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Montane and cloud forest specialists among neotropical *Xylaria* species

D. Jean Lodge[1], Thomas Læssøe[2], M. Catherine Aime[3] and Terry W. Henkel[4]

[1]US Department of Agriculture, Forest Service, Northern Research Station, Center for Forest Mycology Research, PO Box 1377, Luquillo, PR 00773-1377. [2]Dept. of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. [3]Dept. of Plant Pathology and Crop Physiology, Louisiana State University, Agricultural Center, 302 Life Sciences Bldg., Baton Rouge, LA 70803. [4]Dept. of Biological Sciences, Humboldt State University, Arcata, CA 95521.

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Corresponding author: D. Jean Lodge, dlodge@fs.fed.us. Accepted for publication May 23, 2008.

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Abstract: We compared records of neotropical *Xylaria* species among Belize, Ecuador, the Guianas, Mexico, Puerto Rico and Venezuela to determine if there were neotropical taxa consistently found only in cloud forest or high montane forests that might be endangered by climate change. Historical reports were combined with new records from Belize and Guyana. A few collections from the Cerro de la Neblina expeditions in Venezuela were redetermined. Foliicolous (5) and fruit inhabiting (3) species, and species restricted to one country (14) were overrepresented among the 16 species found only in cloud forest as compared to other habitats. The data indicate that several species appear to be specialists of cloud or high montane forests that may be adversely affected by climate change. These include two neotropical cloud forest specialists restricted to that habitat in more than one country (*X. cordovensis,* and *X. magnoliae*), three species reported only from cloud forest and high montane forests (*X. corniculata* ined., *X. pasochoae* ined. and *X. phosporea*), and another 21 species reported from a single country that probably include additional cloud forest or high montane specialists. An additional four widely distributed *Xylaria* taxa occurred primarily in cloud forests and might also be affected by climate change.

Key words: *Xylaria*, cloud forest, montane forest, neotropics, conservation, climate change, fungal ecology, biogeography, meta-analysis, Belize, Ecuador, Guianas, Mexico, Puerto Rico, Venezuela.

Introduction: Recent collections of *Xylaria* (Ascomycota, Xylariaceae) from cloud forests and higher montane habitats in Central and South America have led us to compare our results with those from the earlier, pioneering work of J.D. Rogers and his collaborators (Rogers et al., 1988; San Martín and Rogers, 1989, 1995; San Martín et al., 1997) to determine if there are cloud forest specialist *Xylaria* spp. that could be adversely affected as these habitats decrease in size or disappear due to climate change. A recent analysis by Neelin et al. (2006) found that all of the current climate change models agree on a significant summer drying trend for the Caribbean and Central American region. Such changes could result in a contraction or extirpation of cloud forests on tropical mountains, which may already be occurring in Central America (Foster, 2001; Benning et al. 2002). Climate change is also expected to affect the distribution of cloud forests in biodiversity hotspots of the Andes (Bush et al., 2004) and Hawaii (Benning et al., 2002). Specifically, condensation may move to higher elevations, affecting both cloud forests and higher montane habitats that are currently above the cloud zone.

The first of the earlier studies on neotropical xylariaceous fungi was published by Rogers et al. (1988) on *Xylaria* of the Cerro de la Neblina, a mesa-capped "tepui" mountain in Venezuela, though many of their collections were from around a base camp at much lower elevation than the summit plateau and a few from near the San Carlos de Río Negro airstrip in lowland Amazonian Venezuela. Dr. Rogers also contributed significantly to identification of *Xylaria* species from Puerto Rico, a mountainous island in the Caribbean. The species identified from Puerto Rico were published by Lodge (1996) and incorporated in Minter et al. (2001), and are also available on-line (Lodge, 2003; Cantrell et al., 2006). In a recent paper by San Martín and Rogers (1995), extensive records of *Xylaria* from Mexico were classified by forest type as well as host, providing for an ideal comparison with data from our surveys in Belize, Ecuador, the Guianas and Puerto Rico. Some Ecuadorean and Puerto Rican *Xylaria* species were described or redescribed by Læssøe (1999) and Læssøe & Lodge (1994). Collection information on Ecuadorean *Xylaria* is available (Læssøe and Petersen, 2004).

Records incorporated here were from evergreen lowland broadleaved wet forests, cloud forests at middle elevations, and montane forests at higher elevations above the cloud condensation zone. The cloud forest sites include recent surveys on the highest peak of Belize in Central America known as Doyle's Delight and slopes in the Andes of Ecuador in South America. The high elevation records were all from slopes to the tree line in Ecuador. An attempt was made to segregate data from our recent surveys and previous studies into three classes, i.e., those from high elevations above the level at which atmospheric moisture condenses to form clouds, henceforth referred to as high montane; those within the cloud condensation zone, henceforth referred to as cloud forest; and those from wet, non-deciduous broad-leaved forests occurring at lower elevations, henceforth referred to as lowland wet forest. A few records from moist, semi-deciduous low elevation forests were included if that species occurred in wetter habitats in other countries. Older data from lowland wet forests in Guyana, French Guiana and Venezuela summarized by Dennis (1956, 1957) were also incorporated in our analyses. A few additional distribution records were obtained from the on-line database for fungi of Venezuela from Iturriaga and Minter (2006). Description of new taxa and combinations are not covered here, and will be dealt with elsewhere.

Materials and Methods: Climatic and vegetation or life zones in the tropics generally correspond to elevation, precipitation and temperature according to the Holdridge system (Ewel and Whitmore, 1973). A given life zone, however, occurs at higher elevations on mountains surrounded by highlands than on isolated mountains or peaks. Inversely, comparable life zones are found at lower elevations on mountains of small islands or mountains surrounded by lowland coastal areas, and this is known as the Massenerhebung effect (Foster, 2001). Furthermore, sites in Puerto Rico, Mexico and Belize are classified as subtropical because they occur at higher latitude than tropical locations such as Ecuador, the Guianas and Venezuela, and hence cooler temperatures are encountered at a lower elevation in the subtropics than at comparable elevations close to the equator (Ewel and Whitmore, 1973). Thus, matching of life zones in Belize, Ecuador, Guyana, Mexico, Puerto Rico and Venezuela could not be based solely on elevation. We used the cloud line and characteristic plants in common among regions to classify fungal specimens collected in lowland wet forest, middle elevation cloud forest and high elevation montane habitats. The separations were made as follows:

For Puerto Rico (18° N, 65° W), the division was made at 600 m asl (above sea level), which corresponds to the lower limit of cloud forests (Ewel and Whitmore, 1973; Brown et al., 1983). There are two life zones that are considered cloud forests: subtropical rain forest and lower montane wet forest according to the Holdridge Life Zone system (Ewel and Whitmore, 1973). Cloud forests in Puerto Rico receive ca. 4000-5000 mm annual precipitation, and are comprised of Palo Colorado forest with massive *Cyrilla antillana* and *Magnolia splendens* trees, monodominant palm breaks (variously listed as *Prestoea montana, P. acuminata* or *Euterpe globosa*) in montane wetlands, and elfin/dwarf cloud forest above 800 m. In the Central Mountain Range of Puerto Rico, *Podocarpus coriaceus* L.C. Rich. occurs as a rare cloud forest element, and *Clusia* spp. form dense stands on rocky outcrops.

