

Lianas as a microhabitat for myxomycetes in tropical forests

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Wrigley de Basanta, D., Stephenson, S. L., Lado, C., Estrada-Torres, A. and Nieves-Rivera, A. M. (2008). Lianas as a microhabitat for myxomycetes in tropical forests. *Fungal Diversity* 28: 109-125.

Woody vines (lianas) are common in tropical forests, where they reach the light by using other plants for support. Myxomycetes have been recorded from both living and dead lianas, but the microhabitat represented by these plants has never been examined in detail. In the present study, samples of lianas were obtained from a number of different types of tropical forest in Australia, Cuba, Ecuador, Mexico, Peru and Puerto Rico. Moist chamber cultures prepared with samples from these six study areas yielded several hundred collections representing 65 species of myxomycetes, and at least 87% of all cultures produced some evidence (either plasmodia or fruiting bodies) of these organisms. *Arcyria cinerea*, *Diderma hemisphaericum*, *Didymium squamulosum*, *Physarum pusillum* and *Stemonitis fusca* var. *nigrescens* appear to be among the more consistently abundant and widespread members of the assemblage of myxomycetes associated with lianas, but our cultures also have produced a number of noteworthy collections. Prominent examples are *Perichaena dictyonema*, a rare species described originally from Central Africa, *Physarum hongkongense*, *Ceratiomyxa fruticulosa*, *Physarum melleum* and *Willkommlangea reticulata*. In addition, the total assemblage of species we recorded includes three species (*Physarum hongkongense*, *Stemonitis foliicola* and *Stemonaria gracilis*) not previously known from the Neotropics along with six new records for Australia, 13 new records for Peru and 12 new records for Puerto Rico. Data are provided on the pH and water holding capacity of the samples we processed, and the ecology of lianas as a special microhabitat for myxomycetes is discussed.

Key words: Australia, biodiversity, ecology, Eumycetozoa, Neotropics, tropical forest ecosystems

Article Information

Received 11 December 2006

Accepted 11 July 2007

Published online 31 January 2008

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Introduction

Woody vines (lianas) are a conspicuous feature of most tropical forests, where their leaves can constitute a large proportion of the total leaf surface area of the entire forest community. Lianas, which reach the canopy by using other plants as support, include representatives from many diverse groups of plants, ranging from ferns to angiosperms (Figs 1-2). Some flowering plant families such as the *Bignoniaceae* and *Vitaceae* are particularly rich in species of lianas. All of the species in some genera (e.g., *Serjania*) are lianas, whereas other genera include species of lianas along with

shrubs and trees (Putz and Mooney, 1991). At least some lianas occur in most types of temperate forests and they are particularly abundant in tropical forests. Schnitzer and Bongers (2002) indicated that up to a quarter of the woody plant species in some tropical forest are lianas, and > 1400 liana stems per hectare have been reported in Costa Rica (Mascaro *et al.*, 2003). The ecological significance of lianas is now widely recognized, since they are of vital importance as direct and indirect competitors of trees and in the functioning of ecosystems, as key components of whole-forest transpiration, carbon sequestration and forest regeneration (Putz, 1995; Schnitzer and Bon-

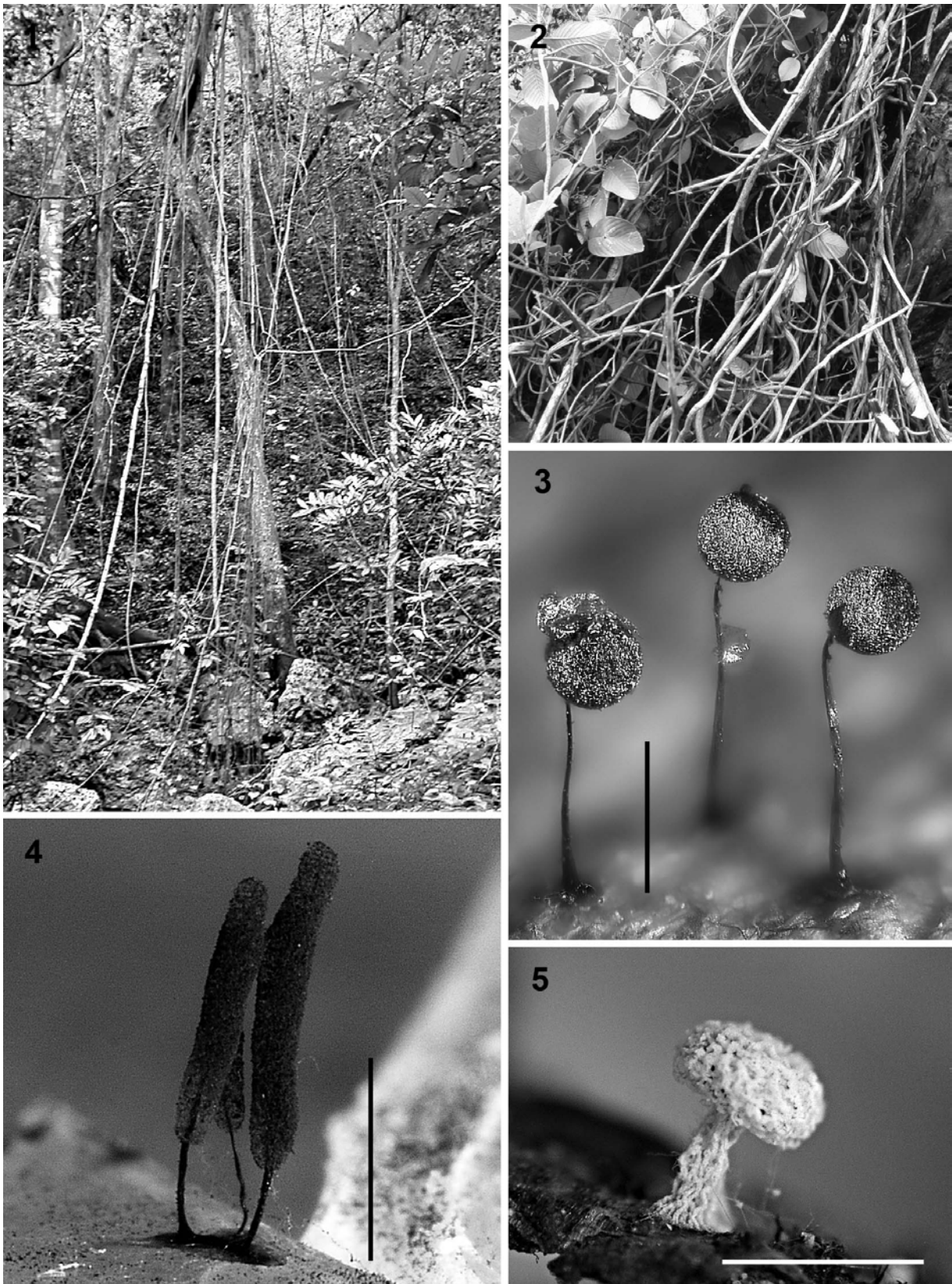


Fig. 1. Lianas in a subtropical wet forest in Puerto Rico. **Fig. 2.** Closer view of lianas from Queensland, Australia. **Fig. 3.** *Collaria arcyronema* (SLS 16952). **Fig. 4.** *Stemonitis foliicola* (dwb 2212), sporocarps. **Fig. 5.** *Didymium squamulosum* (SLS 15387). Figs. 3-5 bars = 1 mm.

gers, 2002).

