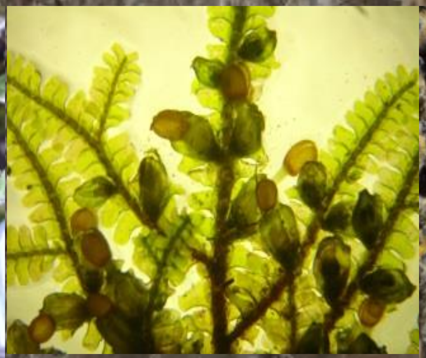

Angel Benitez Chavez-Tesis Doctoral – 2016
Universidad Rey Juan Carlos

EFECTOS DE LA ALTERACIÓN ANTRÓPICA EN BOSQUES TROPICALES SOBRE LA DIVERSIDAD DE ORGANISMOS EPÍFITOS (LÍQUENES Y BRIÓFITOS)

Universidad
Rey Juan Carlos

ÁREA DE
BIODIVERSIDAD
Y CONSERVACIÓN

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Angel Raimundo Benitez Chavez: Tesis Doctoral – 2016

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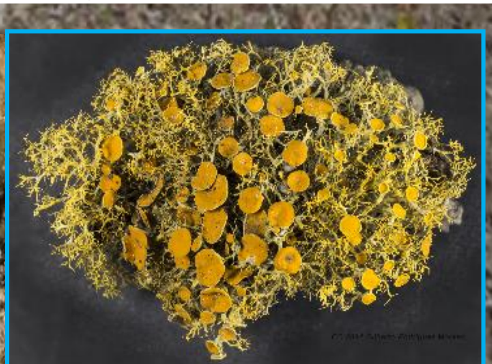
Departamento de Biología y Geología, Física y Química Inorgánica



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TESIS DOCTORAL

EFECTOS DE LA ALTERACIÓN ANTRÓPICA EN BOSQUES TROPICALES SOBRE LA DIVERSIDAD DE ORGANISMOS EPÍFITOS (LÍQUENES Y BRIÓFITOS)

EFFECTS OF TROPICAL FORESTS DISTURBANCE ON EPIPHYTE DIVERSITY (LICHENS AND BRYOPHYTES)

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UNIVERSIDAD REY JUAN CARLOS
Junio de 2016

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Certifican:

Que los trabajos de investigación desarrollado en la memoria de tesis doctoral “Efectos de la alteración antrópica en bosques tropicales sobre la diversidad de organismos epífitos (Líquenes y Briófitos)” se han realizado bajo su supervisión y son aptos para ser presentados por Angel Raimundo Benitez Chavez ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor por la Universidad Rey Juan Carlos.

V°B° Directora de Tesis
Dra. María Prieto Álvaro

V°B° Director de Tesis
Dr. Gregorio Aragón Rubio

A mis padres Gregorio y Esperanza; y la mí amada Anita

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AGRADECIMIENTOS

Agradezco a la Universidad Técnica Particular de Loja (UTPL), Secretaria Nacional de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT) y la Universidad Rey Juan Carlos por brindar las herramientas y los recursos necesarios para el desarrollo de este trabajo de investigación.

A todos los integrantes del departamento de Ciencias Naturales de la UTPL de la ciudad de Loja, de manera especial a Ana Arévalo, Yadira González, Gabriela Cevallos, Geovanny Cango, Fernando Gaona y Elizabeth Guzmán por su colaboración en el trabajo de campo.

Mil gracias a la desaparecida sección de sistemática de la UTPL conformada por Carlos Naranjo, Fani Tinitana, Omar Cabrera, Nixon Cumbicus y Diego Marín por su apoyo y colaboración durante el desarrollo de este trabajo de investigación, es muy grato seguir contando con su amistad y apoyo, mil gracias amigos.

Al Dr. Adrián Escudero, Dra. Isabel Martínez, Dr. José María Iriondo, Dr. Marcos Méndez y Dr. Luis Cayuela de la Universidad Rey Juan Carlos, por su disposición y colaboración desinteresada durante el desarrollo de este trabajo. Adicionalmente agradezco a Silvia Santamaría, Sonia Merinero, Jesús López y Samuel por su colaboración y apoyo durante las diferentes estancias doctorales.

Bueno para mis directores de tesis, empezando con el Dr. Gregorio Aragón solo tengo tres palabras respeto, admiración y sobre todo agradecimiento ya que gracias a su calidad profesional y personal he podido empezar el duro pero gratificante camino de la investigación. Mil Gracias Goyo por el tiempo y dedicación que le pusiste a este trabajo y por darme la oportunidad de hacer investigación en tu campo de estudio. Sin sentimentalismos que yo no soy muy bueno para eso, pero la verdad tengo una gran admiración por el gran trabajo que realizas y la visión que tienes para hacer investigación. A la Dra. María Prieto Álvaro, por todo su apoyo incondicional durante el desarrollo de este trabajo, gracias por seguir confiando en mis capacidades a pesar que muchas de las veces ya sobrepasaba tu gran paciencia. Gracias por enseñarme a determinar los líquenes, sobre todo los costrosos, que ahora ya los llamo crustáceos. Mil gracias a los dos por confiar en mí y darme esta gran oportunidad de que hayan sido mi guía durante este largo camino.

Así mismo quiero agradecer infinitamente al Profesor Robbert Gradstein por su calidad personal y profesional en los diferentes momentos que compartimos durante diferentes salidas de campo e investigaciones que hemos desarrollado en el campo de la briología. Mil gracias profesor por darme la oportunidad y sobre todo por confiar en mis capacidades.

Mil gracias a mi amada familia de España, la familia de Robert, Francisca y Gregorio. De manera especial a Fátima y Johnny por su gran hospitalidad y por hacerte sentir como en casa y sobre todo por apoyarme en los momentos más difíciles durante mis estancias en España. Especialmente quiero agradecer a mi querido y amado sobrino Ismael siempre serás como el hijo que sueño tener, gracias por esperarme siempre con la comida en la mesa y en las mañanas compartir los desayunos sin importante al hora que sea. Mil gracias Isma por todos los momentos compartidos que han sido geniales.

A mis padres que se han convertido en los promotores y sobre todo los impulsores para poder llegar cumplir con esta meta. Además a toda mi familia y sobrinos que gracias a su alegría he podido seguir adelante. Finalmente a la persona que se ha convertido en la alegría y paz que encontraba en los momentos más difíciles de mi vida (Anita), ya que gracias a su apoyo incondicional en las etapas de campo, de laboratorio e investigación he podido cumplir con esta etapa de mi vida, mil gracias por estar siempre para mí y esperarme aunque no haya estado cuando tú me necesitabas debido a mis estancias en España.

RESUMEN

La deforestación es una de las principales causas de pérdida de biodiversidad en los ecosistemas tropicales a nivel global. Los bosques montanos y estacionalmente secos están despareciendo a ritmos alarmantes por lo que han sido catalogados como los más amenazados y de prioridad para la conservación. Estos ecosistemas se caracterizan por sus altos niveles de diversidad y endemismo de flora y fauna, donde los epífitos son un grupo importante en términos de diversidad y funcionamiento. Dentro de los epífitos, una fracción significativa está representada por líquenes y briófitos que, por sus características fisiológicas relacionadas con la disponibilidad de agua y luz, se han convertido en organismos modelo para evaluar cambios en el ambiente. A pesar de ello, los estudios centrados en analizar los efectos de la disturbancia de estos ecosistemas sobre los epífitos no vasculares son muy limitados, de manera especial en los bosques estacionalmente secos. Por este motivo, el objetivo general de esta tesis doctoral se centra en analizar los efectos de la alteración de los bosques tropicales sobre la diversidad de los organismos epífitos (líquenes y briófitos), que permitan un mejor entendimiento de las respuestas de estos organismos a cambios en el ambiente.

En estos dos ecosistemas (bosques montanos y estacionalmente secos), se identificaron manchas de bosques con diferentes tipos de manejo. Se definieron tres categorías de manejo para los bosques montanos, distribuidas en dos manchas de bosques primarios, dos de bosques secundarios y dos de bosques monoespecíficos de *Alnus acuminata*. Para los bosques estacionalmente secos se identificaron cuatro manchas de bosques correspondientes a dos categorías de manejo. En cada bosque se analizaron los cambios en la diversidad de epífitos no vasculares a nivel de árbol y parcela; y se identificaron los factores ambientales (altitud, pendiente y orientación) y de estructura forestal (cobertura del dosel arbóreo, diámetro de los árboles, especie del árbol y textura de la corteza de los árboles) que podrían limitar estas comunidades. Además, se analizaron los efectos de la alteración sobre la diversidad funcional de líquenes epífitos en los bosques montanos y se utilizaron las formas de crecimiento para predecir la riqueza total de líquenes epífitos.

Los resultados muestran que la deforestación disminuye drásticamente la diversidad de epífitos no vasculares en bosques montanos y estacionalmente secos tropicales, donde los bosques primarios mantienen una mayor diversidad en comparación con los bosques secundarios. Los epífitos de sombra (ej. *Leptogium, Lobaria, Sticta, Pannaria,*

Plagiochila) adaptadas a condiciones de alta humedad fueron más afectadas por la pérdida de la cobertura arbolada, debido a cambios microclimáticos relacionados con la disponibilidad de humedad. Sin embargo los epífitos de sol (ej. *Frullania, Graphis, Heterodermia, Usnea*) estuvieron mejor representados en los bosques secundarios, debido a que están adaptadas a condiciones con mayor intensidad lumínica. Por lo tanto, la estructura del bosque relacionada con la cobertura del dosel y los rasgos del forófito, principalmente la especie y diámetro del árbol fueron los factores más influyentes en las comunidades de epífitos no vasculares. Particularmente, los briófitos estuvieron directamente afectados por la disminución de la cobertura arbolada, que implican cambios microclimáticos (luz y humedad), mientras que los líquenes fueron condicionados por el diámetro de los árboles relacionados con el área disponible para su establecimiento y desarrollo. Paralelamente, la diversidad funcional de líquenes epífitos fue afectada por la deforestación, y estuvo condicionada por la cobertura del dosel y el diámetro de los árboles. Las formas de crecimiento (ejemplo, especies con talo gelatinoso, filamentoso y folioso placodioide) se han utilizado para predecir la riqueza total de líquenes en los bosques montanos, y se proponen, por tanto, como herramienta para realizar inventarios rápidos de biodiversidad. A pesar de la aceptada asunción de que en los bosques tropicales la relación entre el forófito y las especies epífitas es nula, en los bosques estacionalmente secos las comunidades de líquenes fueron condicionadas directamente por la especie del árbol hospedador (forófito).

En los muestreos realizados se han encontrado un total de 374 especies epífitas no vasculares en los bosques montanos (307 líquenes y 67 briófitos), mientras que en los bosques estacionalmente secos se registraron 123 especies (122 líquenes y un briófito). Debido al escaso conocimiento de las criptógamas de Ecuador, paralelamente a los estudios realizados se han encontrado nuevas citas regionales, nacionales y provinciales de líquenes y briófitos para Ecuador y Suramérica, que se adjuntan como complementos del trabajo. Así, se han encontrado aproximadamente 200 nuevos registros, lo que demuestra la gran diversidad de líquenes y briófitos en los bosques tropicales de Ecuador.

En conclusión, la deforestación afecta negativamente a la diversidad taxonómica (riqueza y composición de especies) de epífitos no vasculares en los bosques montanos y estacionalmente secos tropicales. Además, los rasgos funcionales de liquenes epífitos fueron afectados negativamente por este factor. De manera consistente la cobertura del dosel relacionada con los factores microclimáticos y los rasgos del forófito fueron los factores más influyentes en la diversidad taxonómica de los epífitos no vasculares. Similar tendencia se observó en los rasgos funcionales de los líquenes epífitos que estuvieron condicionados por estos factores. Las formas de crecimiento de líquenes pueden ser una herramienta prometedora para predecir la riqueza total de epífitos no vasculares en ecosistemas altamente diversos como los bosques montanos tropicales. La conservación de bosques maduros con alta diversidad de especies forestales, gran cobertura arbolada y potenciales forófitos garantizara una gran diversidad de epífitos no vasculares en bosques montanos y estacionalmente secos.