In the highlands of Guyana near Mt. Ayanganna, a narrow band of cloud forest vegetation occurs on ridges at 1500-2000 m elevation (Fanshawe, 1952). The area sampled by Aime (MCA) and Henkel (TWH) on the upper Potaro River basin in the Pakaraima Mountains (5° 18' N, 59° 54' W) ranged from 700-800 m asl, and received 3500+ mm of rain per year, so that site was classified as lowland forest. The vegetation zone is evergreen tropical wet forest (but mean year-round monthly rainfall data are lacking), with dense monodominant stands of a massive emergent tree, *Dicymbe corymbosa*, interspersed with highly diverse broadleaved evergreen forest (Henkel 2003). Records from lower elevation lowland wet forests in Guyana and French Guiana were incorporated from historical records summarized by Dennis (1956, 1957).

In Belize, the break delineating cloud forest was made at 900 m asl, which at Doyle's Delight corresponds to the lowest site with *Cyrilla antillana*; *Magnolia yoroconte* occurred at slightly higher elevations, closer to 950 m asl. (Holst, 2007; Meerman, 2007). Doyle's Delight was sampled by Lodge (DJL) and MCA, and is the highest peak in Belize (16° 29' N, 89° 3' W) situated in a high plateau on the Maya Mountains divide (Meerman, 2007). The Belize Ecosystem Map classifies the life zone as tropical evergreen broad-leaved lower montane palm forest (Meerman, 2007). The ridges (950-1124 m asl) had emergent fan palms (*Colpothrinax cookii*), rare *Podocarpus* and a wide diversity of broadleaved trees in the overstorey including *Quercus* spp., an understorey with many palms (predominantly *Euterpe precatoria*). Stands of *Clusia* sp. grew on rocky outcrops (Holst, 2007; Meerman, 2007). New Belizian records from lowland wet forests were by DJL.

In Ecuador, we considered areas from 1250-2000 m asl as cloud forests, and areas above 2000 m as high montane habitat. Jørgensen et al. (1995) have performed a floristic analysis of the high Andes, and Bush et al. (2004) give the elevation band for lower montane cloud forests as 1,300-2,000 m. We selected a division 50 m lower than indicated by Bush et al. (2004) to avoid splitting of records from the same location. The Ecuadorean sites with extensive sampling were cloud forests on the Pacific slope of the Andes at Mindo (1,600 m) in Pichincha Prov., and on the eastern slope of the Andes at the Cascades de San Rafael (1,250-1,350 m) in Napo Prov., and Baños (1,200-2,000 m) in Tungurahua Prov. A few collections were from cloud forest at La Guanga (1,400 m), in Cotopaxi Prov., and high montane habitats near Cuenca (3,500-4,000 m) in Azuay Prov., the Loja-Zamora road bordering Zamora and Chichipe Prov., at Llanganates (3,500-4,000 m) in Tungurahua Prov., near Maldonado (2,100 m), Guandera (3300-3500 m) in Carchi Prov. and Parque Nat. Podocarpus near Cajanuma (2,800 m) in Loja Prov. Collection records, descriptions and photographs are available on-line (Læssøe and Petersen, 2004). Many insights into Ecuadorean montane forests can be gained from Churchill et al. (1995).

The collection data we used of Mexican *Xylaria* (San Martín and Rogers, 1995) were either from cloud forests (classified as mesophytic montane forest or Bosque Mesófilo de Montaña), or from lowland wet forests (classified as tall non-deciduous broadleaved forest or Selva Alta Perennifolia). Kremsa (n.d.) describes forest types of Mexico with cloud forests occurring from 400-1000 m asl, and lists characteristic species as *Alnus arguta, Juglans mollis, Liquidambar styraciflua, Magnolia dealbata, Nyssa sylvatica, Ostrya virginiana* and *Podocarpus matudae*. *Magnolia* was present in at least some of the cloud forests in Mexico according to host records, indicating a plant genus in common with cloud forests in Puerto Rico and Belize. The mesophytic montane cloud forest areas in Mexico mentioned by San Martín and Rogers (1995) were on the Gulf slope of the Sierra Madre Oriental in Veracruz, the mountains of Chiapas (an area in the same biogeographic region as the highlands of Belize), and Conrado Castillo near Hilalgo in the mountains of Tamaulipas state. Internet searches for these sites and data from Manning (1962) showed them to be in the elevation range for cloud forest, and that they all had some characteristic cloud forest species. Although

Mexico has forests above the cloud zone, these did not correspond to habitats in Ecuador so they were not included in our analyses.

For Venezuela, we delineated forests above 1,000 m asl as cloud forests because the valley below the N side of Pico Phelps (1,000-1,250 m asl, 0° 49' N, 66° 0' W) was classified as cloud forest (Rogers et al., 1988). This eliminated many of the records from the Cerro de la Neblina expeditions (Rogers et al., 1988) as the majority of specimens were collected near a base camp at 140 m asl. Historical records reported in Dennis (1956, 1957, 1970) and incorporated by Iturriaga and Minter (2006) yielded additional sites for a few species, but many of the old records lacked specific locality information.

Collecting by Iturriaga, Rossman and Samuels in lowland Amazonian forest in Venezuela occurred as plot surveys (IVIC plot) and opportunistic collecting near the base camps and airport. Collecting in Ecuador included plot surveys at Cuyabeno and collecting near trails, rivers and roads with repeated visits. Collecting in Puerto Rico also combined repeated plot surveys (16 ha. grid at El Verde) and collecting throughout the island near roads and trails over a 15 yr period. Collecting in Guyana included repeated, multi-year surveys of plots (Henkel, 2003) and opportunistic collecting near the base camp. Collections from Doyle's Delight in Belize were from two 10-day rapid assessments along trails in August 2004 and 2007. Collections from lowlands in Belize were made along trails and forest interiors with repeated visits (2001-2005).

