sterile or lacked spores. Most (56.7 %) were crustose, 40 % foliose and just 3.3 % fruticose. The families with highest species diversity were Graphidaceae (4) and Parmeliaceae (4). Species richness ranged between 1 to 9 lichen species, with 73 % of the trees having from 2 to 6 lichen species. *Senna atomaria* had from 3 to 9 species per tree and hosted 76.7 % of recorded lichen species. Although, most of these lichens were associated with *P. venusta* (83 %, n = 30) and *L. fasciatus* (80 %); a lower association was with *H. lucipeta* (17 %).

Higher lichen occurrence frequency in host trees was recorded for *Buellia spuria* (47 %), *Chrysothrix candelaris* (33 %), *Physcia sorediosa* (33 %) and *Physcia aipolia* (27 %). In addition, regarding with availability of the two most common tree species (Table 1), *B. spuria* was frequently associated with *Lysiloma* sp. (67 %). Otherwise, *C. candelaris* (33 %) and the two mentioned *Physcia* species were associated with *S. atomaria* (50 %).

Although specimens of *B. spuria* and *Platythecium grammitis* were not grazed in a tree of *Lysiloma* sp., grazing traces of tree snails were recorded on 100 % of lichen species. The extent of grazing damage to lichen species seems to vary irregularly with the structure of the lichen community on each tree (Fig. 2). Furthermore, among snail feces samples, we identified two lichen species from their spores: *B. spuria* was in feces of all three tree snail species, and *Coenogonium roumeguerianum* spores were in feces of *P. venusta* and *L. fasciatus*. Four other lichen species were evident from spores but were not identifiable and were recorded as separate entities.

Dispersion of tree snail and corticolous lichen species along the two first NMDS axes (Fig. 3) and the observed frequencies of co-ocurrence between snail and lichen species (Fig. 4) documented an association between the snail *H. lucipeta* and the crustaceous lichens *Platythecium grammitis* (χ^2 = 11.6; df = 1; p < 0.001) and the undetermined lichen species 3 (χ^2 = 100; df = 1; p < 0.001). Nevertheless, *P. venusta* displayed higher association with trees that carried *B. spuria* (χ^2 = 17.6; df = 1; p < 0.001) and *C. candelaris* (χ^2 = 36; df = 1; p < 0.001). The snail *L. fasciatus* significantly associated with the foliose lichens *P. sorediosa* (χ^2 = 36; df = 1; p < 0.001) and *P. aipolia* (χ^2 = 100; df = 1; p < 0.001). In addition, there was a weakly significant association between *L. fasciatus* and *C. candelaris* (χ^2 = 4; df = 1; p = 0.045).

Discussion

Our finding that lichen species richness per host tree ranged from 1 to 9, with most of the trees bearing between 2 to 6 lichen species, could be potentially explained by substrate associations of lichens which vary according to microhabitat features and forest type. Rosabal *et al.* (2012) did not find any trend in species richness related to changes in tree diameter or bark roughness in a semideciduous forest. By contrast, Rosabal *et al.* (2013) later found that lichen species diversity varied in relation to the diameter of the trunk, pH and phenol concentration of the bark in a montane rain forest. In addition, a constrained distribution of lichen species to certain forest types is expected because lichens often grow under specific micro-niche conditions (Soto-Medina *et al.*, 2012) and their distribution is affected by lichenivorous gastropods (Asplund *et al.*, 2018).

We found that 76.7 % of recorded lichen species were hosted by one tree species, *S. atomaria,* which usually has smooth bark. This morphological trait might increase the possibilities of lichen growth on the bark surface. Similarly, *P. venusta* tree snails were associated with smooth bark at Sardinero locality, Santiago de Cuba province, eastern Cuba (Reyes-Tur and González-Rodríguez, 2003). At this other locality, the lichens *Buellia*, *Lecanora*,

Table 1. Data of corticolous lichen species found on 15 host trees of tree snails species (i.e., *Polymita venusta*, *Liguus fasciatus, Hemitrochus lucipeta*) and frequency on the two common host tree species from La Rinconada, Jiguaní municipality, Granma, Cuba. [Growth form]: C, Crustaceous; F, Foliose; FB, Foliose with broad lobes; Fr, Fruticose.