ANTECEDENTES

En la actualidad, la deforestación en los trópicos constituye uno de los problemas ambientales más importantes con serias consecuencias económicas y sociales (Laurance 1999). Este proceso de cambio unido a la fragmentación de hábitats son los principales impulsores del cambio global con efectos negativos para la biodiversidad (Vitousek 1994; Tapia-Armijos et al., 2015). A pesar de que los bosques tropicales albergan el 70% de las especies de animales y plantas del mundo, y de influir en el clima a escala local y mundial (Malhi & Phillips 2004), han sufrido una acelerada perdida de su superficie original (Houghton 1994; Kammesheidt 2002; Garavito et al., 2012; Tapia-Armijos et al., 2015). Así, la deforestación para extracción de madera, actividades agrícolas y ganaderas son las principales amenazas, de manera muy especial sobre los bosques húmedos montanos y los bosques estacionalmente secos (Henderson et al., 1991; Gentry 1995; Churchill et al., 1995; Brummit & Nic-Lughadha 2003; Asner et al., 2005; Barthlott et al., 2005; Gibbs et al., 2010; Fajardo et al., 2005; Miles et al., 2006; Espinosa et al., 2011). Las rápidas transformaciones de estos bosques originales han provocado pérdidas en la biodiversidad de una gran variedad de organismos, entre los que se encuentran especies de árboles (Kessler et al., 2005; Fujisaka et al., 1998, Espinosa et al., 2011), aves (Sodhi 2002; Gray et al., 2007), epífitos vasculares (orquídeas, bromelias, helechos), briófitos, líquenes (Barthlott et al., 2001; Gradstein 2008; Nöske et al., 2008; Werner & Gradstein 2009; Benitez et al., 2015), mariposas (Barlow et al., 2007), escarabajos (Nichols et al., 2007; Gardner et al., 2008), polillas (Beck et al., 2002; Brehm & Fiedler 2005), hormigas y termitas (Lawton et al.,1998).

Bosques húmedos montanos tropicales

La alta diversidad de especies es una de las características de los bosques montanos húmedos tropicales, hecho que le confiere el reconocimiento de ser uno de los puntos calientes de biodiversidad y de prioridad para la conservación (Gentry 1982; Myers et al., 2000; Jørgensen et al., 2011). Estos bosques, con varios estratos de vegetación y un sotobosque relativamente denso, se caracterizan por la ausencia de marcadas estaciones climáticas, presencia constante de nieblas y altas precipitaciones (Bruijnzeel 2005; Richter 2008). La compleja topografía y los constantes deslizamientos incrementan la heterogeneidad de los procesos edáficos, climáticos y por ende en la estructura de la diversidad (Richter 2008). Además, los suelos mantienen gran humedad con alta presencia de materia orgánica, debido a que albergan una elevada proporción de biomasa relacionada principalmente con la gran diversidad de organismos epífitos (Hamilton et al., 1995; Brown & Kappelle 2001; Hamilton 2001). A pesar de ello, la situación es alarmante debido a las diferentes actividades antrópicas que han originado pequeños fragmentos aislados producto de la regeneración natural (vegetación secundaria) dentro en una matriz agrícola y de pastoreo (Gibson et al., 2011; Tabarelli et al., 2010). En consecuencia, la destrucción de los bosques primarios vine acompañada por la expansión de los bosques secundarios de diferentes tamaños y edades en la mayor parte de las zonas tropicales.

Los bosques primarios se han definido como bosques maduros o antiguos que han experimentado poca o ninguna perturbación humana (Gibson et al., 2011). Estos bosques presentan desarrollan coberturas arboladas superiores al 80%; se caracterizan por presentar diferentes estratos, definidos por una vegetación arbustiva, un sotobosque denso, y un dosel arbóreo que alcanzan los 30-50 m de altura dominados principalmente por especies de la familia Podocarpaceae (*Decussocarpus* y *Podocarpus*) y algunas especies del genero *Clusia*, *Cinchona* y *Weinmannia* (Barthlott et al., 2001; Sporn 2009; Benitez et al., 2012).

A diferencia, los bosques secundarios de definen como aquellos ecosistemas que se han originado como consecuencia del impacto humano en los sistemas naturales forestales, excluyendo las plantaciones (Brown & Lugo, 1990). Estos bosques pueden aparecer después de los procesos de deforestación y un posterior abandono de actividades relacionadas con la agricultura y ganadería (Brown & Lugo, 1990; Lugo 2009; Gardner et al., 2009). Es decir, resultan de la regeneración depués de un moderado uso antrópico relacionado con la tala selectiva, pastoreo, recolección de leña, y pequeñas quemas para tierras de cultivos (Brown & Lugo 1990; Holz, 2003). En nuestro caso, provienen de talas selectivas de los bosques primarios de hace 40-50 años, por lo que presentan un dosel arbustivo bien desarrollado; sin embargo, el dosel arbóreo está compuesto de arboles aislados de hasta 30 m de altura que dan como resultado un dosel más abierto (50-75%). Están caracterizados por especies de la familia Bambusaceae (*Chusquea* sp.), Melastomataceae y Lauraceae (Barthlott et al., 2001; Nöske et al., 2008; Benitez et al., 2012).

Otra categoría de vegetación secundaria es producida por la total eiminación de los bosques originales, que dan como resultado bosques secundarios monoespecíficos de *Alnus acuminata* H.B.K. Estos bosques están dominados por arboles jóvenes (10-20 años) de una especie pionera y nativa de los Andes, que gracias a la rápida germinación y crecimiento coloniza eficazmente áreas abiertas como son los pastizales y tierras de cultivo que han sido abandonadas. Estructuralmente se caracterizan por presentar un solo estrato arbóreo, cobertura de dosel inferior al 50% y árboles de hasta 20 m de altura (Hofstede & Aguirre 1999; Fehse et al., 2002). La estructura de los bosques monoespecíficos de *A. cuminata* es muy similar a las plantaciones (*Cedrela* y *Pinus*), muy uniforme debido a la ausencia de un sotobosque (Barthlott et al., 2001), y la diferencia radica en que los primeros e originan de la regeneración natural del bosque.

Bosques estacionalmente secos tropicales

A nivel mundial, los bosques estacionalmente secos tropicales (BTES) ocupan el 42% de la superficie de los bosques tropicales (Miles et al., 2006), y comprenden bosques caducifolios y semicaducifolios que crecen en áreas tropicales sujetas a una severa estacionalidad climática (Espinosa et al., 2012). Para el Neotrópico se distribuyen desde el norte de México hasta el sur brasileño y cubren el 66,7% de la superficie de bosques estacionalmente secos del mundo (Miles et al., 2006). De manera particular, en la región biogeográfica Tumbesina de Ecuador y Perú representa la mayor superficie con 86859 km^2 y están caracterizados por sus altos niveles de endemismos (Dinerstein et al., 1995). Al mismo tiempo, comprenden una de las zonas más amenazadas por las actividades antrópicas (Best & Kessler 1995).

Los bosques estacionalmente secos se caracterizan por una marcada estacionalidad climática, precipitación anual inferior a 1600 mm y un marcado período de sequía que se prolonga hasta 5 o 6 meses al año con una precipitación total menor a 100 mm (Pennington et al., 2000). Una particularidad especial de estos bosques es la pérdida estacional de las hojas (75% de las especies), durante la estación seca, pero durante la estación lluviosa presentan una estructura de bosque siempre verde (Aguirre et al., 2006). En la época seca se produce una acumulación de hojarasca debido a la baja humedad durante esta estación, que se descompone cuando llega la época de lluvias (Pennington et al., 2000), por lo tanto presentan una productividad primaria neta baja (Aguirre et al., 2006). Un factor clave en estos bosques es la disponibilidad de agua, convirtiéndose en una limitante para el establecimiento, supervivencia y desarrollo de las plantas (Ruthemberg 1980). Estos ecosistemas tienen una menor diversidad de especies (Gentry 1995), menor área basal y altura de los árboles que los bosques montanos tropicales (Murphy & Lugo 1986; Moony et al., 1995, Linares-Palomino

2004). Así mismo, la diversidad de epífitas en más baja, debido al incremento de la incidencia lumínica y disminución de la humedad (Gentry & Dodson 1987; Werner & Gradstein 2009) en comparación con los bosques húmedos montanos, sin embargo están caracterizados por un alto grado de especies endémicas (Trejo & Dirzo 2002; Fajardo et al., 2005). Frente a la deforestación, estos ecosistemas tiene los mismos problemas que los bosques húmedos montanos: talas selectivas, extracción de madera y los diferentes usos del suelo para actividades agrícolas o ganaderas (Fajardo et al., 2005; Miles et al., 2006; Espinosa et al., 2011).

Los bosques estacionalmente secos tropicales de Ecuador se localizan en las provincias de Manabí, Guayas, El Oro y Loja entre 0-700 m de altitud. Estos bosques están caracterizados por especies representativas como *Ceiba trichistandra,* (A. Gray) Bakh., especies de la familia Malvaceae (*Eriotheca ruizii* (K. Schum.) A. Robyns) y especies del genero *Tabebuia* (*T. chrysantha* y *T. billbergii*) que son muy importantes recursos maderables (Aguirre et al., 2006). Adicionalmente otras especies del estrato arbóreo son *Bursera graveolens* (Kunth) Triana & Planch., *Cochlospermum vitifolium* (Willd.) Spreng., *Cynophalla mollis* (Kunth) J. Presl, junto con vegetación arbustiva (*Malpighia emarginata* L. y *Croton* sp.pl.). La estructura forestal comprende una densa cobertura entre los 85-90%, con un estrato superior entre los 15-30 m de altura y un estrato denso de arbustos (Werner & Gradstein 2009). En la actualidad estos bosques se han convertido en fragmentos de vegetación secundaria de diferentes tamaños innmersos en un paisaje de cultivos y pastos, dado que muchas de estas zonas poseen excelentes suelos para la agricultura y desarrollo de la ganadería (Kalacska et al., 2005). Además otros tipos de transformaciones se deben a los recursos madereros que ofrecen, dando como resultado la pérdida de cobertura forestal a causa de la extracción de algunas especies arbóreas características de estos bosques (Sánchez et al., 2006; Sanchez-Azofeifa & Portillo-Quintero 2011).

Bajo esta perspectiva, en los últimos años se han incrementado los fragmentos de bosques secundarios que rodean a los bosques originales. Generalmente son el producto de la regeneración natural ligado al abandono de actividades ganaderas, agrícolas, tala selectiva para madera y la recolección de leña (Werner & Gradstein 2009). La cobertura del dosel arbóreo está comprendida entre 40-70% (Werner & Gradstein 2009), y la estructura forestal se caracteriza por antiguos árboles dispersos (*B. graveolens*, *E. ruizii, T. chrysantha, C. mollis* y *Ziziphus thyrsiflora* Benth.) y generalmente no presentan estrato arbustivo.

Epífitos como organismos indicadores de cambios en el ambiente

Los organismos epífitos comprenden una importante fracción de la diversidad de plantas, representando entre el 8-10 % de todas las especies de plantas y entre el 25-50% de especies en los bosques tropicales (Gentry & Dodson 1987; Benzing 1995, 2004). Específicamente para Ecuador los epífitos abarcan más del 25% de la riqueza de especies de plantas vasculares (Küper et al., 2004) y están bien representados por orquídeas, bromelias, helechos, briófitos y líquenes que juegan un importante rol en los ciclos hidrológicos y minerales (Gradstein 2008). Además, brindan refugio y alimento a una variedad de insectos, microrganismos, pequeños reptiles, anfibios y ciertos grupos de aves (Nadkarni & Matelson 1989; Nadkarni & Longino 1990; Yanoviak et al., 2007).

Los epífitos en los bosques húmedos montanos tropicales son muy diversos, debido a la constante humedad de estos ecosistemas (Barthlott et al., 2001; Nadkarni et al., 2001; Gradstein 2008; Mandl et al., 2010), sin embargo un patrón diferente se observa los bosques estacionalmente secos, donde su diversidad desciende debido al incremento de la intensidad lumínica y a una menor disponibilidad hídrica (Gentry & Dodson 1987; Yeaton & Gladstone 1982; Werner & Gradstein 2009; Higuera & Wolf 2010; Vergara-Torres et al., 2010; Rosa-Manzano et al., 2014). A pesar de ello en los bosques estacionalmente secos pueden presentar altos niveles de endemismo y desempeñar un papel importante en el funcionamiento de estos ecosistemas (Werner 2008). Por lo tanto, los epífitos se han definido como elementos característicos de los bosques húmedos montanos y estacionalmente secos tropicales (Mondragón et al., 2004; Gradstein 2008).

Los líquenes y briófitos constituyen un importante componente de la biodiversidad (Pharo & Beattie 1997), representando una parte integral de los ecosistemas forestales (Lesica et al., 1991). Particularmente la mayor parte de especies de estos organismos en los bosques tropicales (bosques húmedos montanos) son epífitos (Gradstein et al., 2001), donde cumplen funciones importantes relacionados con la diversidad, biomasa y funcionamiento de estos ecosistemas (Holz & Gradstein 2005).