The results of our comparisons are presented in tabular form. T. Læssøe (TL) determined Ecuadorean collections; DJL made determinations for the new reports from Belize; for collections from Guyana, DJL determined those by MCA and TL determined ones from TWH; DJL, TL and J.D. Rogers determined collections from Puerto Rico (Callan and Rogers, 1990; Læssøe and Lodge, 1994; Lodge, 1996, 2003; Minter et al., 2001; Cantrell et al., 2006). J.D. Rogers, A.Y. Rossman, C. Rogerson and G. Samuels (Rogers et al., 1988; Samuels and Rogerson, 1990) described collections from the Cerro de la Neblina expeditions in Venezuela, and a few of those collections were redetermined by DJL, some based on substratum differences. Macromycetes in tropical forests rarely fruit on both wood and leaves, though foliicolous species can occur on small twigs (Lodge, 1997). Herbaria where Ecuadorean specimens are deposited (AAU, C, F, FH, K QCNE, and herb. J.D. Rogers) are recorded in the database (Læssøe and Petersen, 2004). Most collections from Puerto Rico were deposited at CFMR with duplicates at C, WSP or herb. J.D. Rogers. Part of all Belizean collections cited have or will be deposited at BRH; duplicates for most Belize records by DJL are deposited at CFMR, while duplicates by MCA are deposited at LSUM. Collections by MCA from Guyana are deposited at BRG with duplicates at LSUM. Herbarium codes are as given in Index Herbariorum (Holmgren and Holmgren, 1998).

Results: *Xylaria* species from neotropical non-deciduous, wet broadleaved forests of Belize, Ecuador, the Guianas, Mexico and Venezuela are presented in Appendix Table 1 (author citations are given in Appendix Table 2). For a few species in which there are differing concepts, an attempt was made to match collections across studies by their descriptions, and these are cross-referenced in the table. A few ambiguous taxa that grade into each other and may represent intraspecific variation [e.g., *X. brasiliensis* (Theiss.) C.G. Lloyd and *X. rhizomorpha* (Mont.) Mont. (Dennis, 1956); *X. telfarii* (Berk.) Fr. and *X. enterogena* (Mont.) Fr. (Dennis, 1956; Rogers et al., 1988; San Martín et al., 1997); *X. pallide-ostiolata* P. Henn. and *X. scruposa* (Fr.) Fr. (Dennis, 1957; San Martín and Rogers, 1989)], and species that are likely to be synonymized in the future [e.g., *X. aristata* Mont. and *X. delicatula* Starbäck (San Martín et al., 1997)] are treated together. The *X.*

squamulosa San Martín & Rogers complex includes *X.* aff. *comosa* (Læssøe, 1999) and possibly *X. areolata* (Berk. & M.A. Curtis) J.H. Miller; this group is unresolved (Læssøe, 1999) and is treated together (except *X. areolata*) in Appendix Table 1 as *X. squamulosa* complex. Rogers (pers. comm. to DJL, 15 Oct. 2007) noted that the taxon identified as *Xylaria* cf. *kegeliana* (Lév.) Fr. in Rogers et al. (1988) was not that species; DJL has redetermined these collections as *X. aenea* Mont. The taxon growing from soil reported as *X.* cf. *trichopoda* Penz. & Sacc. in Rogers et al. (1988) more closely resembled the seed inhabiting species, *X. ianthino-velutina* (Mont.) Fr., than the lignicolous *X. trichopoda* described from Java, so it was assumed by DJL to have been growing from a buried seed.

Problems were encountered in the taxon described in Rogers et al. (1988) as *X.* cf. *brachiata* Sacc. A duplicate of R2233 deposited at BPI and growing on leaves of *Clusia* sp., differed from the description in having a smooth rather than pubescent stipe and spores 9.0-11.4(-11.8) rather than 14.5-16 x 6.5-7 µm. We assumed that the characters described in Rogers et al. (1988) for *X.* cf. *brachiata* refer to another collection, cited as R2284, but we have not examined that material. It is also possible that R2233 was a mixed collection, and that duplicates deposited elsewhere match the description in the text. Collection data for R2284 that was cited under *X.* cf. *brachiata* Sacc. are missing from the final section in Rogers et al. (1988), so the substratum is uncertain. *Xylaria brachiata* was described from the Congo growing on wood, and was synonymized with *X. arbuscula* Sacc. by Dennis (1957), so a part of that record in Rogers et al. has been tentatively assigned here to *X. mellissii* (=*X. arbuscula*).

Problems were also encountered with the records of *X. obovata*. The concept of *X. obovata* in Callan and Rogers (1990, Lodge-186 from Puerto Rico) matches *X. tuberoides* Rehm, i.e, subglobose stromata with a copper-black surface, loose fibrous pink entostroma that disappears with age, and spores 24.5-28(-30) µm long with a short longitudinal germ slit. We are uncertain of the concept of *X. obovata* used in Rogers et al. 1988 (S 1507); while the photograph (Fig. 47) and description of it becoming hollow recalls *X. tuberoides*, the authors noted that some ascospores were as short as 23.5 µm long and some had short oblique germ slits – characters that are more consistent with *X. obovata*, a species also recorded as *X. schweinitzii* from the Cerro de la Neblina expedition. Finally, the concept of *X. obovata* in San Martín and Rogers (1989) matches our concept (synonym *X. schweinitzii*), with ascospores 21-26 µm long and short oblique germ slits.

Sixteen taxa were recorded exclusively from middle elevation cloud forests: *X. anniversaria* ined., *X.* cf. *australis* Cooke, *X. casaamarilliae* ined., *X. ceronii* ined., *X. cordovensis* Berk., *X. eugeniae* F. San Martín, *X. foliicola* ined., *Xylaria* foliicolous spp. 2 and 4 (R2264 and R2284 from Venezuela), *X. intranigra* ined., *X. magnoliae* J.D. Rogers, *X. megaapparati* ined., *X. nodulosa* Lloyd var. *microspora* A. Pande & Waing., *X. persicaria* (Schwein.) Berk., *X. piperarum* ined. and *X. turbinata* comb. ined. Undescribed taxa from Ecuador with provisional names (T. Læssøe) are denoted by ined.; other unnamed taxa are indicated as a numbered foliicolous or lignicolous species. Four species were found in both cloud forest and high montane habitats: *X. corniculata* Sacc., *X. pasochoae* ined., *X. phosphorea* Berk. and *X. subglobosa* ined. Seven species were found exclusively in high montane habitats in Ecuador: *X. andina* ined., *apiculoides* ined., *X. bipapillata* ined., *X. gynoxia* ined., *X. metaeformis* Lév., *X. xylarioides* comb. ined. and *X. zealandica* Cooke. Of the 27 taxa restricted to cloud and/or high montane forests, only *X. cordovensis, X. corniculata, X. magnoliae, X. pasachoae* and *X. phosphorea* were recorded in more than one country and thus may be widespread, though infrequent species. Of these five species, only *X. cordovensis* and *X. magnoliae* were restricted to cloud forest, while the other three were found in both cloud and high montane forests (Appendix Table 1). Four additional widespread but infrequent taxa were recorded predominantly but not exclusively in neotropical cloud forests: *X. apiculata* Cooke, *X.* foliicolous spp. 1 and 3 and *X. platypoda* var. *microspora* J.D. Rogers & A.Y. Rossman.