Although the woody stems of lianas are somewhat similar to those of the trees upon which they depend for support, they differ by possessing large diameter vessels and abundant soft tissues (parenchyma) in the xylem, which makes the stem of a liana much more flexible (Putz and Holbrook, 1991). These large diameter vessels allow for an increased flow rate of water through the xylem. This means that the water conducting capacities of even narrow-stemmed lianas are very large and this enables them to support a much larger leaf area than would otherwise be the case. As such, lianas contribute an unexpectedly high proportion of photosynthetic biomass to the forest (Schnitzer and Bongers, 2002).

Myxomycetes have been reported from both living and dead lianas (Nieves-Rivera *et al.*, 2003), but the microhabitat represented by these plants has never been examined in detail. As one component of biodiversity surveys carried out in several different regions of the world, samples of living and dead lianas were obtained and used to prepare series of moist chamber cultures in an effort to assess lianas as a microhabitat for myxomycetes. The objectives of this paper are (1) to present the results obtained from these cultures, (2) to compare our results with comparable data for other substrates available to myxomycetes in tropical forests and (3) to relate the physical attributes of lianas, as determined from an examination of some of the samples we collected, to these results.

Materials and methods

Samples of bark from living lianas and whole pieces of dead lianas were obtained from several different types of tropical forest in Australia, Cuba, Ecuador, Mexico, Peru and Puerto Rico. These samples were brought back to the laboratory, and used to prepare moist chamber cultures in the manner described by Stephenson and Stempen (1994). A total of 202 moist chamber cultures were prepared. Since substrate pH is an important factor determining the abundance and distribution of myxomycetes (e.g., Stephenson, 1989; Wrigley de Basanta, 2004), the pH of each culture was

recorded at 24 hours before excess water was poured off. Maximum water capacity and the extent of water retention of the substrate upon which they occur appear to represent important factors for myxomycetes, and these parameters also serve as useful comparative measures for sets of moist chamber cultures prepared with different substrates. Samples of the lianas used to prepare moist chamber cultures were tested for maximum water capacity using the method described by Barkman (1958) but without sealing the edges of each piece of liana or liana bark with wax, and without removing visible epiphytes such as mosses and lichens, in an attempt to simulate natural conditions, and those present in the cultures, as closely as possible. Samples consisting of approximately 2 g of air-dried material (either pieces of liana bark or short sections of entire lianas) were weighed and then soaked for 24 hours in a closed container. The surface water was removed from the sample material by blotting and the latter was re-weighed. The difference in weight (as a measure of maximum water capacity) was determined and then expressed as a percentage of the dry mass. To measure water retention, the soaked samples were allowed to remain exposed to laboratory air at 20°C and weighed at intervals. Since the samples reached a constant dry weight at different rates, water retention at a standard interval of 6 hours was determined and expressed as a percentage of the mass of water absorbed. Most samples had dried completely at 24 hours.

List of localities

All of the localities from which samples of lianas were obtained in the context of the study reported herein are listed below. In addition to the records generated from these samples, data are included for myxomycetes appearing in moist chamber cultures prepared with samples of lianas collected from tropical forests in Cuba and Ecuador as part of more comprehensive surveys carried out in these countries. More detailed information on these surveys can be found in Camino *et al.* (in press) for Cuba and in Schnittler *et al.* (2002) for Ecuador.

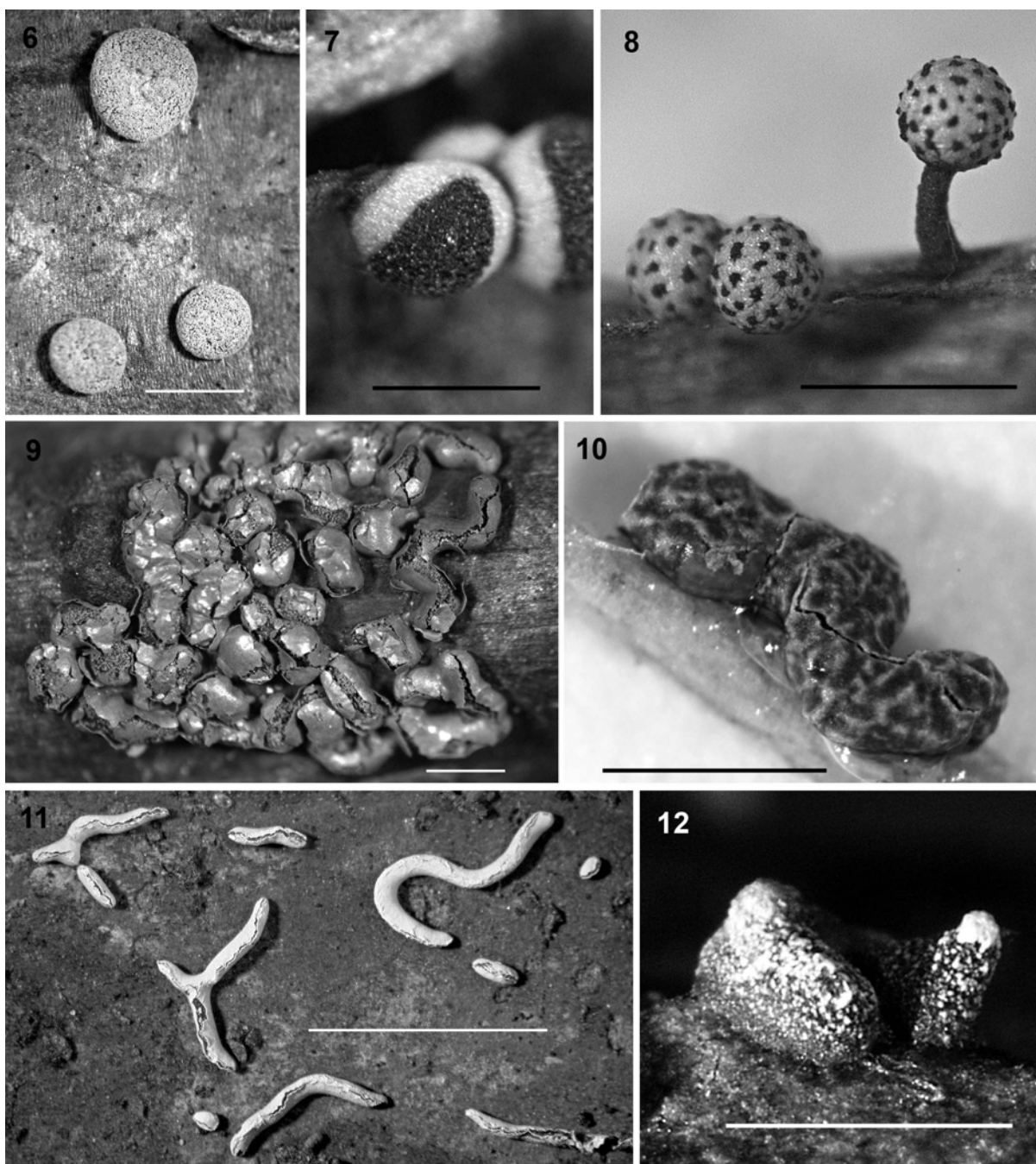


Fig. 6. *Didymium ochroideum* (SLS 16982). **Fig. 7.** *Perichaena dictyonema* (dwb 2432), sessile elliptical sporocarps with dark granular material covering the lid. **Fig. 8.** *Hemitrichia pardina* (SLS 15491), sporocarps a with warted peridium. **Fig. 9.** *Physarum aeneum* (SLS 15735), plasmodiocarps with a glossy outer peridium. **Fig. 10.** *Physarum bogoriense* (dwb 2248), plasmodiocarp. **Fig. 11.** *Physarum hongkongense* (SLS 20427), pale plasmodiocarps with distinct dehiscence lines. **Fig. 12.** *Physarum superbum* (SLS 15521), laterally compressed plasmodiocarp with a nearly limeless lower portion. Figs. 6, 8-10, 12 bars = 1 mm, Fig. 7 bar = 0.5 mm, Fig. 11 bar = 5 mm.