Por sus características fisiológicas relacionadas con la disponibilidad hídrica (organismos poiquilohídricos), los líquenes y briófitos son muy sensibles a cambios ambientales que impliquen pérdida de humedad, ya que no son capaces de regular la captación y pérdida de agua (Nash 1996; Gauslaa et al., 2001; Gradstein 2008;

Kranner et al., 2008). Son también sensibles a cambios en los niveles de irradiación, y especialmente las especies de sombra, asociadas al interior de bosques, que pueden sufrir fotoinhibición por exceso de luz (Nash 1996). Por lo tanto, se han convertido en un grupo modelo para evaluar cambios en el ambiente relacionado con alteraciones antrópicas (Acebey et al., 2003; Holz & Gradstein 2005; Gradstein 2008; Nöske et al., 2008; Aragón et al., 2010; Benitez et al., 2012), contaminación del aire (Käffer et al., 2011; Ochoa-Jimenez et al., 2015) y calentamiento global (Gignac 2001; Hauck 2009).

Partiendo de esta premisa, se han definido dos visiones generales relacionadas con los efectos de la deforestación sobre los organismos epífitos en bosques montanos. La primera sostiene que la riqueza de especies disminuye conforme aumenta la alteración de los bosques (Barthlott et al., 2001; Acebey et al., 2003; Gradstein 2008; Gradstein & Sporn 2010), mientras que la otra corriente mantiene que no existen efectos negativos sobre el número de especies, aunque sí que existen cambios en la composición de las comunidades (Hietz-Seifert et al., 1996; Flores-Palacios & García-Franco 2006; Werner & Gradstein 2009; Larrea & Werner 2010). Esta variación en los patrones observados podría estar relacionado con las diferencias en la taxones estudiados, el nivel de perturbación, la diversidad de especies de árboles o incluso, la edad de la vegetación secundaria (Heitz et al., 2006; Gradstein 2008).

La situación es más alarmante en los bosques secos tropicales, donde el único estudio señala que la riqueza disminuye significativamente al aumentar el grado de alteración, pero los mayores cambios se observan en briófitos (Werner & Gradstein 2009). Sin embargo, estos últimos resultados hay que tomarlos con cautela ya que se limitan a bosques monoespecíficos de *Acacia macracantha.*

Factores que limitan la diversidad y composición de las comunidades epífitas

Los organismos epífitos están condicionados por variables macro y microambientales que afectan su diversidad y distribución a escala local y regional (McCune et al., 1997; Will-Wolf et al., 2006; Sillet & Antoine 2004; Perhans et al., 2007; Gradstein 2008). Las variables orográficas y climáticas (precipitación, temperatura, altitud) son las que condicionan la diversidad de especies (Hauck & Spribille 2005, Marini et al., 2011), mientras que a nivel local son la estructura del bosque y el microclima los principales conductores de la diversidad (Sipman & Harris 1989; Wolseley & Aguirre-Hudson 1997; Holz & Gradstein 2005; Sporn et al., 2009; Norman et al., 2010; Mandl et al., 2010).

La humedad es un factor clave para los epífitos, específicamente para los organismos poiquilohídricos como los líquenes y briófitos que se distribuyen de manera diferente a lo largo de un gradiente de humedad (Sillet & Antoine 2004). Por ejemplo, los líquenes que tienen alga verde como fotobionte son más tolerantes a la desecación que los cianolíquenes, que requieren niveles de hidratación del talo superiores al 80% para poder obtener óptimos fotosintéticos (Nash, 1996); así mismo, los briófitos (incluidas hepáticas) son menos tolerantes a la desecación que los dos grupos antes mencionados (Proctor et al., 2007). Por lo tanto, la diversidad y biomasa de briófitos y cianolíquenes es alta en bosques húmedos, mientras que los clorolíquenes son más abundantes en ambientes con mayor intensidad lumínica (Sillet & Antoine 2004).

La luz también influye sobre la diversidad y distribución de las comunidades epífitas en una amplia gama de bosques (Hauck et al., 2011; Sillet & Antoine 2004). Algunas especies (especialmente las de borde de bosque, o las que viven en zonas más elevadas de los troncos) están adaptadas a alta luminosidad, con saturación fotosintética por encima de los 500 $\mu molm^{-2}s^{-1}$ PFD (Photon Flux Density), mientras que otras que viven en el interior de bosques, y en zonas de la base de los troncos pueden saturarse por encima 150 $\mu molm^{-2}s^{-1}$ PFD (e.g., *Pseudocyphellaria* sp.pl.) (Green et al., 1997). Por ejemplo, los árboles del sotobosque reciben una cantidad de luz menor en comparación con el dosel superior (Hauck et al., 2011), lo que implica una estratificación de las comunidades epífitas en función de estos factores (Sillet & Antoine 2004, Gradstein 2008).

En cuanto a la temperatura, los cianolíquenes están adaptados a temperaturas elevadas con puntos de compensación altos (p.e. *Leptogium phyllocarpum*), pero no resisten temperaturas por debajo de 0 grados (Nash, 2008).

A nivel local, las diferentes transformaciones de los ecosistemas originales tienen directas consecuencias en los organismos epífitos, relacionadas principalmente con los cambios en los siguientes factores:

1. La alteración de la estructura forestal (cobertura arbolada) implicaría un aumento en la incidencia lumínica y disponibilidad de humedad (microclima), que se traduce en un descenso de la disponibilidad hídrica respecto a las condiciones originales (Hedenås & Ericson 2003; Sillet & Antoine 2004; Gradstein 2008; Aragón et al., 2010). Bajo esta premisa se ha determinado una relación negativa entre la disminución de la cobertura

arbolada y la diversidad de epífitos (Gradstein 2008; Werner & Gradstein 2009; Benitez et al., 2015).

2. La tala selectiva implicaría la pérdida del forófito (hospedador) para las especies epífitas, que se traduce en la pérdida de hábitat para su establecimiento y desarrollo. Por ello, la diversidad forestal se ha determinado como un factor limitante en la diversidad de las comunidades epífitas en diferentes bosques (McGee & Kimmerer 2002; Hauck et al., 2011; Nascimbene et al., 2009; Király et al., 2013), muy relacionado con la especificidad del hospedador.

En este ámbito, el debate sobre la relación entre el hospedador y las comunidades epífitas pone en relieve dos visiones opuestas. La primera visión detalla la relación directa entre las epífitas y el árbol, determinado la especificidad entre el hospedador y epífitas (Berg et al., 2002; García-Suárez et al., 2003; Szövényi et al., 2004; Löbel et al., 2006; Hirata et al., 2009; Vergara-Torres et al., 2010; Király et al., 2013). Una visión opuesta detalla poca o ninguna relación entre el árbol huésped y las epífitas (Cornelissen & ter Steege 1989; Cáceres et al., 2007; Soto-Medina et al., 2012; Rosabal et al., 2013). Estas asunciones hacen hincapié sobre la importancia de este factor en la diversidad de epífitas en los bosques montanos y estacionalmente secos tropicales.

3. El tamaño y la edad del hospedador también se han identificado como factores limitantes en la diversidad de las comunidades epífitas relacionadas con en el área y tiempo disponible para la colonización de estos organismos (Fritz et al., 2009; Ranius et al., 2008; Aragón et al., 2010; Benitez et al., 2015).

4. Finalmente las características físicas y químicas de la corteza, como la textura, capacidad de retención de agua, estado de nutrientes y pH son otros factores limitantes de las comunidades epífitas (Callaway et al., 2001; Cáceres et al., 2007; Rosabal et al., 2013).

Estructura funcional de las comunidades epífitas

Generalmente, las especies se describen como entidades taxonómicas, pero también pueden clasificarse a través de sus rasgos funcionales (traits), que son características morfológicas y fisiológicas, medibles a nivel de individuo y que afectan a su desarrollo; por ello, cambios en estos caracteres pueden estar relacionados con cambios en los procesos de los ecosistemas (Violle et al., 2007).

Bajo esta premisa un nuevo enfoque prometedor es la utilización los rasgos funcionales de los organismos epífitos (líquenes y briófitos) como una herramienta que facilite el entendimiento de la estructura y funcionamiento de complejos ecosistemas como los bosques tropicales. Los rasgos funcionales se han determinado como una característica importante para entender el funcionamiento de los ecosistemas (Violle et al., 2007; Mokany et al., 2008), debido a que están directamente influenciados por factores bióticos y abióticos independientemente de la diversidad taxonómica (Webb et al., 2010). La diversidad funcional proporciona información más eficiente relacionada con los procesos y servicios ecosistémicos a diferencia de la diversidad taxonómica que explica muy poco de la variación en dichos procesos (Mokany et al., 2008). A pesar de ello la mayor parte de investigaciones relacionada a los efectos de la deforestación se han realizado en rasgos funcionales de plantas vasculares (Díaz et al., 1999; 2002; 2007; Mabry & Fraterrigo 2009; Laliberte et al., 2010; Sabatini et al., 2014), y muy poco se conoce acerca de los efectos de alteración de los bosques sobre los rasgos funcionales de líquenes epífitos (Stofer et al., 2006; Giordani et al., 2012).

Los rasgos funcionales de los organismos epífitos (líquenes y briófitos) relacionados con la forma de crecimiento, tipo de fotobionte, estrategia de reproducción y presencia de metabolitos secundarios se han utilizado como indicadores efectivos de cambios en el ambiente ligados a diferentes procesos: cambio climático (Ellis & Coppins 2006; Johansson et al., 2007; Marini et al., 2011; Giordani et al., 2012; Pinho et al., 2012; Li et al., 2013, Matos et al., 2015), contaminación del aire (Llop et al., 2012) e indicadores de biodiversidad (Oishi 2009, Pardow et al., 2012; Aragón et al., 2016). Potencialmente los diferentes rasgos funcionales de líquenes epífitos han brindado herramientas para establecer políticas de manejo y conservación (Stofer et al 2006; Pinho et al., 2012; Li et al., 2013). A pesar de ello, la mayor parte de estudios se han enfocado en ecosistemas templados y boreales, por lo que las medidas de conservación no pueden generalizarse a los ecosistemas tropicales donde los estudios son limitados (Koch et al., 2013). De esta forma, el uso combinado de la diversidad taxonómica y funcional puede convertirse en una alternativa eficaz para entender los efectos de la alteración de los bosques tropicales sobre la diversidad de líquenes y briófitos epífitos, debido que estos ecosistemas son rápidamente amenazados por la continua deforestación.

OBJETIVOS Y ESTRUCTURA DE LA TESIS

El objetivo principal de esta tesis es analizar los efectos de la alteración antrópica de los bosques tropicales sobre la diversidad taxonómica y funcional de organismos epífitos (líquenes y briófitos), y ampliar el estado de conocimiento relacionado con la diversidad de estos organismos poco estudiados en Ecuador. En una primera parte tratamos de evaluar los efectos de la alteración sobre los macrolíquenes epífitos. A pesar de los importantes resultados, los macrolíquenes solo constituyen una pequeña fracción de la diversidad de los organismos epífitos. Partiendo de esta premisa, en una segunda etapa nos enfocamos en evaluar la respuesta de epífitos no vasculares (líquenes y briófitos) en relación a la degradación de los bosques. Estos hallazgos se complementaron al analizar los efectos de la degradación de los bosques sobre los rasgos funcionales de líquenes epífitos que permitieron un mejor entendimiento de estos procesos. Simultáneamente, tratamos de analizar los efectos de la alteración de los bosques estacionalmente secos sobre la diversidad de líquenes y briófitos. Estos ecosistemas presentan marcadas diferencias con los bosques montanos relacionadas con la estacionalidad y estructura forestal. Para finalizar, se han recopilado toda la información relativa a la distribución de las especies identificadas, haciendo especial hincapié sobre las que su hallazgo representa hábitats novedosos o ampliaciones considerables en su área de distribución. Para ello, se plantearon los siguientes objetivos específicos:

1. Analizar los efectos de la alteración de los bosques montanos y estacionalmente secos tropicales sobre la diversidad taxonómica (riqueza y composición) de epífitos no vasculares.

2. Evaluar los factores que condicionan la diversidad de líquenes y briófitos epífitos en los bosques montanos y estacionalmente secos tropicales bajo un gradiente de alteración.

3. Analizar la relación de los diferentes rasgos funcionales de líquenes epífitos con la degradación de los bosques montanos tropicales.

4. Determinar la influencia de las características del hospedador sobre la diversidad de líquenes epífitos en los bosques estacionalmente secos.

5. Ampliar el conocimiento sobre la ecología y distribución de las espcies de líquenes y briófitos de Ecuador, en base a nuevos registros provinciales y nacionales.

METODOLOGÍA GENERAL

En este apartado se describen el área de estudio, el diseño, la recolección de datos, así como los análisis estadísticos empleados. Sin embargo, cabe aclarar que en el apartado de “Material y Métodos” de cada capítulo se describe con detalle los métodos utilizados para alcanzar los objetivos planteados.

1. Área de estudio

Se localizan en remanentes de bosques húmedos montanos y bosques estacionalmente secos tropicales con diferentes grados de manejo. Los bosques se localizaron en la provincia de Loja y El Oro de la región sur de Ecuador (Figura 1).