A relatively high proportion of the 60 taxa that were recorded in only one country was found exclusively in cloud forest (13 spp., 22%). In comparison, only two of the 57 species recorded in more than one country (3.5%) were restricted to cloud forests. Striking contrasts were also found in relation to substratum type among species restricted to cloud forests. Leaf inhabiting species comprised five of the 16 species that were restricted to cloud forests (31.3%), versus seven of 47 species found in both cloud and lowland wet forests (14.9%), and seven of 43 species restricted to lowland wet forest (16.3%). Similarly, fruit inhabiting species comprised 18.8% of those restricted to cloud forest, but only 6-7% of the species restricted to lowland wet forests or those found in mixtures of cloud and lowland wet forests. All seven species that were restricted to high montane forest occurred on wood.

Discussion: Both of the widespread species (i.e., recorded in at least two countries) that were restricted to cloud forest, *X. cordovensis* and *X. magnoliae*, were previously reported as occurring exclusively in cloud forests in Mexico (San Martín et al., 1995). There was further agreement between Appendix Table 1 and previous results on *Xylaria* distributions in Mexico (San Martín et al., 1995), with *X. phosphorea* being found exclusively in cloud forest in Venezuela and Mexico, though it was found in high montane forest in Ecuador. Only two of the species that were restricted to cloud forests in Mexico had broader habitat distributions in our wider survey (*X. apiculata* and *X. longipes*; Appendix Table 1).

As noted by San Martín and Rogers (1995), the number of collections from Mexico on which their habitat patterns were based was limited, which constrains confidence and interpretation. Similarly, all neotropical countries, including those in this meta-analysis, have a limited number of collections. Judging habitat restriction based on few records from a single country can therefore be misleading. For example, one might assume that two well-defined, highly distinctive taxa, *X. platypoda* var. *microspora* and *X. griseo-olivacea*, were cloud forest specialists based on records from Belize, but their occurrences at low elevation in South America suggests that they may have a broader ecological range that would be revealed by more collecting. Thus, the meta-analysis presented here overcomes some of these limitations by bringing together data from multiple countries. Appendix table 1 can be used as a crude gap analysis to indicate which species are likely to be found in a particular country where no current records exist, and in which habitat(s) they are likely to be found. For example, it is likely that *X. hyperythra* and *X. meliacearum* occur in lowland wet forest of Venezuela, though not yet recorded from that country.

It should not be assumed, however, that further collecting would show that *X. apiculata* or *X. longipes* also occur outside cloud forests in Mexico. Brunner and Petrini (1992) showed that the two strains of *X. longipes* they tested had different isozymes, and Rodrígues et al. (1993) showed significant heterogeneity in isozymye patterns among cultures derived from the same morphological species of *Xylaria,* such as *X. adscendens, X. allantoidea, X. microceras, X. multiplex* and *X. telfairii*. Thus, cryptic species or incipient speciation may be present within certain morphological species (Rodrígues et al., 1993), and ecotypic differentiation might occur as well. San Martín and Rogers (1995) discussed the possibility of ecotypic variation with regard to habitat separation between *X. longipes* and X. *longipes* var. *tropica*. Similarly, ecotypic variation might explain the disparity in records of *X. apiculata* from only cloud forests in Mexico and Puerto Rico, but from only lowland wet forests in Ecuador and Venezuela.

Many of the 16 taxa reported exclusively in cloud forest appear to have restricted ranges or exhibit certain traits. A disproportionate number of exclusively cloud forest taxa (31.3%) occurred on leaves (*X. casaamarilliae, X. eugeniae, X. foliicoloa*, *Xylaria* foliicolous spp. 1 and 4) or fruits (18.8%; *X. anniversaria*, *X. magnoliae* and *X. persicaria*) as compared to no species that occurred partly or exclusively in high montane forest. Species found exclusively or partly in lowland wet forests also had lower proportions of species inhabiting leaves (15-16%) and fruit (6-7%) than species restricted to cloud forests. Small substrata such as most leaves and fruits dry out quickly in lowland wet forests, limiting growth of some fungi (Lodge, 1997). On the other hand, coarse woody debris often remains waterlogged in cloud forests, which may be responsible for inhibiting fungal growth and decomposition (Torres and González, 2007). Thus an upward shift of the cloud base in the Andes could be detrimental to the seven *Xylaria* species that were restricted to high montane forests in table 1, as they all grow on wood. As noted in Læssøe and Lodge (1994), there is a high frequency of host specificity among leaf- and fruit- inhabiting *Xylaria* species, so it is likely that some of the apparent cloud forest specialists are limited by distribution of their hosts.

Most of the species restricted to cloud forests were reported from only one country (13 of 16 taxa; 81%). Interestingly, species restricted to lowland wet forests also had a disproportionately high number of species reported from only one country (28 of 43; 65%) in comparison to species found in a mixture of lowland wet and mid elevation cloud forests (7 of 47; 15%). Rare species present a problem in that they are easily missed during surveys, but at least *X. cordovensis, X. magnoliae and* some of the other *Xylaria* reported exclusively from cloud forests are likely to be habitat specialists based on consistent patterns in several countries. Van der Gucht (1995) noted four *Xylaria* spp. restricted to montane rain forests (cloud zone) in Papua New Guinea, but of these, only *X. scruposa* was also found in the neotropics. In the neotropical records in Table 1, only a few collections of *X. scruposa* from Puerto Rico occurred in cloud forests, while others from Puerto Rico, Mexico and Venezuela were from lowland wet forests.

Rogers (2000) commented on endemism in Xylariaceae in relation to host specificity, especially among pathogens. Certain high montane specialists known only from Ecuador (e.g., *X. gnoxia* ined. and *X. piperarum* ined.) were apparently host-specific and were possibly pathogenic. Two of the species restricted to cloud forests of Mexico (*X*. cf. *australis* and *X. persicaria*; San Martín and Rogers, 1995) were not recorded from the other neotropical locations in this survey, while 21 of the species in our list of cloud forest and high montane taxa (Appendix Table 1) were only recorded from Ecuador (Læssøe and Petersen, 2004). Whilst Ecuador has a megadiverse biota, the intense collecting activity has undoubtedly contributed to the high species richness in this country. In addition, the other countries in this meta-analysis did not have data from habitats comparable to the high montane forests in Ecuador. *Xylaria persicaria* grows on fruits of *Liquidambar styraciflua* in eastern North America (Rogers 1979, 2000), but it has not been reported further south than Mexico though its host is distributed as far south as Belize, Honduras, Guatemala and Nicaragua. Rogers (2000) surmised that some *Xylaria* species that fruit on seeds and fruits invaded the plants through their flowers. On the other hand, Whalley (1996) indicated that some host-specific *Xylaria* on seeds were strictly litter inhabitants, and Brunner and Petrini (1992) showed that none of the endophytic *Xylaria* strains from *Fagus sylvatica* in Europe matched strains of *X. carpophila* obtained from seeds of the same host. Furthermore, Læssøe and Lodge (1994) showed that some host-specific foliicolous tropical *Xylaria* were present in decaying but not live leaf petioles in Puerto Rico.