Locality 1: AUSTRALIA: Northern Queensland, Australian Canopy Crane near Cape Tribulation, 16°06'S 145°27'E, lowland tropical rainforest, May 2002.

Locality 2: AUSTRALIA: Northern Queensland, Butcher's Creek approximately 90 km from

Kuranda, 17°24'S 145°43'E, complex mesophyll vine forest, June 2002.

Locality 3: AUSTRALIA: Northern Queensland, Kingfisher Park near Julatten, east of Port Douglas,, 16°35'S 145°22'E, lowland tropical rainforest, June 2002.

- Locality 4: MEXICO: Veracruz, Misantla, Cerro Espaldilla, 19°57'N 96°50'W, medium semi-deciduous tropical forest, October 2000.
- Locality 5: MEXICO: Querétaro, Pinal de Amoles, Chuveje Falls, 21°09'N 99°33'W, riverine forest (bosque de galería), September 2004.
- Locality 6: MEXICO: Querétaro, Pinal de Amoles, El Naranjo, 21°18'N 99°38'W, medium semi-deciduous tropical forest, November 2004.
- Locality 7: MEXICO: Querétaro, Arroyo Seco, Sta. María de Cocos, 21°18'N 99°38'W, tropical deciduous forest (selva baja), September 2004.
- Locality 8: MEXICO: Querétaro, Landa de Matamoros, Tancoyol, 21°25'N 99°20'W, tropical deciduous forest (selva baja), July 2003.
- Locality 9: MEXICO: Campeche, Calakmul Biosphere Reserve, 18°15'N 89°49'W, medium semideciduous tropical forest, November 2002.
- Locality 10: MEXICO: Campeche, Calakmul Biosphere Reserve, 18°18'57"N 89°51'23"W, 212 m medium semideciduous tropical forest, November 2002.
- Locality 11: PERU: Mazan, Loreto, 3°28'S 74°55'W, lowland tropical rainforest, April 2002.
- Locality 12: PUERTO RICO: Mayaguez Municipality, Barrio Bateyes, near Finca Rubén Dross, 18°13'S 67°04'W, subtropical wet forest, August 2002.
- Locality 13: PUERTO RICO: Janyuya Municipality, Barrio Coabey, near Piedra Escrita, 18°13'S 66°34'W, subtropical wet forest, August 2002.
- Locality 14: PUERTO RICO: Río Grande Municipality, El Verde Field Station in the Luquillo Mountains, 18°19'S 65°49'W, subtropical wet forest, June and July 1996.
- Locality 15: PUERTO RICO: Lajas Municipality, La Paraguera, west of Ponce, 17°58'S 67°02'W, subtropical dry forest, December 1998.
- Locality 16: PUERTO RICO: Arecibo Municipality, Río Abajo Forest, 18°19'S 66°41'W, subtropical wet forest, June 2002.

Results

Moist chamber cultures prepared with samples of lianas collected in the present study yielded more than 430 collections representing 65 species of myxomycetes. In the list that follows, the myxomycetes we recorded are arranged alphabetically by genus and then species. Nomenclature follows Lado (2001) and Hernández-Crespo and Lado (2005), with the conserved names of several genera (Lado *et al.*, 2005) approved recently by the Committee for Fungi (Gams, 2005) of the IAPT. The

abbreviation 'cf.' in the name of a taxon indicates that the specimen representing the source of the record could not be identified with certainty. Specimens listed herein are deposited in herbarium UARK (SLS numbers) or in the private collection of dwb.

Annotated Species List

Arcyria afroalpina Rammeloo

Locality 1: SLS 15523 (pH 5.9).

Locality 13: SLS 17009 (pH 7.2).

Locality 16: SLS 15386, 15409 (pH 6.6, 7.1).

This species, described originally from Africa by Rammeloo (1981), was first reported from the Neotropics on epiphyllous liverworts by Schnittler *et al.* (2002), who also provided illustrations of this apparently uncommon myxomycete. The typical form is characterized by a long, often somewhat twisted stalk, but some fruitings consist of sporocarps with shorter stalks and are similar in appearance to *Arcyria cinerea*. Our collection represents the first record of this species from Puerto Rico.

Arcyria cinerea (Bull.) Pers.

Locality 1: dwb 2431, 2455, 2458, 2467 (pH 5.7-6.5).

Locality 2: dwb 1974 (pH 6.2).

Locality 5: dwb 2522 (pH 6.6).

Locality 11: dwb 2209, 2217, 2227, 2231 (pH 6.3-6.6).

Locality 12: SLS 16119, 16881, 16882, 16904, 16908, 16909, 16913, 16914, 16915, 16916 (pH 7.3-7.6).

Locality 13: SLS 16907, 16908, 16909, 16913, 16914, 16915, 16916, 16990, 17020, 17317, 20804 (pH 7.3-7.4).

Locality 15: SLS 16859, 16903, 16991, 16992, 17000, 17002 (pH 7.5-8).

Locality 16: SLS 15492, 15404, 15406 (pH 6.6-7).

This common species was reported previously from samples of lianas collected in Mexico (Lado *et al.*, 2003), Cuba (Camino *et al.*, in press) and Ecuador (Schnittler *et al.*, 2002) during other biodiversity surveys in which we have been involved. McHugh (2005) also recorded *Arcyria cinerea* from samples of lianas collected in Ecuador.

Arcyria cf. denudata (L.) Wettst.

Locality 3: SLS 15391 (pH 6.8).

***Arcyria insignis* Kalchbr. & Cooke**

Locality 8: dwb 2402 (pH 6.2).

Locality 9: dwb 2287 (pH 6.8).

***Badhamia melanospora* Speng.**

Locality 12: SLS 16960, 16961, 16962 (pH 7.3-7.4).

Locality 16: SLS 15392 (pH 6.9).

***Badhamia nitens* Berk.**

Locality 1: dwb 2452 (pH 6.4).

Our collection of this species is the first record from Australia.

***Calomyxa metallica* (Berk.) Nieuwl.**

Locality 4: dwb 1905, 1968 (pH 6.2, 6.6).

Locality 8: dwb 2386 (pH 7).

Locality 9: dwb 2298 (pH 7.1).

Specimen dwb 1905 consists of very small rounded sporocarps, and some spores are only 9 µm, but these are probably developmental variables.

***Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr.**

Locality 11: dwb 2241 (pH 6.5).

Although included in virtually all taxonomic treatments of the myxomycetes, this species is more closely related to another group of slime molds (the protostelids) than to the myxomycetes (Olive, 1975). It is common as a field collection in forests throughout the world but only rarely has it been reported as appearing in a moist chamber culture (Stephenson, 1989).

***Clastoderma debaryanum* A. Blytt**

Locality 8: dwb 2422 (pH 6.2).

***Collaria arcyrionema* (Rostaf.) Nann.-Bremek. ex Lado (Fig. 3)**

Locality 1: dwb 2444 (pH 6.4).

Locality 2: SLS 15518, 15451 (pH 6.7, 7).

Locality 12: SLS 16883, 16952, 16954 (pH 7.4-7.7).

Locality 13: SLS 17281, 17338, 17346 (pH 7.5-7.7).

Locality 14: SLS 15531, 15532 (pH 7).

Locality 15: SLS 16933, 16935, 16950, 17324 (pH 7.5-7.8).

Locality 16: SLS 15410 (pH 7).

This species was reported previously from samples of lianas collected in Cuba (Camino *et al.*, in press) and Ecuador (McHugh, 2005).