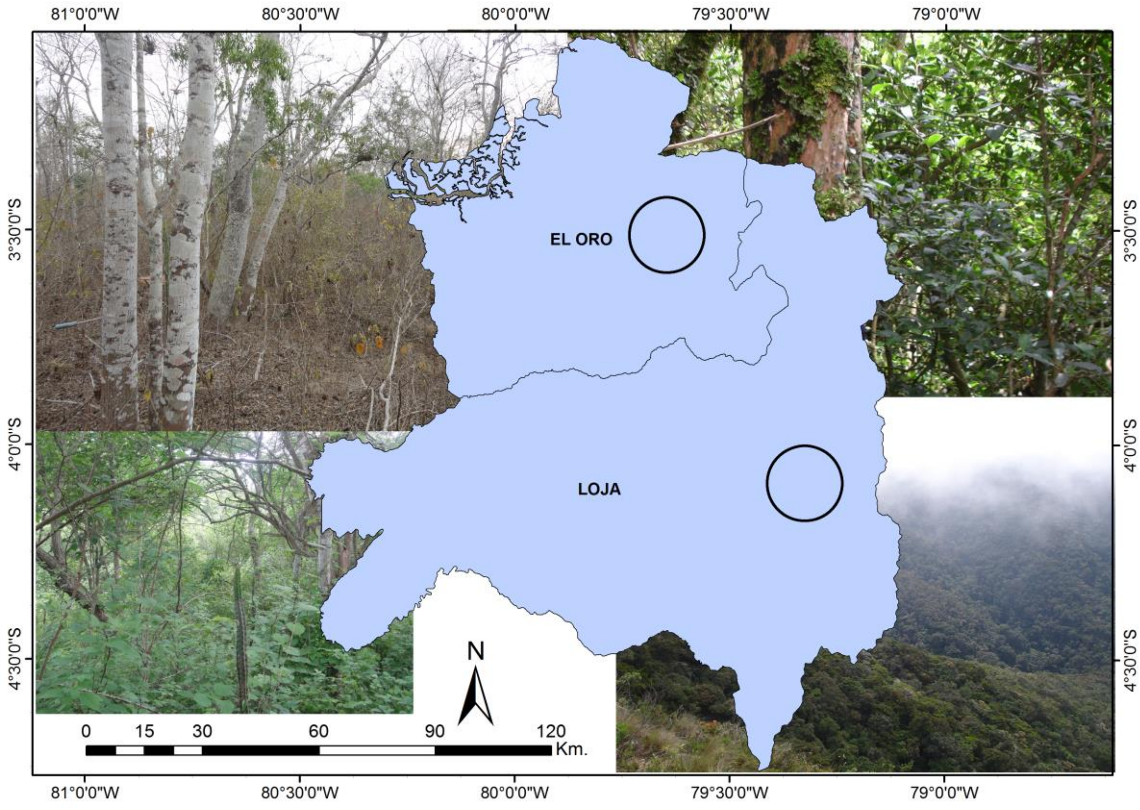

Figura 1. Área de estudio. Provincias de Loja y El Oro de la región del Sur de Ecuador. Bosques montanos y estacionalmente secos tropicales con los diferentes tipos de manejo.

Bosques montanos (Capítulo I, II, III, V y VI)

El estudio se realizó en remanentes de bosques montanos entre los 2200-2800 m de altitud en la provincia de Loja de la Región sur de Ecuador. La temperatura media anual fue de 20 º C, con precipitaciones anuales comprendidas entre los 1700-1900 mm y 80% de humedad relativa (Instituto Nacional de Meteorología en Hidrología INAMI). El trabajo de campo se realizó entre mayo y diciembre de 2010. Se seleccionó tres categorías de manejo con dos remanentes de bosques para cada una de ellas:

1. Fragmentos de bosques primarios (PF, Figura 2A y B): caracterizados por un denso follaje entre el 80-85% de cobertura y grandes árboles (*Podocarpus oleifolius* D. Don)

2. Fragmentos de bosques secundarios (SF, Figura 2C): bosques que se han regenerado depués de sufrir una tala selectiva de los bosques primarios hace 45 años (Brown & Lugo 1990; Holz 2003). La cobertura arbolada esta comprendida entre los 60-70% con especies de la familia Melastomataceae y Lauraceae de hasta 25-30 metros de altura.

3. Fragmentos de bosques monoespecíficos de *Alnus acuminata* Kunth (MF, Figura 2D): bosques jóvenes dominados por una especie nativa y pionera de los Andes. Estos bosques se caracterizan por una estructura uniforme y ausencia de sotobosque. La cobertura arbolada es inferior al 50 % con árboles hasta los 20 metros de altura.

Bosques secos tropicales (Capítulo IV, V y VI)

El estudio se realizó en la Reserva Ecológica Arenillas ubicada en la provincia de El Oro. La vegetación corresponde a una zona de transición entre bosque seco deciduo y matorral seco, con una superficie de 17 hectáreas, comprendida entre los 0-300 m de altitud. El clima está caracterizado por una época seca y una lluviosa con 152 y 515 mm respectivamente, y una temperatura máxima diaria de 25.2 °C (Espinosa et al., 2015). El trabajo de campo se realizó entre enero a diciembre de 2013. Se seleccionaron dos categorías de alteración con dos fragmentos de bosques para cada una de ellas:

1. Fragmentos de bosques secos no alterados (UF, Figura 1E): bosques conservados con especies leñosas predominantes de *Bursera graveolens* (Kunth) Triana & Planch., *Eriotheca ruizii* (K. Schum.) A. Robyns, *Cochlospermum vitifolium* (Willd.) Spreng., *Cynophalla mollis* (Kunth) J. Presl y *Tabebuia chrysantha* G. Nicholson. Las especies características del sotobosque correspondieron a arbustos del genero *Croton*.

2. Remanentes de bosques secos alterados (DF, Figura 1F): bosques alterados caracterizados por tener menos densidad arbórea y escasa vegetación arbustiva. Presumiblemente se establecieron como árboles aislados luego de los diferentes usos del suelo. Las especies dominantes fueron *T. chrysantha*, *C. mollis* and *Ziziphus thyrsiflora* Benth.

2. Diseño y recolección de datos

Bosques montanos (Capítulo I, II, III, V y VI).

Para cada una de las categorías de alteración (3 categorías) se seleccionaron dos fragmentos de bosque (6 bosques). En cada bosque se establecieron 10 parcelas de 5 x 5 m con una separación entre parcelas de más de 50 metros. En cada parcela se seleccionaron 4 árboles, donde se establecieron 6 cuadrantes de 20 cm x 30 cm en dos orientaciones (N y S) y a tres alturas en el tronco de el árbol: altura 1 (0-50 cm), altura 2 (51-150 cm) y altura 3 (151-200 cm). En los 240 árboles se tomaron medidas de presencia y cobertura de todas las especies. A nivel de parcela se tomaron medidas de la cobertura arbolada, inclinación, altitud, orientación, y a nivel de árbol, el diámetro.

Bosques secos tropicales (Capítulo IV, V y VI)

Para cada una de las categorías de alteración (2 categorías) se seleccionaron dos remanentes de bosque (4 bosques). En cada bosque se establecieron 4 parcelas de 20 × 20 m con una separación entre parcelas de más de 100 metros. En cada parcela todos los árboles y arbustos con un DBH > 5 cm fueron identificados. En cada árbol se establecieron 4 cuadrantes de 20 × 30 cm y para los arbustos de 10 × 60 cm en dos orientaciones (N y S) y a dos alturas en el tronco de el árbol: altura 1 (0-100 cm) y altura 2 (101-200 cm). En los 513 árboles se tomaron medidas de frecuencia y cobertura de todas las especies. Para los capítulos I, II, III las condiciones de luz se registraron mediante la medición de la cobertura arbolada (%) y para el capítulo IV como apertura del dosel (%) usando fotografías hemisféricas digitales (Figura 1G y H). Las fotografías fueron registradas siempre en días nublados y la altura del pecho (1,3 metros de altura), con una cámara digital nivelada horizontalmente y con una lente de ojo de pez. Las fotografías fueron analizados utilizando el programa Gap Light Analyzer (GLA) ver. 2.0 (Frazer et al., 2000).

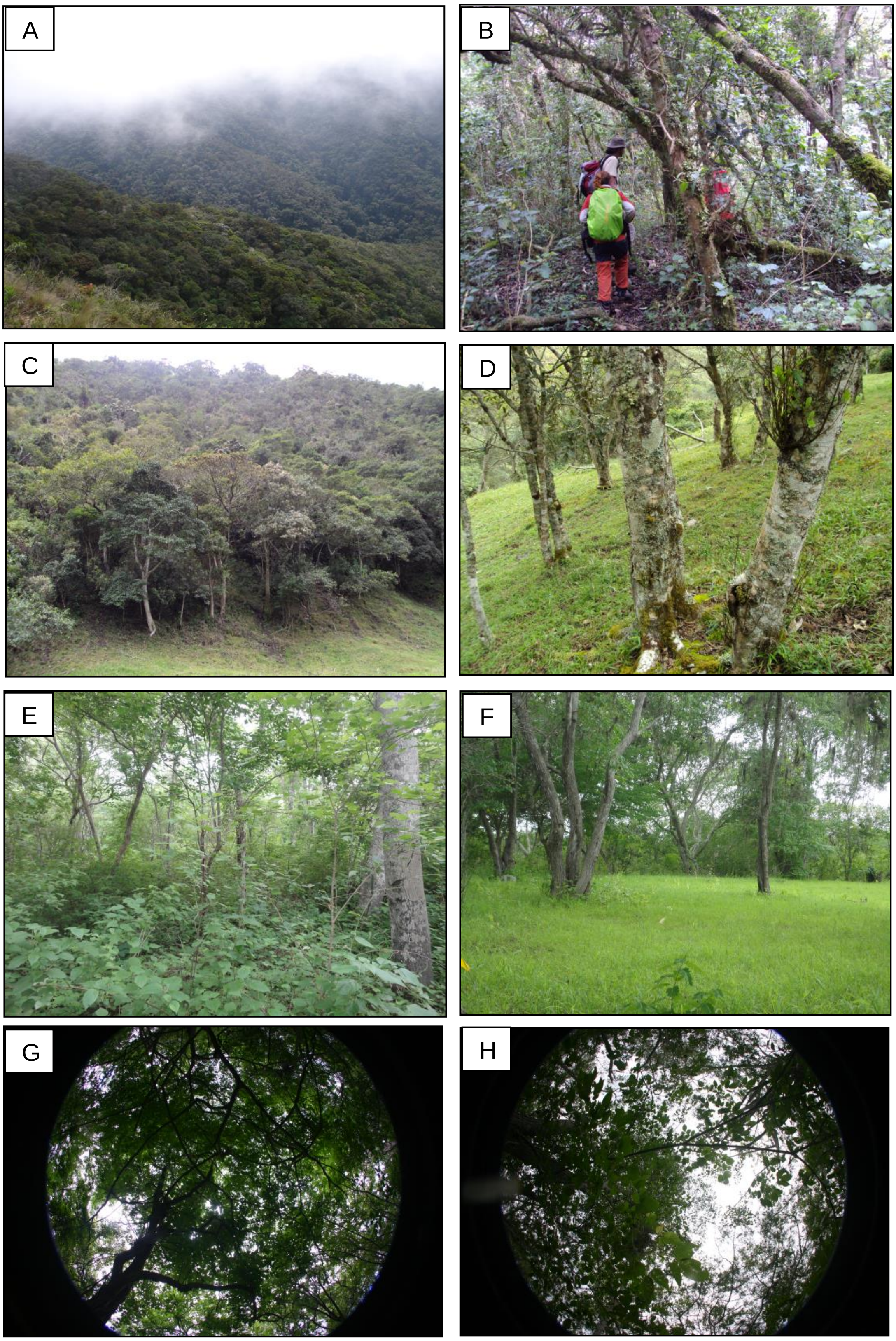

Figura 1. Tipos de bosques estudiados. (A) y (B) Bosques primarios; (C) Bosques secundarios; (D) Bosques monoespecíficos de *A. acuminata*; (E) Bosque seco conservado; (F) Bosque seco alterado; (G) Foto hemisférica de bosques secos no alterado; (H) Foto hemisférica de bosque seco alterado.

3. Análisis de datos

En los capítulos I, II, III, y IV se analizaron los efectos de los factores ambientales (cobertura arbolada, altitud, inclinación, orientación y DBH) sobre la riqueza, diversidad y rasgos funcionales de especies utilizando modelos mixtos lineales generalizados (GLMMS) (McCullagh & Nelder 1989). Dado que los análisis de datos se enfocaron a escala de árbol y parcela se realizaron los modelos mixtos, para incluir el efecto aleatorio del factor parcela o bosque, dependiendo de la escala de trabajo. Todos los GLMMS se realizaron con el programa estadístico SAS (GLIMMIX ver. 8 for SAS/STAT). Adicionalmente para el capítulo IV se realizó modelos lineales generalizados (GLM) para determinar los efectos de los rasgos del hospedador (especie, DBH, tipo de corteza, profundidad de la corteza, inclinación y orientación) sobre la riqueza de especies. Los GLMS fueron realizados en el programa estadístico R con el paquete “nlme” (Pinheiro et al., 2008).