While xylariaceous endophytes are abundant in leaves from tropical trees (Petrini and Petrini, 1985; Rodrígues et al., 1993; Lodge et al., 1996; Arnold et al., 2001), endophytic *Xylaria* appear to be generalists and therefore may not contribute to fungal diversity (Lodge, 1996, 1997). The relationship of endophytic xylariaceous fungi to teleomorphic stromata on decaying vegetation is unclear (Rogers, 2000; Polishook et al., 2001). Brunner and Petrini (1992) found large isozyme differences between 15 of their 17 endophytic strains resembling *X. polymorpha* in culture in comparison to 13 stromata of *X. polymorpha* from Switzerland. Rodríges et al. (1993) found a similar divergence in isozyme patterns between teleomorphs and endophytic strains of *Xylaria* that clustered with them, mainly taxa from the neotropics. Rodrígues et al. (1993) therefore suggested the possibility that xylariaceous endophytes in leaves of tropical trees have largely abandoned sexual reproduction and are no longer connected with teleomorphic stromata (see also Lodge, 1997 and Rogers, 2000). The factors that contribute to host-specificity in *Xylaria* are therefore in need of further research (Rogers, 2000). Nevertheless, much of the difference between our list of cloud and montane forest taxa as compared to the previous publication that was restricted to Mexico (San Martín and Rogers, 1995) suggests a preponderance of cloud forest and high montane forest species with limited geographical as well as ecological ranges. The apparent cloud forest specialists among the widespread neotropical *Xylaria* species are likely to be adversely affected by regional drying and lifting of the cloud base. Cloud forests in the Caribbean and Central America are expected to contract or disappear, as may already be occurring at Monte Verde in Costa Rica, putting organisms that are restricted to such habitats and that already have fragmented and discontinuous distributions in danger of extinction (Foster, 2001; Benning et al., 2002). In addition to imperiled cloud forest communities in the Caribbean Basin, climate change is expected to cause rapid changes in the elevation at which clouds condense in the Andes, putting organisms in these high diversity ecosystems at risk (Bush et al., 2004). Wood inhabiting *Xylaria* species that were restricted to areas that are normally above the clouds in high montane forests of Ecuador could also be adversely be affected by wetter conditions associated with lifting of the cloud base. Cloud forest and high montane forest specialists that have limited geographic ranges may be in even greater danger of extinction than the widespread specialists, but it is difficult to know how many of the rare cloud forest and high montane forest *Xylaria* species were truly endemic or restricted to that habitat. Nevertheless, the fact that a significant proportion of rare *Xylaria* species occurred on leaves or fruits in cloud forest, and that many *Xylaria* in that trophic niche are host-specific (Læssøe and Lodge, 1994), a high proportion of these species may become as endangered as their host plants in response to unprecedented rapid changes in climate (Bush et al., 2004).

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Appendix Table 1. Presence of *Xylaria* species reported from various neotropical broadleaved wet forest areas. Country reports exclusively from high elevation above cloud forest are denoted by !! and highlighted in violet; reports exclusively from cloud forest are noted by ** and highlighted in blue; mixed reports from cloud forest and higher are denoted by *! And highlighted in blue and violet; mixed reports from both cloud forest and below the cloud condensation line are noted by * and highlighted in green; reports exclusively from lowland areas lack these superscripts and are highlighted in cream (wet forest) or salmon (moist forest). Unpublished species and combinations from Ecuador are from T. Læssøe. Un-named, numbered taxa are listed at the end by substratum type. Collection numbers are cited for new reports, re-determinations that are reported here for the first time, or to avoid confusion among sources; previously published reports (including those under other names) and literature on synonymies are noted with a superscript corresponding to numbered citations at the end.