Tabla 1. Datos de las especies de líquenes cortícolas encontradas sobre 15 árboles hospederos de moluscos arborícolas (i.e., *Polymita venusta, Liguus fasciatus, Hemitrochus lucipeta*) y su frecuencia sobre las dos especies de árboles más comunes como hospederas, en La Rinconada, municipio Jiguaní, Granma, Cuba. [Forma de crecimiento]: C, Crustáceo; F, Foliáceo; FB, Foliáceo con lóbulos anchos; Fr, Fruticuloso.

Family/ Species	Occurrence frequency (%)	Frequency on *Senna atomaria* (%)	Frequency on *Lysiloma* sp. (%)
Arthoniaceae			
Arthonia cinnabarina (DC.) Wallr. [C]	20	33.3	0
Arthopyreniaceae			
Bogoriella subfallens (Müll. Arg.) Aptroot & Lücking [C]	6.7	16.7	0
Caliciaceae			
Buellia spuria (Schaer.) Anzi [C]	46.7	33.3	66.7
Dirinaria picta (Sw.) Clem. [F]	13.3	33.3	0
Pyxine sp. [F]	6.7	16.7	0
Chrysotrichaceae			
Chrysothrix candelaris (L.) J.R. Laundon [C]	33.3	33.3	0
Coenogoniaceae			
Coenogonium roumeguerianum (Müll. Arg.) Kalb [C]	20	16.7	0
Graphidaceae			
Graphis adpressa Vain. [C]	13.3	33.3	0
Graphis sp. [C]	6.7	0	0
Platythecium grammitis (Fée) Staiger [C]	20	16.7	66.7
Undetermined species 1 [C]	20	16.7	66.7
Parmeliaceae			
Parmotrema cristiferum (Taylor) Hale [FB]	20	50	0
Parmotrema hypotropum (Nyl.) Hale [FB]	6.7	16.7	0
Parmotrema praesorediosum (Nyl.) Hale [FB]	6.7	16.7	0
Platismatia sp. [F]	13.3	33.3	0
Physciaceae			
Physcia aipolia (Ehrh. *ex* Humb.) Fürnr. [F]	26.7	50	0
Physcia americana G. Merrill [F]	6.7	16.7	0
Physcia sorediosa (Vain.) Lynge [F]	33.3	50	0
Pyrenulaceae			
Pyrenula leucostoma Ach. [C]	6.7	0	0
Ramalinaceae			
Ramalina peruviana Ach. [Fr]	6.7	0	0
Strigulaceae			
Strigula griseonitens R.C. Harris [C]	13.3	16.7	33.3
Trypetheliaceae			
Astrothelium subcatervarium (Malme) Aptroot & Lücking [C]	6.7	16.7	0
Trypethelium eluteriae Spreng. [C]	6.7	16.7	0
Unknown Family			
Undetermined species 2 [C]	6.7	0	0
Undetermined species 3 [C]	6.7	0	33.3
Undetermined species 4 [F]	6.7	0	0
Undetermined species 5 [F]	6.7	0	0
Undetermined species 6 [C]	6.7	16.7	0
Undetermined species 7 [F]	6.7	16.7	0
Undetermined species 8 [C]	6.7	0	0