En los capítulos I, II, IV se analizaron los cambios en la composición de especies en función del grado de alteración mediante análisis multivariados con base en permutaciones (PERMANOVA) en el programa estadístico PRIMER 6.1.11. (Anderson et al., 2008). Adicionalmente se realizó un análisis de ordenación multidimensional MDS con los valores de cobertura de las especies que fueron transformados a log10(x+1) y se utilizó la medida de distancia Bray–Curtis. En el capítulo III se realizaron análisis de especies indicadoras (ISA, Dufrêne & Legendre 1997; Koch et al., 2013) para determinar qué grupo funcional es el mejor indicador de la alteración de los bosques y correlaciones lineales de Pearson para predecir la riqueza total de especies de líquenes en función de las formas de crecimiento. En los capítulos II y IV para identificar qué factores influyen en la composición de las comunidades epífitas se realizó una correlación (r^2) entre los dos primeros ejes del NMDS y las variables ambientales con el paquete ‘vegan’ (Oksanen et al., 2011). Los NMDS fueron realizados en el programa estadístico R.

DISCUSIÓN GENERAL

A pesar, que en la última década se ha hecho aportes sustanciales para entender los efectos de la deforestación sobre la diversidad taxonómica (riqueza y composición) de los organismos epífitos en ecosistemas tropicales (bosques montanos y estacionalmente secos), los estudios se han orientado a epífitos vasculares, en menor grado a briófitos y casi de manera nula en líquenes (Werner et al., 2005; Gradstein 2008; Nöske et al., 2008, Werner & Gradstein 2009; Gradstein & Sporn 2010). En este contexto, los resultados limitados y controversiales no han permitido definir un patrón general de la respuesta de estos organismos a los procesos de deforestación de los bosques. Un nuevo enfoque y con resultados importantes en bosques templados y boreales lo constituiría el uso de la diversidad funcional de líquenes epífitos en repuesta a los cambios ambientales derivados de la deforestación (Stofer et al., 2006, Girodani et al., 2012). La diversidad funcional permite un mejor entendimiento de los diferentes procesos involucrados en el funcionamiento en estos ecosistemas (Mokany et al., 2008). Por este motivo, esta tesis incluye un estudio enfocado en analizar los efectos de la alteración de los bosques montanos y estacionalmente secos sobre la diversidad taxonómica (riqueza y composición) y funcional de las comunidades de epífitas no vasculares (líquenes y briófitos). También consideramos los factores ambientales y de estructura del bosque que influyen sobre estas comunidades.

De manera general, comprobamos que la diversidad taxonómica de las comunidades epífitas no vasculares (macrolíquenes, microlíquenes y briófitos) fue drásticamente afectada por la deforestación, y especialmente por cambios en la cobertura del dosel, tamaño de los árboles (diámetro), especies de hospedador, e incluso la rugosidad de la corteza (Capítulos I, II, IV). En un primer enfoque, se determinó que los macrolíquenes “epífitos de sombra”, que incluyen a las epecies con cianobacteria (cianolíquenes) y aquellas que no sitentizan metabolitos secundarios en córtex o médula (p.e., *Leptogiun, Lobaria, Sticta*) fueron más abundantes en los bosques primarios y las más afectados por la deforestación (Capítulo I). Muchos de estos cianolíquqnes están restringidos a bosques maduros, con elevada cobertura arbolada y árboles de gran tamaño, que garantizan condiciones de alta humedad. Son especies con unos requerimientos hídricos muy elevados, ya que alcanzan óptimos fotosintéticos con hidrataciones entre el 80-300% de su peso seco, y además sufren fotoinhibición con la excesiva irradiación (Lange et al., 1993; Jovan & McCune, 2004; Kranner et al., 2008; Marini et al., 2011). Por el contrario, las especies más fotófilas denominadas como “epífitas de sol” (p.e., *Heterodermia, Parmotrema, Usnea*), que presentan adaptaciones morfológicas o anatómicas a los ambientes más secos y de mayor intensidad lumínica (presencia de metabolitos secundarios en córtex superior que permiten cierta opacidad a la irradiación, presencia de cristales de oxalato cálcico que reflejan la luz solar), estuvieron mejor representadas en los bosques secundarios, con un dosel más abierto (Capítulo I). A pesar de los importantes resultados de esta investigación, hay que tomar en consideración que los macrolíquenes representan menos de un tercio de todas las especies de epífitas de los bosques montanos tropicales. Por tanto, estos resultados no pueden generalizarse para toda la comunidad de epífitas no vasculares que son elementos característicos en términos de diversidad, biomasa y funcionamiento de estos ecosistemas.

Bajo esta premisa en un segundo enfoque evaluamos los efectos de la deforestación sobre las epífitas no vasculares en las que incluimos los macrolíquenes, microlíquenes y briófitos (Capítulo II). Los resultados señalaron un patrón similar a los del capítulo I, sin embargo los factores que influyen en la diversidad fueron diferentes para briófitos y líquenes. Así, la diversidad de epífitas no vasculares (líquenes y briófitos) mostró cambios relacionados con la alteración de los bosques y estuvieron condicionados principalmente por la cobertura arbolada y el diámetro de los árboles. La diversidad fue más alta en bosques primarios al compararlos con la vegetación secundaria, además los bosques secundarios albergan mayor diversidad que los bosques monospecíficos de *Alnus acuminata* (Capítulo II). En este contexto, la estructura forestal de los bosques primarios (árboles de gran diámetro, mayor cobertura arbolada y alta diversidad de especies) garantiza una gran diversidad de epífitos en los bosques montanos tropicales (Acebey et al., 2003; Gradstein 2008).

La riqueza de brióffitos fue menor en los bosques secundarios debido a la alteración de la cobertura arbolada que implica cambios ambientales drásticos como disminución de humedad y mayor incidencia lumínica. En general, los briófitos (hepáticas foliosas en nuestro caso) dependen estrechamente de la humedad, necesaria para completar su ciclo vital, tienen altas demandas hídricas y son muy sensibles a altos niveles de radiación solar (Sillett & Antoine, 2004; Gradstein, 2008; Gradstein & Sporn 2010; Pardow & Lakatos 2013).

La riqueza de líquenes también disminuyó considerablemente conforme aumentó la alteración de los bosques, sin embargo, no estuvo ligada a los cambios en la cobertura arbolada. Existe un remplazamiento de las “especies de sombra” por “especies de sol”, que suelen ser dominantes en bosques secundarios. Como señala Nöske et al. (2008), la vegetación secundaria puede albergar una alta riqueza de líquenes epífitos, sin embargo la mayor parte de especies corresponden a las epífitas de sol que han reemplazado a las epífitas de sombra pobremente representadas en estos bosques. Sin embargo, la riqueza de líquenes se ve muy afecta por la eliminación de árboles de gran porte (talas selectivas), y la pérdida estuvo relacionada con líquenes especialistas de sustratos relacionados con la mayor edad de los árboles (fisuras, grietas, oquedades, presencia de briófitos y humus) y al tiempo necesario para la colonización (e.g. Fritz et al., 2009; Johansson et al., 2007; Király et al., 2013). Por lo tanto las comunidades de epífitas no vasculares estuvieron condicionadas por la disminución de potenciales hospederos (árboles con mayor diámetro) y cambios microclimáticos a causa de la disminución de la cobertura arbolada (Capítulo II).

A pesar de los importantes resultados relacionados con la diversidad taxonómica de epífitos no vasculares en respuesta a deforestación (Capítulo I, II y IV), es de conocimiento general que la información florística explica muy poca variación en los procesos del ecosistema (Mokany et al., 2008). Frente a esta limitante nos hemos enfocado en analizar los efectos de la deforestación sobre la diversidad funcional de líquenes epífitos en los bosques montanos (Capítulo III). El uso de la diversidad funcional permite un mejor entendimiento de los conjuntos biológicos relacionados con el funcionamiento de los ecosistemas, sin embargo, los estudios relacionados a los efectos de la deforestación sobre la diversidad funcional de líquenes epífitos son nulos en los bosques montanos tropicales y solo se han limitado a los bosques templados y boreales (Stofer et al., 2006, Girodani et al., 2012).

En este contexto la diversidad funcional de líquenes epífitos fue negativamente afectada por la deforestación en los bosques montanos tropicales, donde los factores relacionados con la estructura forestal del bosque, por ejemplo la cobertura del dosel y el tamaño de los árboles (diámetro) fueron los principales factores limitantes (Capítulo III). Claramente el tipo de fotobionte, la forma de crecimiento, estructura de reproducción y la presencia de metabolitos secundarios fueron los mejores indicadores de la deforestación de los bosques montanos tropicales (Capítulo III). Estos rasgos funcionales han sido documentados previamente como adecuados indicadores de cambios en el ambiente (Ellis & Coppins, 2006; Stofer et al., 2006; Marini et al., 2011).

La prácticamente ausencia de algunos rasgos funcionales relacionados con la forma de crecimiento (talos crustáceos con protalo, gelatinosos o placodioides) o tipo de alga (presencia de cianobacteria), en bosques secundarios, y especialmente en los monoespecíficos de *Alnus acuminata*, tiene que ver con los requerimientos hídricos e incluso con las adaptaciones del talo para libera el exceso de agua. Las especies gelatinosas presentan talos muy finos, muy adaptados a la capatción y pérdida de agua en muy poco tiempo, las especies placodioides, liberan agua através de las hifas del cortex inferior, que se estructuran en forma de canales y, las crustáceas con protalo, carecen de cortex superior, y la médula hidrófoba expuesta al medio ambiente repele el exceso de humedad (Pardow et al., 2012). Además, como ya se ha indicado con anteriordad, las espcies con cianobacterias presentan unos requerimientos hídricos mayores que las especies que contiene alga verde, ligado a las hidrataciones del talo para alcanzar los óptimos fotosintéticos. Por esta razón, las especies con estos rasgos funcionales están restringidas a los bosques primarios (Capítulo III). Bajo esta visión algunos estudios han documentado que las especies de líquenes con similares características (p.e. especies con cianobacteria) están restringidos a al ambiente forestal de bosques maduros y bien conservados (Belinchón et al., 2007; Kranner et al., 2008; Normann et al., 2010; Aragón et al., 2010; Marini et al., 2011; Benitez et al., 2012).

Por el contrario lo líquenes con talos foliosos estrechos, lirelas como estructura de reproducción y con presencia de metabolitos en cortex superior o médula (p.e.. ácido úsnico, vulpínico,lecanórico) fueron mejor representados en los bosques más alterados (Capítulo III). Estos rasgos funcionales se han identificado como adaptaciones de las especies de líquenes a mayores intensidades de luz (Lücking, 1999; Koch et al., 2013). Por ejemplo, especies con atranorina, ácido úsnico, acído vulpínico o parietina protegen al alga de la excesiva irradiación absorbiendo luz incidente y además actúan como filtros rente a la radiación ultravioleta (Molnar & Farkas, 2010). Evidentemente, la mayoría de las especies, y especialmente los macrolíquenes que viven en el interior de bosques primarios carecen de la protección que les infiere algunos de los metabolitos secundarios.

Adicionalmente se evidenció que la riqueza de especies con formas de crecimiento gelatinosa, filamentosa y foliácea placodioide pueden ser utilizados para predecir la riqueza total de líquenes epífitos en los bosques montanos tropicales (Capítulo III). A pesar de los importantes resultados basados en este nuevo enfoque, pocos estudios han utilizado de manera eficaz la riqueza de las diferentes formas de crecimiento o formas de vida de epífitos no vasculares (líquenes y briófitos) para predecir la riqueza total en ecosistemas con alta diversidad (Oishi 2009; Aragón et al., 2016). Desde el punto de vista de inventarios rápidos de biodiversidad de estos organismos en ecosistemas altamente amenazados y muy diversos como los bosques montanos tropicales, este enfoque se convierte en una alternativa viable, debido a que pueden ser aplicados por personas no especializada en taxonomía de líquenes y briófitos (Capítulo III).

En un siguiente apartado, nos enfocamos en analizar los efectos de la deforestación sobre los epífitos no vasculares en bosques estacionalmente secos tropicales, que hasta la fecha constituye el primer estudio orientado en esta temática a nivel de país (Capítulo IV). Los bosques estacionalmente secos tropicales presentan una marcada estacionalidad, árboles deciduos y menor diversidad de especies en comparación con los bosques húmedos. A pesar de la baja diversidad de epífitos, pueden albergar altos grados de endemismo y cumplir importantes funciones en estos ecosistemas (Werner 2008).