***Comatricha laxa* Rostaf.**

Locality 1: dwb 2433 (pH 6.6).

Locality 12: SLS 17333 (pH 7.4).

Locality 16: SLS 15395 (pH 7).

The material represented by collection dwb 2433 is scanty, and our identification is not definitive.

***Comatricha cf. pulchella* (C. Bab.) Rostaf.**

Locality 16: SLS 15520 (pH 6.6).

This species was also reported from samples of lianas collected in Cuba (Camino *et al.*, in press) and Ecuador (Schnittler *et al.*, 2002). If confirmed, our collection represents the first record of this species from Puerto Rico.

***Comatricha tenerrima* (M.A. Curtis) G. Lister**

Locality 1: dwb 2449 (pH 6).

Locality 3: SLS 15412, 15542 (pH 7.1, 7.5).

Locality 11: dwb 2190, 2242, 2243 (pH 6.5-7.1).

Locality 12: SLS 16941, 17309, 17209 (pH 7.4-7.5).

This species was reported previously from samples of lianas collected in Los Tuxtlas, Mexico (Lado *et al.*, 2003) and in Cuba (Camino *et al.*, in press). Our collection represents the first record of this species from Peru and Puerto Rico.

***Craterium aureum* (Schumach.) Rostaf.**

Locality 11: dwb 2252 (pH 6.5).

Schnittler *et al.* (2002) commented on material they recorded on lianas from Ecuador, which they list as *Physarum cf. galbeum* but without dehiscence lines. They suggested that the forms they collected may be closely related to this species. Our collection represents the first record of this species from Peru.

***Cribraria microcarpa* (Schrad.) Pers.**

Locality 14: SLS 15533 (pH 7).

***Cribraria violacea* Rex**

Locality 8: dwb 2360, 2370 (pH 6.1, 6.4).

Locality 13: SLS 17260 (pH 7.4).

This species was also reported from samples of lianas collected in Cuba (Camino *et al.*, in press).

***Diderma effusum* (Schwein.) Morgan**

Locality 13: SLS 16902 (pH 7.2).

***Diderma hemisphaericum* (Bull.) Hornem.**

Locality 2: dwb 2460 (pH 5.9).

Locality 11: dwb 2223, 2253 (pH 6.4, 6.6).

Locality 12: SLS 16977, 16978, 16981 (7.5-8.1).

This species was also reported from samples of lianas collected in Cuba (Camino *et al.*, in press). Our collection represents the first record of this species from Peru.

***Didymium anellus* Morgan**

Locality 15: SLS 16968 (pH 7.4).

***Didymium difforme* (Pers.) Gray**

Locality 6: dwb 2512 (pH 6.9).

***Didymium iridis* (Ditmar) Fr.**

Locality 1: dwb 2443, 2441 (pH 5.7, 6.2); SLS 15397, 15484 (pH 6.2, 7.1)

Locality 2: SLS 15397 (pH 6.3).

This species was also reported from samples of lianas collected in Cuba (Camino *et al.*, in press) and Ecuador (Schnittler *et al.*, 2002).

***Didymium nigripes* (Link) Fr.**

Locality 3: SLS 16863 (pH 6.9).

Locality 12: SLS 16985, 16986, 16987 (pH 7.3-7.6).

Locality 16: SLS 15384 (pH 7.1).

This species was also reported from samples of lianas collected in Ecuador (Schnittler *et al.*, 2002).

***Didymium cf. ochroideum* G. Lister (Fig. 6)**

Locality 15: SLS 16982 (pH 8.1).

This species was also reported from samples of lianas collected in Ecuador (McHugh, 2005). Some collections of this species from the tropics have larger and more strongly marked spores than described in most monographs on the myxomycetes (e.g., Martin and Alexopoulos, 1969). It is possible that more than a single species is involved. Our collection represents the first record of this species from Puerto Rico.

***Didymium squamulosum* (Alb. & Schwein.) Fr. (Fig. 5)**

Locality 2: SLS 15414 (pH 6.8)

Locality 10: dwb 2289, 2291, 2303 (pH 7-7.4).

Locality 11: dwb 2215, 2247 (pH 6.8, 7.1).

Locality 16: SLS 15387 (pH 6.6)

This species was reported previously from samples of lianas collected in Cuba (Camino *et al.*, in press) and also is known from Yasuni, Ecuador (unpubl. data).

***Echinostelium apitectum* K.D. Whitney**

Locality 1: dwb 2425 (pH 6.4).

***Echinostelium minutum* de Bary**

Locality 1: dwb 2426, 2427 (pH 5.4, 6.4).

Locality 2: dwb 2428 (pH 5.9).

Locality 10: dwb 2286 (pH 7).

Locality 11: dwb 2197, 2201, 2207, 2226 (pH 6.3-6.8).

Our collection represents the first record of this species from Peru.

***Hemitrichia calyculata* (Speg.) M.L. Farr**

This species was reported previously on lianas from Ecuador (Schnittler *et al.*, 2002).

***Hemitrichia pardina* (Minakata) Ing (Fig. 8)**

Locality 16: SLS 15491 (pH 6.6).

This species was also reported from samples of lianas collected in Los Tuxtlas, Mexico (Lado *et al.*, 2003), in Cuba (Camino *et al.*, in press) and in Ecuador (McHugh, 2005). In most earlier treatments of the myxomycetes, it is listed as *Hemitrichia minor* G. Lister or *Perichaena minor* (G. Lister) Hagelst. Our collection represents the first record of this species from Puerto Rico.

***Licea biforis* Morgan**

Locality 1: SLS 15418B (pH 7).

***Licea erecta* var. *erectoides* (Nann.-Bremek. & Y. Yamam.) Y. Yamam.**

Locality 1: SLS 15418 A (pH 7).

This species was reported previously from samples of dead lianas collected in Cuba (Camino *et al.*, in press). Our collection is the first record of the species from Australia.

***Licea operculata* (Wingate) G.W. Martin**

Our collections of this species from Mexico and Peru, recorded on lianas were described in Wrigley de Basanta and Lado (2005), as was a collection from Ecuador on lianas.

***Licea rugosa* var. *fuiokana* (Y. Yamam.) D. Wrigley & Lado**

Locality 6: dwb 2513 (pH 6.9).

The collection reported herein is the first report of this species from lianas, which represent a new substrate for what appears to be a rare species. It has been recorded also

from other substrates in Mexico (Wrigley de Basanta and Lado, 2005).

Licea scyphoides T.E. Brooks & H.W. Keller

Our collections of this species on lianas from Cuba and Peru lianas were reported in Wrigley de Basanta and Lado, (2005).

Macbrideola martinii (Alexop. & Beneke) Alexop.

Locality 4: dwb 1899, 1857, 1879 (pH 6.4-6.6).

This species was reported previously on lianas from the Los Tuxtlas Tropical Biology Station in Veracruz, Mexico (Lado *et al.*, 2003)

Macbrideola scintillans* var. *verrucosa (Nann.-Bremek. & Y. Yamam.) Y. Yamam.

Locality 4: dwb1882 (pH 6.6).

This species was reported previously on samples of lianas from the Los Tuxtlas Tropical Biology Station in Veracruz, Mexico (Lado *et al.* 2003).

Perichaena chrysosperma (Curr.) Lister

Locality 3: SLS 15485, 15737 (pH 6.7, 6.8).

Locality 12: SLS 17319 (pH 7.5).

Locality 16: SLS 15411 (pH 7).