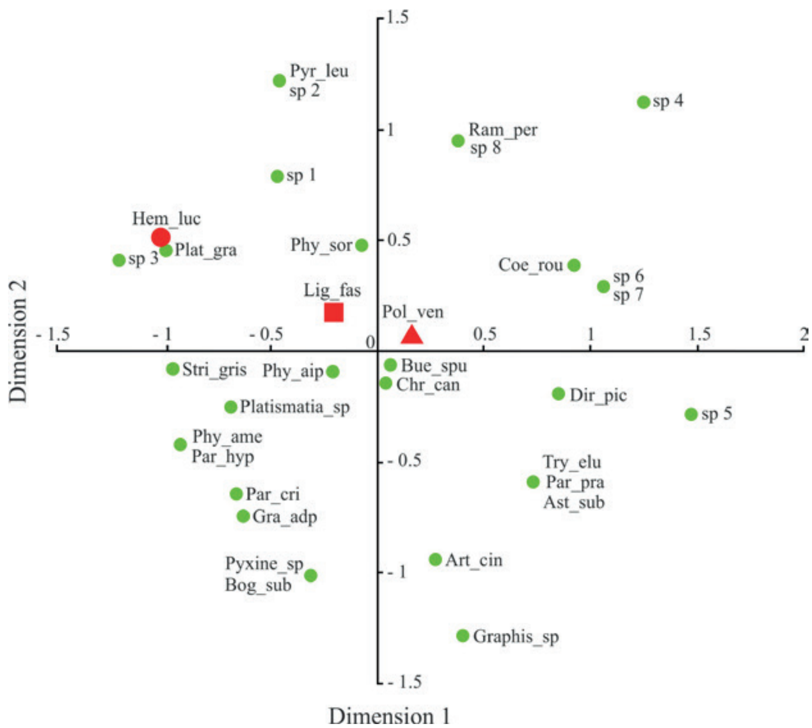

Figure 3. Non-metric multidimensional scaling (NMDS) plot of the corticolous lichen community (green circles) in relation with three tree snails species (red symbols) from La Rinconada, Jiguaní municipality, Granma, Cuba. Lichen species names: Art_cin = *Arthonia cinnabarina*, Ast_sub = *Astrothelium subcatervarium*, Bog_sub = *Bogoriella subfallens*, Bue_spu = *Buellia spuria*, Chr_can = *Chrysothrix candelaris*, Coe_rou = *Coenogonium roumeguerianum*, Dir_pic = *Dirinaria picta*, Gra_adp = *Graphis adpressa*, Par_cri = *Parmotrema cristiferum*, Par_hyp = *Parmotrema hypotropum*, Par_pra = *Parmotrema praesorediosum*, Phy_aip = *Physcia aipolia*, Phy_ame = *Physcia americana*, Phy_sor = *Physcia sorediosa*, Plat_gra = *Platythecium grammitis*, Pyr_leu = *Pyrenula leucostoma*, Ram_per = *Ramalina peruviana*, Stri_gris = *Strigula griseonitens*, Try_elu = *Trypethelium eluteriae* var. *citrinum*, sp 1 = Undetermined species 1, sp 2 = Undetermined species 2, sp 3 = Undetermined species 3, sp 4 = Undetermined species 4, sp 5 = Undetermined species 5, sp 6 = Undetermined species 6, sp 7 = Undetermined species 7, sp 8 = Undetermined species 8, Tree snail species names: Hem_luc = *Hemitrochus lucipeta*, Lig_fas = *Liguus fasciatus*, Pol_ven = *Polymita venusta*.

Figura 3. Representación gráfica del Escalamiento multidimensional no métrico (EMDN) de la comunidad de líquenes cortícolas (círculos verdes) relacionada con tres especies de moluscos arborícolas (símbolos rojos) en La Rinconada, municipio Jiguaní, Granma, Cuba.

Opegrapha and *Graphis* were frequent. In general, it seems that Cuban tree snails such as *Polymita* or *Liguus* are associated with smooth-barked trees. There is often higher crustose lichen abundance on smooth bark (Díaz-Piferrer, 1961; Milera and Martínez, 1987). For *P. muscarum*, Bidart (1997) found an abundance of fungi such as *Aspergillus* sp. and *Pericoma* sp. in the most used host trees (*Eugenia* sp. and *Lysiloma* sp.). Therefore, crustose lichens and non-lichenized fungi could play an important role in the diet of *Polymita* species.

At our Rinconada site we found a significant snail-specific association with certain corticolous lichen species. The species *L. fasciatus* showed a highly significant association with two foliose species frequently associated with *S. atomaria* tree species, *P. sorediosa* and *P. aipolia*. By contrast, the tree snail *H. lucipeta*, restricted to the host *Lysiloma* sp., seems to be associated with the crustose lichens *P. grammitis* and another unknown species. Interestingly, *P. venusta* displayed higher associations with the crustose lichens *B. spuria* and *C. candelaris*, when these were living on *Lysiloma* sp. and *S. atomaria*, respectively. These species-specific association patterns suggest niche segregation by diet as reported by Baur *et al.* (1992, 1994) in two European snails, *Chondrina clienta* (Westerlund, 1883) and *Balea aspersa* (Linnaeus, 1758). They reported a difference between grazed lichen species and they proposed, as an alternative explanation, that divergence of niche diminishes the interspecific competition.