Estas peculiares características han generado una interrogante relacionada a entender si los efectos de la deforestación sobre la diversidad de epífitos siguen el mismo patrón que en los bosques húmedos. Solo un estudio ha determinado que la deforestación en los bosques secos disminuye la diversidad de epífitos (briófitos) y que los factores relacionados con la cobertura del dosel y el microclima condicionan estas comunidades. Sin embargo estos resultados se restringen a bosques monospecíficos de árboles de hoja perenne de *Acacia macracantha* (Werner & Gradstein 2009), que no presentan las mismas características estructurales y funcionales de los bosques estacionalmente secos. Por tanto, se han convertido en ecosistemas de gran interés para evaluar los efectos de la deforestación en los organismos epífitos.

A pesar que la deforestación tiene efectos negativos en la diversidad de los organismos epífitos en los bosques estacionalmente secos, las características del hospedador de manera especial la especie del árbol fue el factor limitante de estas comunidades (Capítulo IV). La pérdida de diversidad forestal de estos bosques implica la disminución de la cobertura arbolada junto con la eliminación de potenciales hospedadores con consecuencias negativas para estos organismos. En este contexto varios estudios en bosques templados y boreales han determinado que la diversidad de árboles es un factor limitante para la diversidad de epífitos no vasculares (Nascimbene et al., 2009; Király et al., 2013).

En nuestra área de estudio los líquenes crustáceos fueron los elementos dominantes (90% de especies) y solamente se encontró una especie de briofito, debido a que estos últimos están restringidos a zonas con mayor humedad. Partiendo de esta idea comprobamos que las mayor parte de especies (líquenes crustáceos) presentan especificidad por un pequeño grupo de potenciales hospedadores, como es el caso de *Eriotheca ruizii* y *Cochlospermum vitifolium* caracterizados por un mayor tamaño y corteza más lisa respecto al resto de forófitos (Capítulo IV).

En los bosques tropicales se ha determinado una ausencia de especificidad del hospedador por las especies epífitas, debido principalmente a la compleja estructura de estos ecosistemas, relacionados con la alta diversidad de especies de árboles que forman diferentes estratos arbóreos y diversos habitas para el establecimiento de las especies (Cáceres et al., 2007; Rosabal et al., 2013). Sin embargo estos resultados no pueden generalizarse para los bosques estacionalmente secos, con una diversidad menor de especies arbóreas de hojas deciduas y con una marcada estacionalidad.
En un trabajo previo, Vergara-Torres et al. (2010) evidenciaron un alto grado especificidad del hospedador y sus epífitas vasculares en estos ecosistemas. En este contexto se ha podido determinar que la especie del hospedor es un factor limitante en los bosques estacionalmente secos para las comunidades de líquenes epífitos en comparación con los bosques húmedos tropicales (Capítulo IV).

Finalmente los resultados de los capítulos I, II, III y VI han supuesto importantes avances en el conocimiento de la ecología y distribución de las especies de líquenes y briófitos, generando además un incremento considerable de nuevos registros provinciales, nacionales y regionales (Capítulo V, VI). Ecuador se ha caracterizado por una alta diversidad de líquenes y briófitos, donde se han reportado 950 especies de musgos, 700 especies de hepáticas y antoceros (Churchill, 1994; Churchill et al., 2000; León-Yánez et al., 2006) y cerca de 900 especies de líquenes (Cevallos 2012). A pesar de los avances en el área de la briología y liquenología de nuestro país los estudios siguen siendo limitados y se han enfocado en área específicas; por ejemplo únicamente para las Islas Galápagos se han descrito 797 especies de líquenes (Bungartz et al., 2013) y 253 especies de briófitos (Ziemmeck et al., 2011). Sin embargo, estos números son desalentadores, ya que si comparamos el número de especies para Ecuador continental y las Islas Galápagos, podemos observar que son casi similares a pesar de la diferencia en superficie y la diversidad de ambientes.

En este contexto podemos mencionar que se ha descrito más de 200 nuevos registros provinciales y nacionales de briófitos y líquenes para Ecuador (Capítulo V, VI). Por ejemplo, *Diplolabia afzelii* (Ach.) A.Massal. es nuevo registro provincial. Además, destacan nuevos registros para Ecuador continental de *Ramonia valenzueliana* (Mont.) Stizenb. y *Trypethelium eluteriae* Spreng., que previamente habían sido citados en las Islas Galápagos*.* Dentro de los registros nacionales destacan *Mazosia carnea* (Eckfeldt) Aptroot & M. Cáceres*, Notothylas vitalii* Udar & D.K. Singh (Capítulo V) y *Syncesia effusa* (Fée) Tehler (Figura 3)*.* En lo que respecta a registros para Sur América incluimos a *Chapsa diploschistoides* (Zahlbr.) Frisch, *Fibrillithecis halei* (Tuck. & Mont.) Mangold y *Pyrenula psoriformis* Zahlbr. (Capítulo VI)*.* Adicionalmente se encuentra estudiando algunos especímenes del género *Fissurina*, *Graphis* y *Gyalidea* (Figura 4), que posiblemente correspondan a especies nuevas para la ciencia que más adelante podrán ser descritas.

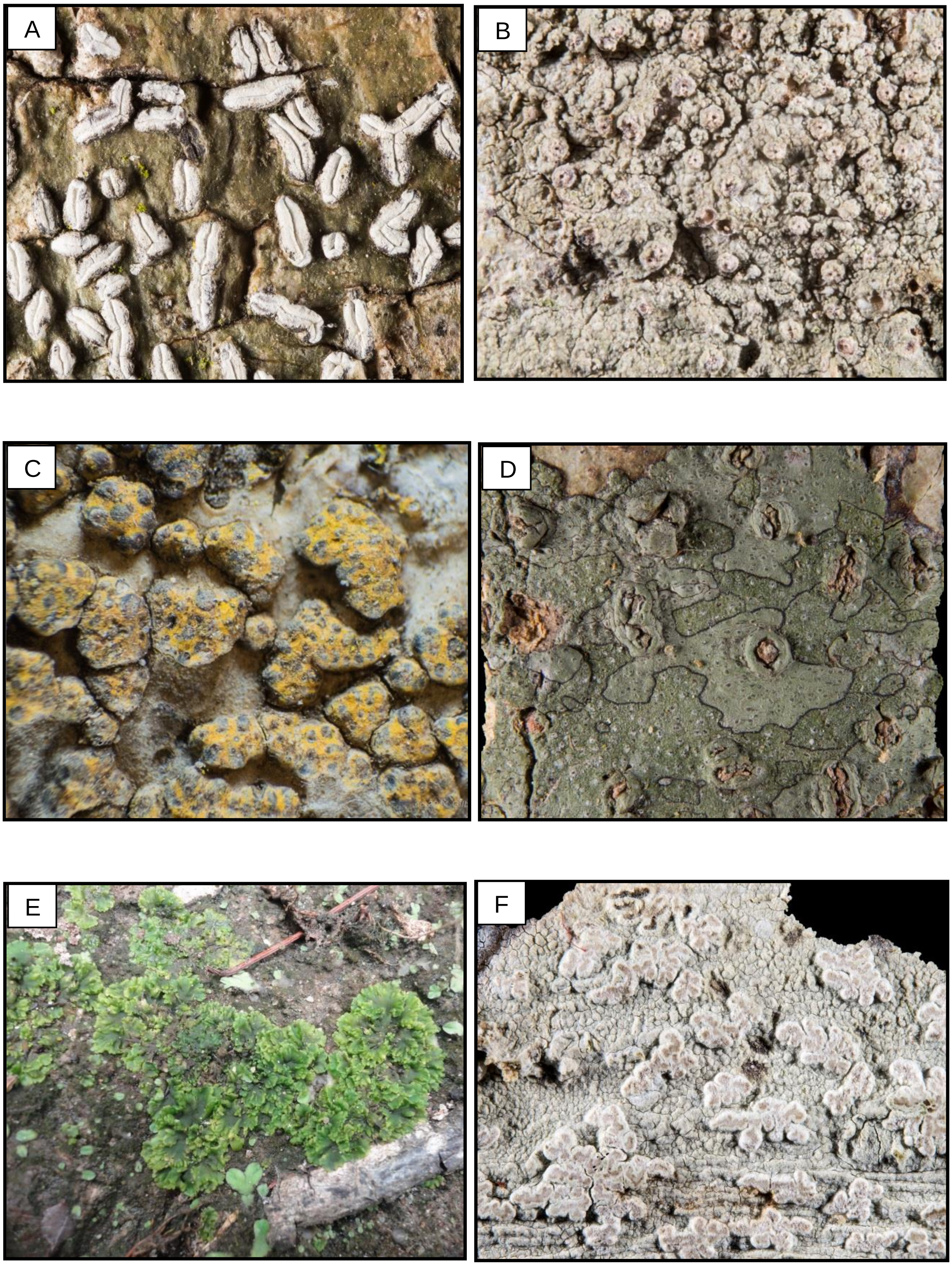

Figura 3. Nuevas aportaciones provinciales, para el continente y para Ecuador. (A) *Diplolabia afzelii* (Ach.) A.Massal.; (B) *Ramonia valenzueliana* (Mont.) Stizenb.; (C) *Trypethelium eluteriae* Spreng.; (D) *Mazosia carnea* (Eckfeldt) Aptroot & M. Cáceres; (E) *Notothylas vitalii* Udar & D.K. Singh; y (D) *Syncesia effusa* (Fée) Tehler.

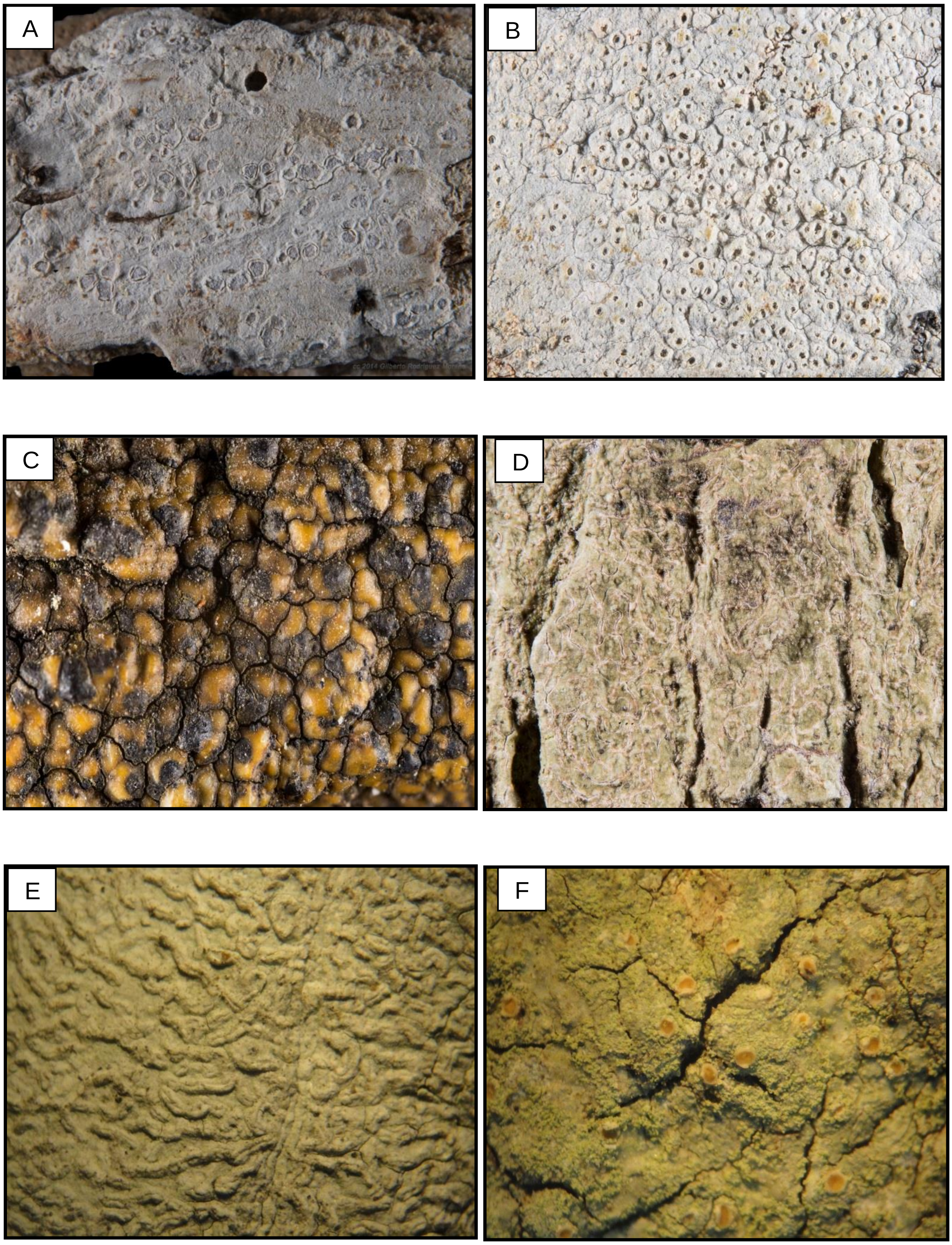

Figura 4. Nuevas aportaciones de líquenes para Sur América y posibles especie nuevas para la ciencia. (A) *Chapsa diploschistoides* (Zahlbr.) Frisch; (B) *Fibrillithecis halei* (Tuck. & Mont.) Mangold; (C) *Pyrenula psoriformis* Zahlbr.; (D) *Fissurina*; (E) *Graphis* y (F) *Gyalidea*.