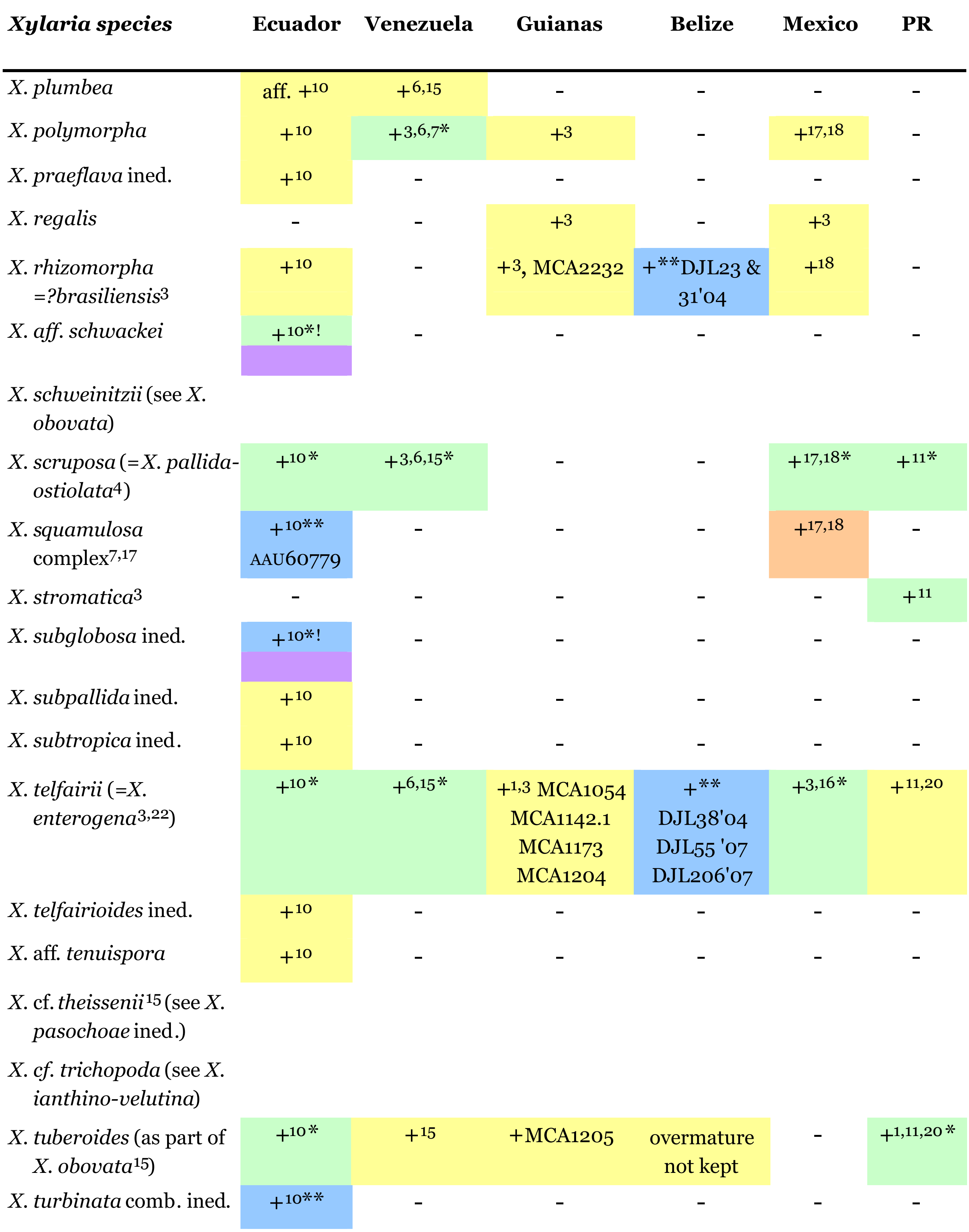
Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. aff. *aburiensis*	+[10]	-	-	-	-	-
X. adscendens	+[10]**	+[3,6]	+[1]	-	+[17,18]*	+[11]
X. aemulans	+[10]*	-	-	-	-	-
X. aenea (as *X. aenea* & cf. *kegeliana*[6,15])	-	+[3,6] Rossman 6 coll., S1427, S1451[15]	+[3]	-	+[17]**	-
X. albonigra ined.	+[10]	-	-	-	-	-
X. allantoidea	+[10]	-	+[1]	-	+[16]	+[11,20]
X. andina ined.	+[10]!!	-	-	-	-	-
X. anisopleura[3,6,12,15] (see *X. globosa*)						
X. anniversaria ined.	+[10]**	-	-	-	-	-
X. apiculata (*s.l.*)	+[10]	+[6,15]	-	-	+[18]**	+[11]**
X. apiculoides ined.	+[10]!!	-	-	-	-	-
X. appendiculata	+[10]	-	-	-	-	+[11]
X. arbuscula (see *X. mellisii*)						
X. areolata	+[10]	-	-	DJL-61'04**	-	+[11]

Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. aristata *(=?* X. delicatula[19]*)*	-	-	+[3] MCA2320	-	+[17,18,19]	+[11,20]
X. asperata	-	+[6,15]	-	-	-	-
X. cf. *australis*	-	-	-	-	+[18]**	-
X. axifera	-	-	+[3]	-	-	+[8,11,20]*
X. berkeleyi (see *X. cordovensis*)						
X. berteri	+[10]*	-	-	-	-	+[11]
X. bipapillata ined.	+[10]!!	-	-	-	-	-
X. boergesenii (as *H. conostomum* in PR)	-	-	-	-	+[18]	WSP 62101
X. brachiata[15,19] (see *X. mellisii* & *Xylaria* foliicolous sp. 2)						
X. cappariformis ined.	+[10]	-	-	-	-	-
X. casaamarilliae ined.	+[10]**	-	-	-	-	-
X. ceronii ined.	+[10]**	-	-	-	-	-
X. chordiformis	+[10]*	-	-	-	-	+[11]
X. claviceps	-	-	-	-	+[17,18]	-
X. clusiae[15,16]	-	S1353[15,16]	-	-	-	-
X. coccophora	+[10]	+[6]	+[3]	-	+[17,18]	+[10,11]
X. comosa[8]	+[8,10]	+[6,15]	-	-	cf. +[17,18]	-
X. aff. *comosa*[8] (also see *X. squamulosa*)	+[8,10]	-	-	-	-	-
X. comosoides[8]	+[8,10]	-	-	-	-	-
X. cf. complanata	-	-	-	-	+[18]	-
X. compressa	+[10]	+[3]	+[3]	-	-	-
X. cordovensis (=*X. berkeleyi*[3])	-	+S1264[6,15]**	+[3] no location	-	+[18]**	+** PR606
X. corniculata ined.	+[10]*!	-	-	-	cf. +[17]**	-

Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. corniformis (=*X. feejeensis* & *X. rhytidophloea*[3,7,17,22])	+[10]	+[15]	+[3] MCA1802	-	+[17,18]	+[1,11,20]
X. cubensis	+[10]*	+[6,15]*	+[3]	+DJL-30'07* DJL-42'01	+[17,18]*	+[11,20]
X. culleniae	-	+[15]	-	-	-	-
X. curta	+[10]*!	+[6]*	+[1,3]	+DJL-18'01	+[17,18]*	+[10,11]
X. dealbata (see *X. fockei*)						
X. earlei ined.	+[10]*	-	-	-	-	-
X. enterogena[15,16,17](see *X. telfairii*)						
X. enteroleuca	-	-	-	-	+[18]*	-
X. eugeniae	-	-	-	-	+[19]**	-
X. aff. *fastigiata*	+[10]	-	-	-	-	-
X. feejeensis (see *X. corniformis*)						
X. fockei (=*X. dealbata*[5,10,22])	+[10,21]	+[6,15]	+[3]	-	+[16]	+[11,20]
X. foliicola ined.	+[10]**	-	-	-	-	-
X. fuscopurpurea ined.	+[10]*	-	-	+DJL40'07**	-	+
X. globosa[10,11,12](as *X. anisopleura*[15,17])	+[10]	+[3,6,15]*	+[3]*	+DJL37 '04**	+[17,18]*	+[10,11]
X. grammica	+[10]	+[3,6]	-	+DJL-119 '02	+[17,18]*	-
X. griseo-olivacea	+[8,10]	+[6,15]	-	DJL-112' 07**	-	-
X. aff. *guaranitica*	+[10]	-	+MCA1198 TH 8491	-	-	-
X. guyanensis	+[10]*	+[3,6]	+[3]	-	+[17,18]	-
X. gynoxia ined.	+[10]!!	-	-	-	-	-

Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. cf. heliscus (aff. *feejeensis*)	+[10]*	-	+[4]	-	-	-
X. hirtella	+[10]	-	-	-	-	-
X. cf. holmbergi	-	-	-	-	+[18]	-
X. hyperythra (as *X. olobapha*[20], Chardon)	+[10]	-	+[3] MCA2336	DJL-31 '07** MCA3395	+[18]	+[11,20]
X. ianithinovelutina (as *X.* cf. *trichopoda* and *X.* aff. *magnoliae*[15])	+[10]	+[6,15]* R1740 on pod S1342 on soil[15] seed?	+ MCA 1061 MCA 1371	-	+[3,1718]	+[11]
X. aff. *intracolorata*	+[10]	-	-	-	-	-
X. intranigra ined.	+[10]**	-	-	-	-	-
X. irearteae ined.	+[10]	-	-	-	-	-
X. juniperus var. asperula	-	-	-	-	+[17,18]	-
X. juruensis s.l.	+[10]	S1364[15]**	-	-	+[17]	-
X. kegeliana	+[10]	-	-	-	+[17,18]	+[11]
X. kretchmarioidea	aff. +[10]	+[6,15]	-	-	-	-
X. laevis	-	-	-	-	+[17,18]	-
X. lagerheimii ined.	+[10]*	-	-	-	-	-
X. cf. lhermii	-	-	-	-	+[17,18]	-
X. cf. *longiana*	+[10]	-	-	-	+[17,18]	-
X. longipes	aff. +[10]	+[3,6]	-	-	+[17,18]**	-
X. longipes var. tropica	-	-	-	-	+[17,18]	-
X. lutea	-	+[6,15]	-	-	-	-
X. magnoliae[15,17]	-	-	-	+** DJL-24, 60 & 107 2004	+[17,18]**	-
X. megaapparati ined.	+[10]**	-	-	-	-	-
X. melanura	-	+[6]	-	-	+[18]**	-
X. meliacearum	+[10]	-	cf. + MCA2302 MCA2075	+* DJL-46'04 DLL-11'02 ASM 9317	-	+[8,11]

Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. mellisii (= *X. arbuscula*[3])	+[10]*	+[3,6,12]*	+[3]	-	+[17,18]*	+[11]
X. metaeformis	+[10]!!	-	-	-	-	-
X. mexicana	-	-	-	-	+[19]	-
X. microceras	+[10]	+[6,15]*	+[3] MCA2350	-	+[17,18]	+[1,11]
X. mindoensis ined.	+[10]*	-	-	-	-	-
X. multiplex	+[10]*	+[3,15]*	+[3] MCA1292	+ DJL-14 '02	+[17,18]	+[11]
X. nigrescens	-	-	-	-	+[17,18]	+[11]
X. nodulosa var. microspora	-	+[15]**	-	-	-	-
X. obovata (see also *X. schweinitzii*[17,18,20] & *X. tuberoides*[15,22])	+[10]*	+[15]*	+ MCA1142.2	-	+[17]	+[11,20]*
X. cf. *olobapha* var. *camptospora*	-	-	-	-	+[17,18]	-
X. oxycanthae	-	-	-	-	+[17,18]*	-
X. pallida-ostiolata[17,18] (see *X. scruposa*[4])						
X. palmicola	+[10]	-	-	-	-	+[3,20]**
X. pasochoae ined. (as *X.* cf. *theissenii*[15])	+[10]*!	+I 594[6,15]**	-	-	-	-
X. persicaria	-	-	-	-	+[16]**	-
X. phosphorea	cf. +[10,14]!!	+[6]**	-	-	+[18]**	-
X. phyllocharis	+[10]	-	+[3], MCA1269 MCA1760	-	+[17,18,19]	+[11]*
X. piperarum ined.	+[10]**	-	-	-	-	-
X. platypoda var. *microspora*	-	+[15]	-	+DJL136'07 MCA3397**	-	-
X. platypoda var. platypoda	+[10,13]!	-	-3	-	-	-



Xylaria species	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. plumbea	aff. +[10]	+[6,15]	-	-	-	-
X. polymorpha	+[10]	+[3,6,7]*	+[3]	-	+[17,18]	-
X. praeflava ined.	+[10]	-	-	-	-	-
X. regalis	-	-	+[3]	-	+[3]	
X. rhizomorpha =*?brasiliensis*[3]	+[10]	-	+[3], MCA2232	+**DJL23 & 31'04	+[18]	-
X. aff. schwackei	+[10]*!	-	-	-	-	-
X. schweinitzii (see *X. obovata*)						
X. scruposa (=*X. pallida-ostiolata*[4])	+[10]*	+[3,6,15]*	-	-	+[17,18]*	+[11]*
X. squamulosa complex[7,17]	+[10]** AAU60779	-	-	-	+[17,18]	-
X. stromatica[3]	-	-	-	-	-	+[11]
X. subglobosa ined.	+[10]*!	-	-	-	-	-
X. subpallida ined.	+[10]	-	-	-	-	-
X. subtropica ined.	+[10]	-	-	-	-	-
X. telfairii (=*X. enterogena*[3,22])	+[10]*	+[6,15]*	+[1,3] MCA1054 MCA1142.1 MCA1173 MCA1204	+** DJL38'04 DJL55 '07 DJL206'07	+[3,16]*	+[11,20]
X. telfairioides ined.	+[10]	-	-	-	-	-
X. aff. *tenuispora*	+[10]	-	-	-	-	-
X. cf. *theissenii*[15] (see *X. pasochoae* ined.)						
X. cf. trichopoda (see *X. ianthino-velutina*)						
X. tuberoides (as part of *X. obovata*[15])	+[10]*	+[15]	+MCA1205	overmature not kept	-	+[1,11,20]*
X. turbinata comb. ined.	+[10]**	-	-	-	-	-

***Xylaria* species**	**Ecuador**	**Venezuela**	**Guianas**	**Belize**	**Mexico**	**PR**
X. xylarioides comb.ined.	+[10]!!	-	-	-	-	-
X. zealandica	+[10]!!	-	-	-	-	-
Xylaria foliicolous sp. 1	-	+[15]* R2023 R2233	-	+** DJL117'07	-	-
Xylaria foliicolous sp. 2 (as *X.* cf. *brachiata*[15])	-	+[15]** R2284	-	-	-	-
Xylaria foliicolous sp. 3	-	+[15] R1741	-	+** DJL31'04	+[17]** CJ 102B	-
Xylaria foliicolous sp . 4	-	+[15]**R 2264	-	-	-	-
Xylaria foliicolous sp. 5	-	+[15] S 1330	-	-	-	-
Xylaria foliicolous & lignicolous sp. 6	-	+[15] S 1364	-	-	-	-

[1]Callan and Rogers, 1990. [2]Cantrell et al., 2006. [3]Dennis, 1956. [4] Dennis, 1957. [5] Dennis, 1970. [6] Iturriaga and Minter, 2006. [7] Læssøe, 1987. [8] Læssøe, 1999. [9] Læssøe and Lodge, 1994. [10] Læssøe and Petersen, 2004. [11]Lodge 1996, 2003. [12]Minter et al., 2001. [13]Patouillard and Lagerheim, 1882. [14]Patouillard and Lagerheim, 1895. [15]Rogers et al., 1988. [16]Samuels and Rogerson, 1990. [17]San Martín and Rogers, 1989. [18]San Martín and Rogers, 1995. [19]San Martín et al., 1997. [20] Stevenson, 1975 (untraced records not cited). [21] Sydow, 1939. Note comments regarding *X. fockei* in Læssøe and Petersen 2004 regarding mixed location. information and unlikely (erroneous?) habitat report. [22] Van der Gucht, 1995.