This species was reported previously on samples of lianas from the Los Tuxtlas Tropical Biology Station in Veracruz, Mexico (Lado *et al.*, 2003) and also from Cuba (Camino *et al.*, in press) and from Ecuador (Schnittler *et al.*, 2002). McHugh (2005) commented on the similarities and differences that he found to exist between this species and *Perichaena pedata* in his collections on lianas from Ecuador. Our collection represents the first record of this species from Puerto Rico.

Perichaena depressa Lib.

Locality 7: dwb 2519 (pH 7.1).

Locality 14: SLS 15530 (pH 6.7).

This species was reported previously on lianas from the Los Tuxtlas Tropical Biology Station in Veracruz, Mexico (Lado *et al.*, 2003) and also from Cuba (Camino *et al.*, in press). Our collection represents the first record of this species from Puerto Rico.

Perichaena dictyonema Rammeloo (Fig. 7)

Locality 1: dwb 2432 (pH 6.2).

Locality 3: SLS 15483 (pH 7.5).

Locality 12: SLS 17321, 17337, 17381 (pH 8).

Our collections represent the first records for both Australia and Puerto Rico and the second time the species has been recorded from lianas in the Neotropics, since it was reported previously by McHugh (2005) from Ecuador. Schnittler *et al.* (2002) recorded it on other substrates from Ecuador.

Perichaena vermicularis (Schwein.) Rostaf.

Locality 1: SLS 15487 (pH 6.7).

Locality 11: dwb 2191, 2192, 2195, 2216, 2222 (pH 7.1-7.3).

This species was reported previously on lianas from Cuba (Camino *et al.*, in press). Our collection represents the first record of this species from Peru.

Physarum aeneum (Lister) R.E. Fr. (Fig. 9)

Locality 14: SLS 15735 (pH 5.6).

Our collection represents the first record of this species from Puerto Rico

Physarum album (Bull.) Chevall.

Locality 2: SLS 15453 (pH 6.1).

Locality 5: dwb 2504 (pH 7.1).

Physarum bogoriense Racib. (Fig. 10)

Locality 11: dwb 2248 (pH 6.4).

Comments on the similarities and differences of this species and *Physarum hongkongense* are provided in the information given with the latter. Our collection represents the first record of this species from Peru.

Physarum cinereum (Batsch) Pers.

Locality 3: SLS 15394 (pH 7.1).

Physarum compressum Alb. & Schwein.

Locality 1: dwb 2442 (pH 6.4); SLS 15415 (pH 6.9).

Locality 10: dwb 2302, 2300 (pH 6.8, 7.1).

Locality 11: dwb 2221, 2234 (pH 7, 7.1).

Locality 12: SLS 16925, 16927, 16926 (pH 7.7-8.1).

Locality 15: SLS 16926, 16929, 16937 (pH 7.5-8.1).

Locality 16: SLS 15537, 16901, 17313 (pH 6.9-7.4).

Specimen dwb 2300 consists of sporocarps with rounded reniform and lobate sporothecae instead of the flattened fan-shaped form that is typical for the species, and the stalks are dark at the base. However, the capillitium and spores fit the description of *Physarum compressum*, and Martin and Alexopoulos (1969) mention these variations.

This species was reported previously on lianas from Cuba (Camino *et al.*, in press) and from Ecuador (Schnittler *et al.*, 2002; McHugh, 2005). Our collection represents the first record of this species from Peru.

Physarum crateriforme Petch

Locality 16: SLS 15390 (pH 6.6).

Our collection represents the first record of this species from Puerto Rico.

Physarum decipiens M. A. Curtis

Locality 11: dwb 2202, 2238 (pH 6.3, 6.5).

Our collection represents the first record of this species from Peru.

Physarum didermoides (Pers.) Rostaf.

Locality 5: dwb 2521 (pH 7.1).

Locality 9: dwb 2297 (pH 6.8).

Locality 12: SLS 17322, 17332 (pH 7).

This species was reported previously on dead lianas from Cuba (Camino *et al.*, in press), and from Ecuador (McHugh, 2005).

Physarum globuliferum (Bull.) Pers.

Locality 11: dwb 2235 (pH 6.8).

Our collection represents the first record of this species from Peru.

Physarum cf. gyrosum Rostaf.

Locality 12: SLS 17185 (pH 7.6).

Locality 15: SLS 16965, 16966, 16975 (pH 7.2-7.4).

Our collection, if confirmed, represents the first record of this species from Puerto Rico.

Physarum hongkongense Chao H. Chung

Locality 4: dwb 1972 (pH 6.2).

Our one specimen of this species consists of more than 60 sporocarps. Most of these are plasmodiocarps with a distinct preformed line of dehiscence and regularly warted spores 7.5-9 µm in diameter. The outer peridium has the characteristic two tones caused by thick lime deposits on the inner surface but is paler yellow than described by Chung (1997). *Physarum hongkongense* can be distinguished from *P. bogoriense* primarily on the basis of the yellow colour of the sporocarps (Chung *et al.*, 1998), and these authors mentioned that they have found the two species occurring together on a single leaf. It is possible that *P. bogoriense*

exhibits a wide range of variation that encompasses what is recognized as *P. hongkongense* at one extreme. However, this specimen and our one specimen (dwb 2248) of *P. bogoriense* are macroscopically very different (Figs 10-11). Our specimen of *P. hongkongense* apparently represents the first published record of the species from the Neotropics.

Physarum leucophaeum Fr.

Locality 1: dwb 2466 (pH 6.2).

Physarum melleum (Berk. & Broome) Masee

Locality 11: dwb 2251 (pH 7.3).

Physarum nicaraguense T. Macbr.

Locality 12: SLS 17003, 17008 (pH 7.4, 7.7).

Locality 15: SLS 16951, 16993, 16994, 16995, 16996, 16997, 16998 (pH 6.5-7.9).

Physarum oblatum T. Macbr.

Locality 1: dwb 2453, 2454 (pH 6.4, 6.9).

Physarum pusillum (Berk. & M.A. Curtis) G. Lister

Locality 9: dwb 2293 (pH 6.8); SLS 15539 (pH 6.9).

Locality 11: dwb 2196, 2204, 2218, (pH 6.6-7.3).

Locality 12: SLS 16894, 16923, 16944, 16945, 16947, 16948, 16949, 16942, 16946 (pH 7.2-7.8).

Locality 14: SLS 15388 (pH 6.7).

Locality 15: SLS 11329, 16889, 16930, 16931, 16934, 16936, 16938 (pH 7.4-8.1).

This species was reported previously on dead lianas from Cuba (Camino *et al.*, in press) and from Ecuador (Schnittler *et al.*, 2002; McHugh, 2005). Our collection represents the first record of this species from Peru.

Physarum stellatum (Masee) G.W. Martin

Locality 5: dwb 2506 (pH 7.1).

Physarum superbum Hagelst. (Fig. 12)

Locality 1: SLS 15416 (pH 7.3).

Locality 11: dwb 2239, 2240 (pH 7).

The sporocarps of these collections are laterally compressed, especially when fused to form plasmodiocarps or sub-plasmodiocarps, with some solitary sporocarps that are almost conical. The peridium is double, with the inner peridium membranous and iridescent and without lime below but encrusted with lime above. Peridial lime is egg-yolk orange, sometimes fading to yellow, and the lime nodes

of the capillitium are bright orange when fresh. Spores are pale violaceous, minutely verrucose and (7) 8-10µm in diameter. Our collections represents the first records of this species from Australia and Peru.

***Physarum cf. viride* (Bull.) Pers.**

Locality 1: SLS 15454 (pH 6.7).

***Stemonaria gracilis* Nann.-Bremek. & Y. Yamam.**

Locality 11: dwb 2200, dwb 2211 (pH 6.7-7.1).