CONCLUSIONES

Los resultados obtenidos en la presente investigación han permitido entender algunos procesos relacionados con la respuesta de las comunidades epífitas no vasculares (líquenes y briófitos) a la alteración de los bosques tropicales (bosques montanos y bosques estacionalmente secos), a partir de los cuales se extraen las siguientes conclusiones generales:

1. La riqueza de líquenes y briófitos epífitos se reduce considerablemente conforme aumenta la alteración de los bosques montanos y bosques estacionalmente secos tropicales.

2. Los cambios en la composición de las comunidades de macrolíquenes epífitos en los bosques montanos, se atribuyeron a la perdida severa de las epífitas de sombra, debido a su intolerancia a la excesiva irradiación, derivados deun aumento de la apertura del dosel, de los bosque secundarios y monospecíficos de *Alnus acuminata*.

3. La respuesta de líquenes (macro y micro líquenes) y briófitos frente a la alteración de los bosques montanos tropicales fue diferente. Los líquenes estuvieron más influenciados por variaciones en el tamaño (diámetro) de los árboles, y los briófitos por cambios en los factores microclimáticos como mayor incremento en la irradiación y una disminución de la humedad, provocada por una mayor apertura del dosel.

4. En los boques montanos tropicales los rasgos funcionales de líquenes y la media ponderada de cada rasgo a nivel de comunidad (CWM), respondieron eficazmente a las alteraciones antrópicas y estuvieron determinados consistentemente por la cobertura arbolada y el diámetro de los árboles. Por lo tanto la diversidad funcional (rasgos funcionales) permitieron un mejor entendimiento de los efectos de la deforestación sobre las comunidades epífitas que la diversidad taxonómica.

5. Los rasgos funcionales relacionados con el tipo de fotobionte (cianobacterias), formas de crecimiento (gelatinosa, foliácea placodioidea, crustácea con prótalo), estructura de reproducción y la presencia de metabolitos secundarios resultaron ser indicadores eficaces de la alteración de los bosques montanos.

6. Las formas de crecimiento gelatinosa, crustácea con prótalo, foliácea placodioidea, filamentosa y escuamulosa estuvieron fuertemente correlacionados con la riqueza total de líquenes en los bosques montanos. En este sentido, se puede utilizar como una herramienta para realizar inventarios rápidos de biodiversidad en estos ecosistemas, que han sido catalogados como uno de los más amenazados de todo el planeta.

7. A pesar de que la alteración antrópica en los bosques estacionalmente secos provocó una disminución en la diversidad de las comunidades epífitas relacionada con la apertura del dosel, las características del hospedador se han identificado como los principales conductores de las comunidades epífitas en estos bosques. De manera especial, la especie del árbol fue el principal factor limitante de las comunidades de líquenes epífitos en los bosques estacionalmente secos.

8. Los resultados de esta investigación han permitido resaltar la importancia de la conservación de los bosques montanos y bosques secos no alterados como prioritarios para mantener una alta diversidad de líquenes y briófitos, debido a la alta heterogeneidad de hábitats y estructura forestal que proporcionan estos ecosistemas.

9. Por último, hemos podido constatar el escaso conocimiento que se tiene de las especies que viven en estos ambientes. Son numerosas las aportaciones a la ecología y distribución de las especies de líquenes y briófitos que han sido identificadas durante la realización de esta memoria.

LISTA DE MANUSCRITOS

La tesis se ha estructurado en base a cinco artículos en inglés y uno en español para su publicación en revistas científicas internacionales. A continuación se detalla el título, la lista de coautores y el estado de publicación de cada capítulo.

Bosques Montanos Tropicales

Capítulo I	Benítez, Á., Prieto, M., González, Y., & Aragón, G. (2012). Effects of tropical montane forest disturbance on epiphytic macrolichens. *Science of the Total Environment*, 441, 169-175.
Capítulo II	Benítez, Á., Prieto, M., & Aragón, G. 2015. Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *Forestry*, 88(5), 521-527.
Capítulo III	Benítez, Á., Prieto, M., González, Y., & Aragón, G. Functional traits of epiphytic lichens as indicators of forest disturbance and predictors of total richness in a tropical montane rainforest of Ecuador. Manuscrito inédito

Bosques Secos Tropicales

Capítulo IV	Benítez, Á., Prieto, M., & Aragón, G. Lichen diversity in tropical dry forest is influenced by host preference more than disturbance. Manuscrito inédito

Aportaciones a la ecología y distribución de las especies

Capítulo V	Benitez, A., Gradstein, S.R., Prieto, M., Aragón, G., León-Yánez, S., Moscoso, A. & Burghardt, M. 2012. Additions to the bryophyte flora of Ecuador 2. *Tropical bryology* 34: 99–106.
Capítulo VI	Benítez, Á., Aragón, G., González, Y. & Prieto, M. More than one hundred new records of lichens from Ecuador. Manuscrito inédito

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REFERENCIAS

Acebey, A., Gradstein, S. R., & Krömer, T. (2003). Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of tropical ecology, 19(01), 9-18.

Aguirre, Z., Kvist, L. P., & Sánchez, O. (2006). Bosques secos en Ecuador y su diversidad. Botánica económica de los Andes Centrales, 2, 162-187.

Anderson, M.J., Gorley, R.N., & Clarke, K.R. (2008). PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth, UK: PRIMER-E.

Aragón, G., Belinchón, R., Martínez, I., & Prieto, M. (2016). A survey method for assessing the richness of epiphytic lichens using growth forms. Ecological Indicators, 62, 101-105.

Aragón, G., López, R., & Martínez, I. (2010). Effects of Mediterranean dehesa management on epiphytic lichens. Science of the total environment, 409(1), 116-122.

Asner, G. P., Knapp, D. E., Broadbent, E. N., Oliveira, P. J., Keller, M., & Silva, J. N. (2005). Selective logging in the Brazilian Amazon. Science, 310(5747), 480-482.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A., & Peres, C. A. (2007). The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. Journal of Applied Ecology, 44(5), 1001-1012.

Barthlott W, Mutke J, Rafiqpoor MD, Kier G, Kreft H (2005) Global centres of vascular plant diversity. Nova Acta Leopoldina NF, 92, 342: 61-83

Barthlott, W., Schmit-Neuerburg, V., Nieder, J., & Engwald, S. (2001). Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecology, 152(2), 145-156.

Beck, J. A. N., Schulze, C. H., Linsenmair, K. E., & Fiedler, K. (2002). From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. Journal of tropical ecology, 18(01), 33-51.

Belinchón, R., Martínez, I., Escudero, A., Aragón, G., & Valladares, F. (2007). Edge effects on epiphytic communities in a Mediterranean Quercus pyrenaica forest. Journal of Vegetation Science, 18(1), 81-90.

Benítez, Á., Prieto, M., & Aragón, G. (2015). Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. Forestry, 88(5), 521-527.

Benítez, Á., Prieto, M., González, Y., & Aragón, G. (2012). Effects of tropical montane forest disturbance on epiphytic macrolichens. Science of the Total Environment, 441, 169-175.

Benzing, D. H. (1995). The physical mosaic and plant variety in forest canopies.*Selbyana*, *16*(2), 159-168.

Benzing, D. H. (2004). Vascular epiphytes. *Forest canopies*, *2*, 175-211.

Berg, A., Gärdenfors, U., Hallingbäck, T., & Norén, M. (2002). Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden–analyses of data from a national survey. Biodiversity & Conservation, 11(8), 1479-1503.

Best, B.J., Kessler, M. 1995. Biodiversity and Conservation in Tumbesian Ecuador and Peru. Pp.: 218 BirdLife I. BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, U.K.

Brehm, G., & Fiedler, K. (2005). Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. Journal of Research on the Lepidoptera, 38, 1-14.

Brown, A. D., & Kappelle, M. (2001). Introducción a los bosques nublados del neotrópico: una síntesis regional. Bosques nublados del neotrópico, 27-40.

Brown, S., & Lugo, A. E. (1990). Tropical secondary forests. Journal of tropical ecology, 6(1), 1-32.

Bruijnzeel L.A. (2005). Tropical montane cloud forests: a unique hydrological case. In: Bonell M, Bruijnzeel LA (eds) Forests, water and people in the humid tropics. Cambridge University Press, Cambridge, pp 462–483.

Brummitt, N., & Lughadha, E. N. (2003). Biodiversity: where's hot and where's not. Conservation Biology, 17(5), 1442-1448.

Bungartz, F., Ziemmeck, F., Yánez Ayabaca, A., Nugra, F., Aptroot, A. (2013). CDF Checklist of Galapagos Lichenized Fungi - FCD Lista de especies de Hongos liquenizados de Galápagos. *In*: Bungartz, F., Herrera, H., Jaramillo, P., Tirado, N., Jiménez-Uzcátegui, G., Ruiz, D., Guézou, A. & Ziemmeck, F. (eds.). Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin.

Cáceres, M. E., Lücking, R., & Rambold, G. (2007). Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycological Progress, 6(3), 117-136.

Callaway, R. M., Reinhart, K. O., Tucker, S. C., & Pennings, S. C. (2001). Effects of epiphytic lichens on host preference of the vascular epiphyte *Tillandsia usneoides*. Oikos, 94(3), 433-441.

Cevallos Solórzano, G. (2012). Checklist de líquenes y hongos liquenícolas de

Ecuador Continental.

Churchill, S. P. (1994). New synonyms and deletions for the moss floras of Colombia and Ecuador. Bryophyte Diversity and Evolution, 9(1), 1-4.

Churchill, S. P., Griffin III, D. A. N. A., Lewis, M., Balslev, H., Forero, E., & Luteyn, J. L. (1995). Moss diversity of the tropical Andes. In Biodiversity and conservation of Neotropical montane forests. Proceedings of a symposium, New York Botanical Garden, 21-26 June 1993. (pp. 335-346). New York Botanical Garden.

Churchill, S.P., Griffin, D. & Muñoz, J. (2000).A Checklist of the Mosses of the tropical Andean countries. Ruizia 17: 1–203.

Cornelissen, J. T., & Ter Steege, H. (1989). Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology*, *5*(02), 131-150.

Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E., & Araníbar, J. (1999). Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. Journal of Vegetation Science, 10(5), 651-660.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences, 104(52), 20684-20689.

Díaz, S., McIntyre, S., Lavorel, S., & Pausas, J. G. (2002). Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. New Phytologist, 154(1), 7-9.

Dinerstein, E; Olson, DM; Graham, DJ; Webster, AL; Primm, SA; Bookbinder, MP; Ledec, G. 1995. A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean. The World Bank, Washington, DC., USA.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological monographs, 67(3), 345-366.

Ellis, C. J., & Coppins, B. J. (2006). Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. Journal of Biogeography, 33(9), 1643-1656.

Espinosa, C. I., Cabrera, O., Luzuriaga, A. L., & Escudero, A. (2011). What Factors Affect Diversity and Species Composition of Endangered Tumbesian Dry Forests in Southern Ecuador?. Biotropica, 43(1), 15-22.

Espinosa, C. I., Cruz, M., Jara-Guerrero, A., Gusmán, E., & Escudero, A. (2015). The effects of individual tree species on species diversity in a tropical dry forest change throughout ontogeny. Ecography, 39 (3) 329–337.

Espinosa, C. I., De la Cruz, M., Luzuriaga, A. L., & Escudero, A. (2012). Bosques tropicales secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e implicaciones para la conservación. *Revista Ecosistemas*, *21*(1-2).

Fajardo, L., González, V., Nassar, J. M., Lacabana, P., Portillo, Q., Carlos, A., & Rodríguez, J. P. (2005). Tropical Dry Forests of Venezuela: Characterization and Current Conservation Status1. Biotropica, 37(4), 531-546.

Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A., & Sevink, J. (2002). High altitude tropical secondary forests: a competitive carbon sink?.*Forest Ecology and Management*, *163*(1), 9-25.

Flores-Palacios, A., & García-Franco, J. G. (2006). The relationship between tree size and epiphyte species richness: testing four different hypotheses. Journal of Biogeography, 33(2), 323-330.

Frazer, G. W., Canham, C. D., & Lertzman, K. P. (2000). Gap light analyzer, version 2.0.

Fritz, Ö., Niklasson, M., & Churski, M. (2009). Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Applied Vegetation Science, 12(1), 93-106.