Appendix Table 2. Authors of *Xylaria* species noted in the text and Appendix Table 1.

X. aburiensis (Dennis) D. Hawksw.
X. adscendens Fr.
X. aemulans Starbäck
X. aenea Mont.
X. allantoidea (Berk.) Fr.
X. andina nom. prov., Læssøe, ined.
X. anisopleura (Mont.) Fr.
X. anniversaria nom. prov., Læssøe, ined.
X. albonigra nom. prov., Læssøe, ined.
X. apiculata Cooke
X. apiculoides nom. prov., Læssøe, ined.
X. appendiculata Ferd. & Winge
X. arbuscula Sacc.
X. areolata (Berk. & M.A. Curtis) Y.M. Ju & J.D. Rogers
X. aristata Mont.
X. asperata J.D. Rogers, Rossman & Samuels
X. australis Cooke
X. axifera Mont.
X. berkeleyi Mont.
X. berteri (Mont.) Cooke
X. bipapillata nom. prov., Læssøe, ined.
X. boergesenii (Ferd. & Winge) P.F. Cannon
X. brachiata Sacc.
X. brasiliensis (Theiss.) Lloyd
X. cappariformis nom. prov., Læssøe, ined.
X. casaamarilliae nom. prov., Læssøe, ined.
X. ceronii nom. prov., Læssøe, ined.
X. chordiformis Lloyd
X. claviceps F. San Martín & J.D. Rogers
X. clusiae K.F. Rodrigues, J.D. Rogers & Samuels
X. coccophora Mont.
X. coccophora Mont.
X. comosa Mont.
X. comosoides nom. prov., Læssøe, ined.
X. complanata Ces.
X. compressa Pat. & Gaillard
X. cordovensis P. Leroy & Mornand
X. corniculata nom. prov., Læssøe, ined.
X. corniformis (Fr.) Fr.
X. cubensis (Mont.) Fr.
X. culleniae Berk. & Broome
X. curta Fr.
X. dealbata Berk. & M.A. Curtis
X. delicatula Starbäck
X. earlei nom. prov., Læssøe, ined.
X. enterogena Mont.
X. enteroleuca (Speg.) P.M.D. Martin
X. eugeniae F. San Martín
X. fastigiata Fr.
X. feejeensis (Berk.) Fr.
X. fockei (Miq.) Cooke
X. foliicola nom. prov., Læssøe, ined.
X. fuscopurpurea nom. prov., Læssøe, ined.
X. globosa (Spreng. Ex Fr.) Mont.
X. grammica (Mont.) Mont.
X. griseo-olivacea J.D. Rogers & Rossman
X. guaranitica (Speg.) Dennis
X. guyanensis (Mont.) Fr. (*X. guianensis* in Index Fungorum
X. gynoxia nom. prov., Læssøe, ined.
X. heliscus (Mont.) J.D. Rogers & Y.M. Ju
X. hirtella Wakef.
X. holmbergi Speg.
X. hyperythra Mont.
X. ianithinovelutina (Mont.) Fr.
X. intracolorata (J.D. Rogers, Callan & Samuels) J.D. Rogers & Y.M. Ju
X. intranigra nom. prov., Læssøe, ined.
X. irearteae nom. prov., Læssøe, ined.
X. juniperus Starbäck *var. asperula* Starbäck
X. juruensis Henn.
X. kegeliana (Lév.) Fr.
X. kretchmarioidea nom. prov., Læssøe, ined.
X. laevis Lloyd
X. lagerheimii nom. prov., Læssøe, ined.
X. lhermii Pat.
X. longiana Rehm
X. longipes Nitschke
X. longipes var. tropica F. San Martín & J.D. Rogers
X. lutea Beeli
X. magnoliae J.D. Rogers
X. megaapparati nom. prov., Læssøe, ined.
X. melanura Lév.
X. meliacearum Læssøe
X. mellisii (Berk.) Cooke
X. metaeformis Lév.

X. mexicana F. San Martín, J.D. Rogers & P. Lavín
X. microceras (Mont.) Berk.
X. mindoensis nom. prov., Læssøe, ined.
X. multiplex (Kunze) Fr.
X. nigrescens (Sacc.) Lloyd
X. nodulosa Lloyd *var. microspora* A. Pande & Waing.
X. obovata (Berk.) Berk.
X. olobapha Berk. var. *camptospora* Penz. & Sacc.
X. oxyacanthae Tul. & C. Tul.
X. pallida-ostiolata Henn.
X. palmicola G. Winter
X. pasochoae nom. prov., Læssøe, ined.
X. persicaria (Schwein.) Berk. & M.A. Curtis
X. phosphorea Berk.
X. phyllocharis Mont.
X. piperarum nom. prov., Læssøe, ined.
X. platypoda (Lév.) Fr. var. *microspora* J.D. Rogers & Rossman
X. platypoda (Lév.) Fr. var. *platypoda*
X. plumbea J.D. Rogers & Samuels
X. polymorpha (Pers.) Grev.
X. praeflava nom. prov., Læssøe, ined.
X. regalis Cooke
X. rhizomorpha Mont.
X. rhytidophloea Mont.
X. schwackei Henn.
X. schweinitzii Berk. & M.A. Curtis
X. scruposa (Fr.) Berk.
X. squamulosa F. San Martín & J.D. Rogers
X. stromatica Lloyd
X. subglobosa nom. prov., Læssøe, ined.
X. subpallida nom. prov., Læssøe, ined.
X. subtropica nom. prov., Læssøe, ined.
X. telfairii (Berk.) Sacc.
X. telfairioides nom. prov., Læssøe, ined.
X. tenuispora (Dennis) D. Hawksw.
X. cf. *theissenii* Lloyd
X. trichopoda Penz. & Sacc.
X. tuberoides Rehm
X. turbinata (Ellis & Everh.) Læssøe, comb. ined.
X. xylarioides (Speg.) Læssøe, comb. ined.
X. zealandica Cooke