We related our new findings to the phenomenon that snail behavior on tree trunks is integrated with defecation activities. We found spores of six lichen species in tree snails feces, with

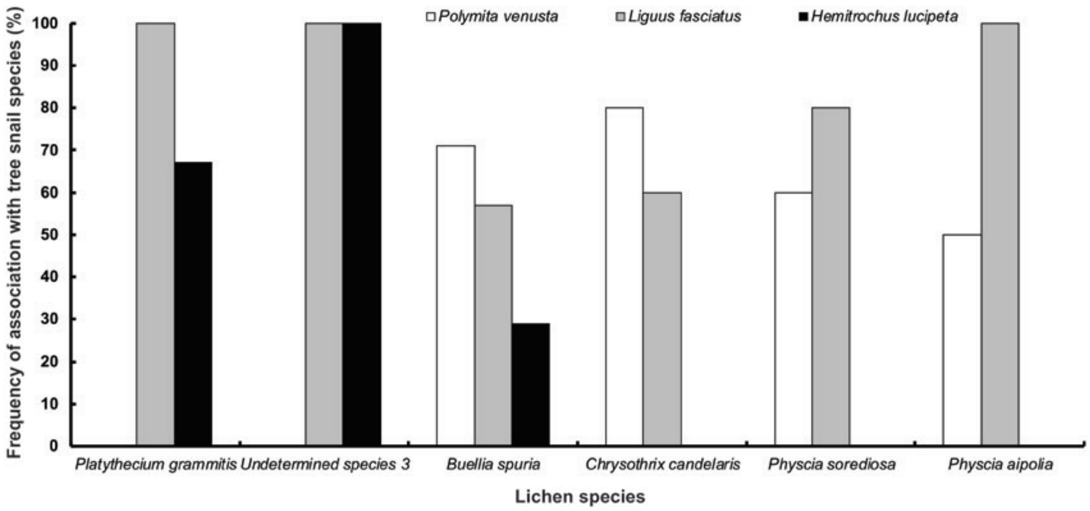

FIGURE 4. Frequency of co-occurrence of tree snail and lichen species with significant association on host trees from La Rinconada, Jiguaní municipality, Granma, Cuba.
FIGURA 4. Frecuencia de coincidencia de las especies de líquenes y moluscos arborícolas asociadas significativamente, sobre árboles hospederos en La Rinconada, municipio Jiguaní, Granma, Cuba.

the highest frequencies for *C. roumeguerianum* and *B. spuria* spores in all the studied tree snails. *Polymita venusta* is associated with trees with *B. spuria* as apparently this lichen is an important part of its diet. For *P. venusta*, Reyes-Tur (2004) reported that defecation was a frequent behaviour at the beginning of nocturnal activity. During and immediately after defecation these snails rubbed different parts of their soft bodies with their fresh feces. During daytime most of these individuals (70 %) returned to the sites where they rubbed feces the night before. Hence, in agreement with suggestion of Cook (2001) for other land snail species, it could be possible that *P. venusta* labels suitable feeding and resting sites through substances present in the fecal components (*e.g.*, spores). The evidence of spore diversity within feces and grazed traces both revealed that most of recorded lichen species were consumed by two tree snails, *P. venusta* and *L. fasciatus*. This suggests that at least these two tree snails are generalist herbivores despite spatial association for habitats with particular lichen species.

In conclusion, we described associations between three species of Cuban tree snails and epiphytic lichens on their host trees. Most of the tree snail and lichen species were associated with *S. atomaria*, a tree species that usually has smooth bark. Further, there was not only a significant snail species-specific association for habitats with particular lichen species but also our findings suggested that two species of studied snails were generalist herbivores. However, in order to provide a thorough account of the patterns of snail-lichen association, more replication is needed to increase the sample size. In addition, we need to increase our knowledge and understanding of the relative palatability of the different lichen species to the three species of tree snail.

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