In our collections the sporocarps are 3-4 mm tall and dull brown. The stalk is black and one third of the total height. The hypothallus is dark orange-red and the columella reaches the apex. The capillitium is stout and even with some paler anastomoses but with no surface net. The spores are 8-10 µm and spiny-reticulate. These are the first records of this species for the Neotropics.

***Stemonitis flavogenita* E. Jahn**

Locality 15: SLS 16963, 16976 (pH 7.2).

Our collection represents the first record of this species from Puerto Rico.

***Stemonitis foliicola* Ing (Fig. 4)**

Locality 1: dwb 2459, 2450, (pH 6.4, 6.5).

Locality 2: dwb 2429, 2456, 2457 (pH 5.9-6).

Locality 11: dwb 2220, 2228, 2230, 2224, 2212, 2236 (pH 5.7-6.8).

Specimen dwb 2236 consists of about 60 sporocarps, which are taller (almost 5 mm) than the other specimens recorded for this species, and the spores are more prominently spiny. However, the spore size of 7.5-9 µm and other characters fit the description of *Stemonitis foliicola*. Our collections represent the first records of the species from Australia and the first records from the Neotropics.

***Stemonitis fusca* var. *nigrescens* (Rex) Torrend**

Locality 1: dwb 2430, 2440 (pH 5.4, 6.5); SLS 15524 (pH 6.9).

Locality 11: dwb 2210 (pH 6.3).

Locality 12: SLS 16957 (pH 7.4).

Locality 13: SLS 17318 (pH 7.6).

Locality 14: SLS 15526, 16956 (pH 5.6, 6.5).

Locality 15: SLS 17323 (pH 7.6).

Our collection represents the first record of this species from Peru.

***Stemonitis mussooriensis* G.W. Martin, K.S. Thind & Sohi**

This species was reported previously on lianas from the Los Tuxtlas Tropical Biology Station in Veracruz, Mexico (Lado *et al.*, 2003).

***Trichia cf. munda* (Lister) Meyl.**

Locality 2: SLS 15535 (pH 5.6).

Locality 3: SLS 15417 (pH 5.6).

***Willkommlangea reticulata* (Alb. & Schwein.) Kuntze**

Locality 1: dwb 2461, (pH 5.7).

Locality 11: dwb 2219, 2237 (pH 6.3, 6.4).

Our collection represents the first record of this species from Peru.

Discussion

The 202 moist chamber cultures prepared with lianas yielded more than 430 collections of myxomycetes representing 65 species in 21 genera (Table 1). One hundred and seventy-five of the 202 cultures (87%) produced some evidence (either plasmodia or sporocarps) of myxomycetes. The genus *Physarum* alone accounted for 29% of all species recorded. The most common species (*Arcyria cinerea*, *Didymium squamulosum* and *Physarum compressum*) were recorded from all six study areas. Seven other species (*Collaria arcyrionema*, *Comatricha tenerrima*, *Diderma hemisphaericum*, *Hemitrichia pardina*, *Perichaena chrysosperma*, *Physarum didermoides* and *Physarum pusillum*) were recorded from four or five of the study areas, another 19 in two or three areas and 36 species were recorded from only a single study area (Table 2). Certain species of *Physarum* were noteworthy for their extensive fruitings. For example, one collection of *Physarum globuliferum* consisted of 120 sporocarps in a single moist chamber, and a collection of *Physarum hongkongense* consisted of 60 sporocarps. The total assemblage of species recorded from lianas included three species (*Physarum hongkongense*, *Stemonitis foliicola* and *Stemonaria gracilis*) not previously known from the Neotropics, six new records for Australia, 13 new records for Peru, and 12 new records for Puerto Rico.

Table 1. Summary data on moist chamber cultures

Study site	No. of cultures	% positive	No. of species	S/G ratio
Australia	60	85	29	2.2
Cuba	27	78	16	1.6
Ecuador*	55	-	15	1.9
Mexico	33	85	23	1.8
Peru	17	100	21	1.6
Puerto Rico	61	89	29	2.6
Total	*253			

*includes data from Schnittler *et al.* (2002) and McHugh (2005)

In a survey of the myxomycetes associated with various microhabitats in semideciduous tropical dry forests of the Yucatán Peninsula in Mexico (Stephenson *et al.*, 2003), moist chamber cultures prepared with samples of aerial litter (87% positive) and forest floor litter (87% positive) yielded comparable results, although there were fewer cultures than in the present study. Both types of litter were more productive than bark (74% positive). The assemblages of species associated with the two types of litter and bark were compositionally different, and all three differed from the assemblage of species we recovered from lianas. These data would seem to indicate that each of the different microhabitats potentially available for myxomycetes in a tropical forest supports a distinct assemblage of species. If this is the case, then all of these microhabitats must be considered in order to develop a complete understanding of the overall biodiversity of these organisms in tropical forest ecosystems.

The mean number of species per genus (S/G) has been used as a measure of taxonomic diversity in several studies of myxomycetes (e.g., Stephenson *et al.*, 1993; Tran *et al.*, 2006). As has been pointed out in these studies, a biota in which the species are divided among many genera is intuitively more 'diverse' than one in which most species belong to only a few genera. Consequently, a low value for S/G implies a higher overall diversity than a high value. On this basis, the assemblages of species associated with lianas would seem particularly diverse. Two thirds of the individual data sets (Table 1) had a S/G ratio below 2, whereas data

sets obtained for several different substrates in four forest types in Costa Rica generally had values of about 3 (Schnittler and Stephenson, 2000) and a value of 2.4 was reported for data sets compiled for bark and litter in temperate deciduous forests at a study site in the eastern United States. However, the S/G value calculated from pooled data for samples of lianas from all six study areas was somewhat higher (3.1).

Coefficient of community (CC) indices (*sensu* Stephenson, 1988) calculated for all pairwise combinations of the assemblages of species from the six study area ranged from 0.27 to 0.58, with a mean value of 0.42. The assemblage of species recorded for samples of lianas from Cuba was the most similar (mean CC value of 0.50) to those of the other study areas, whereas the assemblage of species recorded for Peru was the least similar (mean CC value of 0.37).

As a general observation, myxomycetes regarded as primarily corticolous, including species in such genera as *Echinostelium*, were not well represented on samples of lianas, and their fruitings tended to consist of lower numbers of sporocarps than for sets of cultures prepared with substrate material from other types of microhabitats. *Macbrideola martinii* and *M. scintillans* were recorded only from samples collected in Mexico but were common on that set of samples. In addition, our samples yielded several rare or unusual species. For example, *Perichaena dictyonema*, a rare myxomycete described from Central Africa, appeared in two cultures prepared with samples from Australia, one from Puerto Rico and has also been reported from Ecuador (McHugh, 2005), also on lianas. *Arcyria afroalpina*, also described from Africa, was recorded from lianas in Australia and Puerto Rico. As already noted, our specimen of *Physarum hongkongense* from Mexico apparently represents the first record for this species from the Neotropics. This species was described originally from Hong Kong (Chung, 1997) and since then has been reported from Taiwan (Chung and Tzean, 1998) and New Zealand (Stephenson, 2003). All of the previous records were from ground litter, either the leaves of angiosperms or old palm fronds. This same microhabitat is

Table 2. Occurrence of myxomycetes on samples of lianas collected in the six study areas. Note: NSA = number of study areas in which the species was recorded. ¹Camino *et al.* (in press); ²McHugh (2005); ³Schnittler *et al.* (2002).

Species	Australia	Cuba ¹	Ecuador ^{2,3}	Mexico	Peru	Puerto Rico	NSA
<i>Arcyria afroalpina</i>	+					+	2
<i>Arcyria cinerea</i>	+	+	+	+	+	+	6
<i>Arcyria</i> cf. <i>denudata</i>	+						1
<i>Arcyria insignis</i>				+			1
<i>Badhamia melanospora</i>						+	1
<i>Badhamia nitens</i>	+						1
<i>Calomyxa metallica</i>				+			1
<i>Ceratiomyxa fruticulosa</i>					+		1
<i>Clastoderma debaryanum</i>				+			1
<i>Collaria arcyronema</i>	+	+	+			+	4
<i>Comatricha laxa</i>	+					+	2
<i>Comatricha tenerrima</i>	+	+		+	+	+	5
<i>Comatricha</i> cf. <i>pulchella</i>			+			+	2
<i>Craterium aureum</i>					+		1
<i>Cribraria microcarpa</i>						+	1
<i>Cribraria violacea</i>		+		+		+	3
<i>Diderma effusum</i>						+	1
<i>Diderma hemisphaericum</i>	+	+			+	+	4
<i>Didymium anellus</i>						+	1
<i>Didymium difforme</i>				+			1
<i>Didymium iridis</i>	+	+	+				3
<i>Didymium nigripes</i>	+		+			+	3
<i>Didymium</i> cf. <i>ochroideum</i>			+			+	2
<i>Didymium squamulosum</i>	+	+	+	+	+	+	6
<i>Echinostelium apitectum</i>	+						1
<i>Echinostelium minutum</i>	+			+	+		3
<i>Hemitrichia calyculata</i>			+				1
<i>Hemitrichia pardina</i>		+	+	+		+	4
<i>Licea biforis</i>	+						1
<i>Licea erecta</i> var. <i>erectoides</i>	+	+					2
<i>Licea operculata</i>			+	+	+		3
<i>Licea rugosa</i> var. <i>fujiokana</i>				+			1
<i>Licea scyphoides</i>		+			+		2
<i>Macbrideola martinii</i>				+			1
<i>Macbrideola scintillans</i> var. <i>verrucosa</i>				+			1
<i>Perichaena chrysosperma</i>	+	+	+	+		+	5
<i>Perichaena depressa</i>		+		+		+	3
<i>Perichaena dictyonema</i>	+		+			+	3
<i>Perichaena vermicularis</i>	+	+			+		3
<i>Physarum aeneum</i>						+	1
<i>Physarum album</i>	+			+			2
<i>Physarum bogoriense</i>					+		1
<i>Physarum cinereum</i>	+						1

Table 2 (continued). Occurrence of myxomycetes on samples of lianas collected in the six study areas. Note: NSA = number of study areas in which the species was recorded. ¹Camino *et al.* (in press); ²McHugh (2005); ³Schnittler *et al.* (2002).

Species	Australia	Cuba ¹	Ecuador ^{2,3}	Mexico	Peru	Puert o Rico	NSA
<i>Physarum compressum</i>	+	+	+	+	+	+	6
<i>Physarum crateriforme</i>						+	1
<i>Physarum decipiens</i>					+		1
<i>Physarum didermoides</i>		+	+	+		+	4
<i>Physarum globuliferum</i>					+		1
<i>Physarum cf. gyrosum</i>						+	1
<i>Physarum hongkongense</i>				+			1
<i>Physarum leucophaeum</i>	+						1
<i>Physarum melleum</i>					+		1
<i>Physarum nicaraguense</i>						+	1
<i>Physarum oblatum</i>	+						1
<i>Physarum pusillum</i>		+	+	+	+	+	5
<i>Physarum stellatum</i>				+			1
<i>Physarum superbum</i>	+				+		2
<i>Physarum cf. viride</i>	+						1
<i>Stemonaria gracilis</i>					+		1
<i>Stemonitis flavogenita</i>						+	1
<i>Stemonitis foliicola</i>	+				+		2
<i>Stemonitis fusca</i> var. <i>nigrescens</i>	+				+	+	3
<i>Stemonitis mussooriensis</i>				+			1
<i>Trichia cf. munda</i>	+						1
<i>Willkommlangea reticulata</i>	+				+		2
Total: 65	29	16	15	23	21	28	

shared by other foliicolous species that we recorded on lianas. Examples include *Diderma hemisphaericum* and *Stemonitis foliicola*. *Collaria arcyronema* was recorded only on samples from Australia and Cuba. Two species (*Physarum melleum* and *Willkommlangea reticulata*) not usually reported from moist chamber cultures were recorded on samples of lianas from Australia, and the latter species also was collected on lianas from Peru. *Ceratiomyxa fruticulosa* rarely appears in moist chamber cultures but was recorded from lianas. In addition to the species appearing on lianas in moist chamber culture, myxomycetes also can be recorded from lianas in the field. Some of the species we have observed include *Fuligo megaspora* (Lado *et al.*, 2003), *Arcyria cinerea*, *Didymium iridis*, *Didymium squamulosum* and *Physarum compressum* (unpublished data).

Some of the species recorded as common on lianas were also recovered from samples represented by other aerial microhabitats (e.g., dead leaves of vascular epiphytes) collected in same study area in Australia (Black *et al.* 2004). *Arcyria cinerea* and *Didymium squamulosum* were especially common, and all but one (*Physarum cf. lateritium*) of the species recorded from aerial microhabitats other than lianas also occurred on lianas. Species recorded from lianas but not from other aerial microhabitats included *Comatricha tenerrima*, *Echinostelium minutum* and *Perichaena vermicularis*. Although the number of moist chamber cultures prepared in this other study was lower than the number we prepared for lianas, the proportion of cultures of lianas yielding evidence of myxomycetes was essentially the same as was the case for other types of aerial microhabitats.

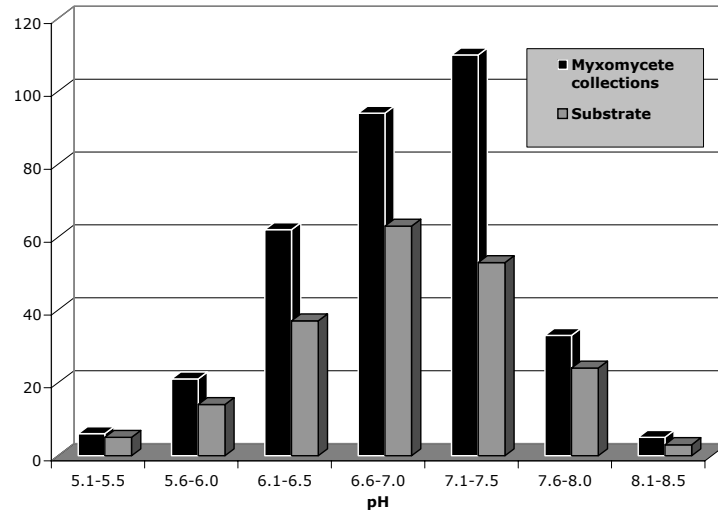


Fig. 13 The productivity of lianas in relation to the pH of the substrate.

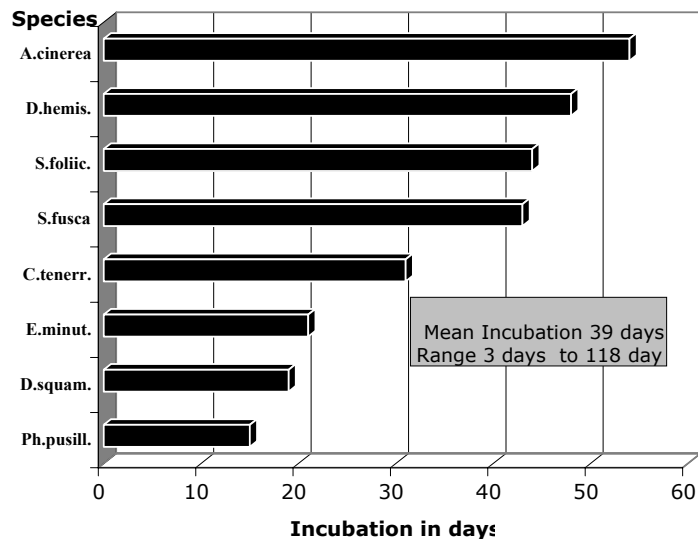


Fig. 14 The incubation times of the most characteristic species appearing on lianas.

[Species: *Arcyria cinerea*, *Diderma hemisphaericum*, *Stemonitis foliicola*, *Stemonitis fusca*, *Comatricha tenerrima*, *Echinostelium minutum*, *Didymium squamulosum* and *Physarum pusillum*]

Values of pH recorded for all moist chamber cultures prepared with samples of lianas ranged from 5.4 to 8.5, but the mean value was exactly neutral (7). When productivity was compared to the pH of the substrate (Fig. 13), the highest numbers of specimens were associated with cultures with a circumneutral pH. However, the pH interval of 7.1 to 7.5 appeared to have a higher overall yield than any of the other intervals. The apparent association of many species of

myxomycetes with substrates characterized by a circumneutral pH is consistent with the results obtained from studies of the species appearing on bark in moist chamber cultures (Wrigley de Basanta, 2000, 2004). Cultures with a substrate pH either much higher or much lower tend to be much less productive. However, there are some myxomycetes that appear to be restricted to certain substrates characterized by a more extreme pH. For example, species such as *Licea succulenticola*

Table 3. Mean values of maximum water capacity and water retention obtained for sets of samples of different substrates. SD = standard deviation.

Substrate	Mean water capacity (% dry mass) \pm SD	Mean water retention (% water absorbed) \pm SD	
		6 hrs open to air	24 hrs open to air
Liana whole (dead)	139 \pm 52	64 \pm 11	6 \pm 6
Liana bark	183 \pm 79	56 \pm 17	6 \pm 8
Bark of cacti	48 \pm 21	26 \pm 8	3 \pm 6
European tree bark	83 \pm 18	26 \pm 12	0
Neotropical tree bark	89 \pm 27	65 \pm 9	26 \pm 20

(Mosquera *et al.*, 2003) occur on the remains of succulent plants with a pH of 10, and the acidic bark of some conifers consistently yields certain species (e.g., *Enerthenema papillatum*) at a pH below 4 (Stephenson, 1989). Data reported by Snell and Keller (2003) from studies in the Great Smoky Mountains National Park in the United States indicated that trees with a similar bark pH also had similar assemblages of myxomycetes present. All of the trees sampled in this study had a bark pH below 7, but the most acidic bark was characterized by the lowest species richness and most of the common species were more abundant on trees with bark at the highest pH values (5.7 and 6.7).

The moisture content of the substrate appears to be another critical abiotic factor for myxomycetes (Ing, 1994). The high value for maximum water capacity recorded for lianas indicates that this substrate is capable of absorbing nearly twice the amount of water as some other similar substrates (Table 3). The liana bark also reflected this large water capacity. The values for water retention indicate that more half of the water remains after 6 hours, but most of the water has been lost at twenty-four hours. Over 90% of the absorbed water was lost, which shows that a high rate of evaporation occurred under these experimental conditions. Considering the fact that the high moisture levels in tropical forests - from rainfall, constant cloud cover and transpiration - create intense local humidity, then water retention is not a critical factor for these plants, and in fact much of the transpired water is generated by the lianas themselves as a result of the large leaf surface area they can support. In this humid environment, evaporation would be slower. Although a

controlled comparative study would properly clarify whether the water absorption and retention of the substrate is a significant factor in myxomycete distribution, some other data we have collected previously is presented here (Table 3) for comparison. The bark or outer layer of the stem of tree cacti (*Cactaceae*) absorbs comparatively little water and retains it poorly, as can be seen from the table. In these xerophilous plants, the bark as observed in culture is often waxy, probably with the role of protecting the interior reservoir of water and minimising evaporation in ultra-dry surroundings. The tree bark from the Neotropics was mainly from arid or semi-arid areas, and it shows the best retention of water of the examples used. The bark from Europe was from temperate species of *Quercus* and *Pinus* growing in areas with generally more water available. The high water capacity of lianas demonstrated here could be one reason why they are such good substrates for myxomycetes. In moist chamber cultures, the artificially maintained humidity may account for why a number of plasmodia could not be induced to fruit. In their natural environment, lianas would undergo periods of drying, which is quite unlike the forest floor, tree bark and other microhabitats that may remain continuously moist, a condition that would not favor the production of fruiting bodies. Perhaps the suggestion that myxomycetes do not appear to reach their biodiversity optimum in tropical rain forests primarily because of the high moisture levels (Schnittler and Stephenson, 2000) does not take into account the fact that these organisms have been displaced to different microhabitats, such as lianas. Information from myxomycetes associated with other aerial microhabitats (Black *et al.*,

2004) also seems to suggest that this might be the case.

Although the moist chamber cultures we prepared with samples of lianas were productive, the myxomycetes appearing in these cultures seemed to require a longer period of time to develop than those reported for the same species in cultures prepared with samples of bark (Fig. 14). In 84 cultures monitored to determine the first appearance of myxomycete sporocarps, the mean number of days was 39, which is almost a week longer than the mean (33 days) recorded for a similar number of mixed bark cultures from the Neotropics (Wrigley de Basanta, 2002). Two common species that were abundant in moist chamber cultures of *Quercus ilex* in Spain and common on lianas in the present study, showed longer average incubation times on lianas. *Echinostelium minutum* required 21 days versus 10 days, whereas *Arcyria cinerea* required 54 days versus 34 days (Wrigley de Basanta, 1998). The longest incubation time for any species appearing in cultures of lianas was 118 days (*Perichaena depressa*), and the shortest time was three days (*Arcyria insignis* and *Echinostelium minutum*). These very short incubation times are probably because the myxomycete was on the liana in the form of microcysts or sclerotia not spores. It may be that the longer average incubation times are due to the availability of water, which enables them to remain longer as myxomonads or plasmodia in this favourable microhabitat, and so they are slower to produce fruiting bodies. Agar culture work has shown that the spores of some species can take up to a month to germinate (Haskins and Wrigley de Basanta, in press), so reaching exact germination conditions may be another reason for differences. It has been suggested that opportunists, such as the “casual corticoles” reported by Ing (1998), take longer than true bark species to develop. In these cultures of lianas and liana bark, however, 82% of the results were produced in the first two months, and of the remaining results the longest incubation time was a collection of *Perichaena depressa*, a common bark species.

In summary, the results obtained in the present study indicate that lianas are a very productive substrate for myxomycetes, both in

terms of species richness and the abundance of fruiting bodies. Certainly, they have been the most productive set of moist chamber results the authors have obtained from Mexican moist forests thus far, and the Peruvian and Puerto Rican liana results were also exceptionally good. Presumably, in this elevated microhabitat, myxomycetes can take advantage of year-round climatic stability, abundant moisture, plentiful food resources and suitable pH conditions high above the forest floor, a strategy that for these organisms, as well as many others, is clearly a success.

Acknowledgements

The research reported herein was supported in part by the Spanish Ministry of Education and Science (grants REN2002-00445/GLO and CGL2005-00320/BOS), the US National Science Foundation (grants DEB-9705464, DEB-0316284 and INT-0139547) and the Australian Biological Resources Study Participatory Program.

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