Fujisaka, S., Castilla, C., Escobar, G., Rodrigues, V., Veneklaas, E. J., Thomas, R., & Fisher, M. (1998). The effects of forest conversion on annual crops and pastures: Estimates of carbon emissions and plant species loss in a Brazilian Amazon colony. Agriculture, ecosystems & environment, 69(1), 17-26.

Garavito, N. T., Álvarez, E., Caro, S. A., Murakami, A. A., Blundo, C., Espinoza, T. B., ... & León, B. (2012). Evaluación del estado de conservación de los bosques montanos en los Andes tropicales. Revista Ecosistemas, 21(1-2).

García-Suárez, M. D., Rico-Gray, V., & Serrano, H. (2003). Distribution and abundance of Tillandsia spp. (Bromeliaceae) in the Zapotitlán Valley, Puebla, México. Plant ecology, 166(2), 207-215.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology letters*, *12*(6), 561-582.

Gardner, T. A., Hernández, M. I., Barlow, J., & Peres, C. A. (2008). Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. Journal of Applied Ecology, 45(3), 883-893.

Gauslaa, Y., Ohlson, M., Solhaug, K. A., Bilger, W., & Nybakken, L. (2001). Aspect-dependent high-irradiance damage in two transplanted foliose forest lichens, *Lobaria pulmonaria* and *Parmelia sulcata*. *Canadian Journal of Forest Research*, *31*(9), 1639-1649.

Gauslaa, Y., Palmqvist, K., Solhaug, K. A., Holien, H., Hilmo, O., Nybakken, L., Myhre, C. & Ohlson, M. (2007). Growth of epiphytic old forest lichens across climatic and successional gradients. Canadian Journal of Forest Research, 37(10), 1832-1845.

Gentry, A. H. (1995) Diversity and floristic composition of neotropical dry forests. Seasonally dry tropical forests (ed. By S. H. Bullock, H. A. Mooney and E. Medina), pp. 146–194. Cambridge University Press, Cambridge.

Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular epiphytes. Annals of the Missouri Botanical Garden, 74(2), 205-233.

Gentry, A.H. (1982) Patterns of neotropical plant species diversity. Evolutionary Biology, Vol. 15 (edsM.K.Hecht, B.Wallace & G.T.Prance), pp. 1 – 84. Plenum Press, New York, NY, USA.

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences, 107(38), 16732-16737.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. Nature, 478(7369), 378-381.

Gignac, L. D. (2001). Bryophytes as indicators of climate change. The bryologist, 104(3), 410-420.

Giordani, P., Brunialti, G., Bacaro, G., & Nascimbene, J. (2012). Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. Ecological Indicators, 18, 413-420.

Gradstein, S. R., & Sporn, S. G. (2010). Land-use change and epiphytic bryophyte diversity in the tropics. Cambio en el uso de la tierra y diversidad de briófitas epífitas en los trópicos. Nova Hedwigia., 138, 311-323.

Gradstein, S.R. (2008). Epiphytes of tropical montane forests—impact of deforestation and climate change. In: The tropical mountain forest. Patterns and Processes in a Biodiversity Hotspot. Gradstein, S.R., Homeier, J. and Gansert, D. (eds). University Press, Göttingen, pp. 51–65.

Gradstein, S.R., Churchill, S.P. & Salzar, N. (2001). Guide to the bryophytes of tropical America. Mem.N. Y.Bot.Gard.86, 1–577.

Gray, M. A., Baldauf, S. L., Mayhew, P. J., & Hill, J. K. (2007). The response of avian feeding guilds to tropical forest disturbance. Conservation Biology, 21(1), 133-

141.

Green, T. G. A., Büdel, B., Meyer, A., Zellner, H., & Lange, O. L. (1997). Temperate rainforest lichens in New Zealand: light response of photosynthesis.*New Zealand Journal of Botany*, *35*(4), 493-504.

Hamilton, L. S. (1995). Mountain cloud forest conservation and research: a synopsis. Mountain Research and Development, 259-266.

Hamilton, L.S. (2001). Una campaña para los bosques nublados: ecosistemas únicos y valiosos en peligro. Pp. 41-49, in M. Kappelle y A.D Brown (eds.): Bosques nublados del neotrópico. INBio, Costa Rica.

Hauck, M. (2009). Global warming and alternative causes of decline in arctic-alpine and boreal-montane lichens in North-Western Central Europe. Global change biology, 15(11), 2653-2661.

Hauck, M. (2011). Site factors controlling epiphytic lichen abundance in northern coniferous forests. Flora-Morphology, Distribution, Functional Ecology of Plants, 206(2), 81-90.

Hauck, M., & Spribille, T. (2005). The significance of precipitation and substrate chemistry for epiphytic lichen diversity in spruce-fir forests of the Salish Mountains, northwestern Montana. Flora-Morphology, Distribution, Functional Ecology of Plants, 200(6), 547-562.

Hedenås, H., & Ericson, L. (2003). Response of epiphytic lichens on *Populus tremula* in a selective cutting experiment. Ecological Applications, 13(4), 1124-1134.

Henderson, A., Churchill, S. P., & Luteyn, J. L. (1991). Neotropical plant diversity. Nature, 351, 21-22.

Hietz, P., Buchberger, G. and Winkler, M. (2006) Effect of forest disturbance on abundance and distribution of epiphytic bromeliads and orchids. Ecotropica 12, 103–112.

Hietz-Seifert, U., Hietz, P., & Guevara, S. (1996). Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biological conservation, 75(2), 103-111.

Higuera, D., & Wolf, J. H. (2010). Vascular epiphytes in dry oak forests show resilience to anthropogenic disturbance, Cordillera Oriental, Colombia. Caldasia, 32(1), 161-174.

Hirata, A., Kamijo, T., & Saito, S. (2009). Host trait preferences and distribution of vascular epiphytes in a warm-temperate forest. Plant Ecology, 201(1), 247-254.

Hofstede, R., & Aguirre, N. (1999). Biomasa y dinámica del carbono en relación con las actividades forestales en la Sierra del Ecuador. *El páramo como espacio de mitigación de carbono atmosférico. Serie Páramo*, *1*, 29-51.

Holz, I. (2003). Diversity and ecology of bryophytes and macrolichens in primary and secondary montane Quercus forests, Cordillera de Talamanca, Costa Rica (Doctoral dissertation, PhD Thesis, University of Göttingen, Göttingen, Alemania).

Holz, I., & Gradstein, R. S. (2005). Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica–species richness, community composition and ecology. Plant Ecology, 178(1), 89-109.

Houghton, R. A. (1994). The worldwide extent of land-use change. BioScience, 44(5), 305-313.

Johansson, P., Rydin, H., & Thor, G. (2007). Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience, 14(1), 81-91.

Jovan, S., & McCune, B. (2004). Regional variation in epiphytic macrolichen communities in northern and central California forests. The Bryologist, 107(3), 328-339.

Käffer, M. I., de Azevedo Martins, S. M., Alves, C., Pereira, V. C., Fachel, J., & Vargas, V. M. F. (2011). Corticolous lichens as environmental indicators in urban areas in southern Brazil. Ecological Indicators, 11(5), 1319-1332.

Kalacska, M.E.R., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Rivard, B., Quesada, M. 2005. Effects of Season and Successional Stage on Leaf Area Index and Spectral Vegetation Indices in Three Mesoamerican Tropical Dry Forests. Biotropica 37:486-496.

Kammesheidt, L. (2002). Perspectives on secondary forest management in tropical humid lowland America. AMBIO: A Journal of the Human Environment, 31(3), 243-250.

Kessler, M., Keßler, P. J., Gradstein, S. R., Bach, K., Schmull, M., & Pitopang, R. (2005). Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. Biodiversity & Conservation, 14(3), 547-560.

Király, I., Nascimbene, J., Tinya, F., & Ódor, P. (2013). Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. Biodiversity and Conservation, 22(1), 209-223.

Koch, N. M., de Azevedo Martins, S. M., Lucheta, F., & Müller, S. C. (2013). Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. Ecological indicators, 34, 22-30.

Kranner, I., Beckett, R., Hochman, A., & Nash III, T. H. (2008). Desiccation-tolerance in lichens: a review. The Bryologist, 111(4), 576-593.

Küper, W., Kreft, H., Nieder, J., Köster, N., & Barthlott, W. (2004). Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests.*Journal of*

Biogeography, *31*(9), 1477-1487.

Laliberte, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., & McNamara, S. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology letters, 13(1), 76-86.

Lange, O. L., Büdel, B., Meyer, A., & Kilian, E. (1993). Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. The Lichenologist, 25(02), 175-189.

Larrea, M. L., & Werner, F. A. (2010). Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. Forest Ecology and Management, 260(11), 1950-1955.

Laurance, W. F. (1999). Reflections on the tropical deforestation crisis. Biological Conservation, 91(2), 109-117.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., & Stork, N. E. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature, 391(6662), 72-76.

León-Yánez, S., Gradstein, S. R., & Wegner, C. (2006). Hepáticas y antoceros del Ecuador. Herbario QCA, Quito.

Lesica, P., McCune, B., Cooper, S. V., & Hong, W. S. (1991). Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany*, *69*(8), 1745-1755.

Li, S., Liu, W. Y., & Li, D. W. (2013). Bole epiphytic lichens as potential indicators of environmental change in subtropical forest ecosystems in southwest China. Ecological indicators, 29, 93-104.

Linares-Palomino, R. (2004). Los bosques tropicales estacionalmente secos: II. Fitogeografía y composición florística. Arnoldia, 11(1), 103-138.

Llop, E., Pinho, P., Matos, P., Pereira, M. J., & Branquinho, C. (2012). The use of lichen functional groups as indicators of air quality in a Mediterranean urban environment. Ecological Indicators, 13(1), 215-221.

Löbel, S., Snäll, T., & Rydin, H. (2006). Species richness patterns and metapopulation processes–evidence from epiphyte communities in boreo-nemoral forests. Ecography, 29(2), 169-182.

Lücking, R. (1999). Ecology of foliicolous lichens at the ‘Botarrama’trail (Costa Rica), a neotropical rainforest. IV. Species associations, their salient features and their dependence on environmental variables. The Lichenologist, 31(03), 269-289.

Lugo, A. E. (2009). The emerging era of novel tropical forests. *Biotropica*, *41*(5), 589-591.

Mabry, C. M., & Fraterrigo, J. M. (2009). Species traits as generalized predictors of forest community response to human disturbance. Forest Ecology and Management, 257(2), 723-730.

Malhi, Y., & Phillips, O. L. (2004). Tropical forests and global atmospheric change: a synthesis. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 359(1443), 549-555.

Mandl, N., Lehnert, M., Kessler, M., & Gradstein, S. R. (2010). A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. Biodiversity and Conservation, 19(8), 2359-2369.

Marini, L., Nascimbene, J., & Nimis, P. L. (2011). Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. Science of the Total Environment, 409(20), 4381-4386.

Matos, P., Pinho, P., Aragón, G., Martínez, I., Nunes, A., Soares, A. M., & Branquinho, C. (2015). Lichen traits responding to aridity. Journal of Ecology, 103(2), 451-458.

McCullagh, P. and Nelder, J.A. (1989). Generalized linear models. Second Edition. Monographs on statistics and applied probability 37. Chapman and Hall/CRC, New York, USA.

McCune, B., Dey, J., Peck, J., Heiman, K., & Will-Wolf, S. (1997). Regional gradients in lichen communities of the southeast United States. The Bryologist, 145-158.

McGee, G. G., & Kimmerer, R. W. (2002). Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. Canadian Journal of Forest Research, 32(9), 1562-1576.

Miles, L., A. Newton, R. Defries, C. Ravilious, I. May, S. Blyth, V. Kapos, & J. Gordon. (2006). A global overview of the conservation status of tropical dry forests. Journal of Biogeography, 33, 491–505.

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Ecology, 96(5), 884-893.

Molnár, K., & Farkas, E. (2010). Current results on biological activities of lichen secondary metabolites: a review. *Zeitschrift für Naturforschung C*, *65*(3-4), 157-173.

Mondragón, D., Durán, R., Ramírez, I., & Valverde, T. (2004). Temporal variation in the demography of the clonal epiphyte *Tillandsia brachycaulos* (Bromeliaceae) in the Yucatán Peninsula, Mexico. Journal of Tropical Ecology, 20(02), 189-200.

Mooney, H.A., Bullock, S.H., Medina, E., (1995). Introduction, In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge

University Press, Cambridge, pp. 146–194.

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. Annual review of ecology and systematics, 67-88.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Nadkarni, N.M., M.C. Merwin & J. Nieder. (2001). Forest canopies: plant diversity. Pp. 27-40 in S. Levin, ed. Encyclopedia of Biodiversity. Academic Press, San Diego, California, USA.

Nascimbene, J., Marini, L., Motta, R., & Nimis, P. L. (2009). Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. Biodiversity and Conservation, 18(6), 1509-1522.

Nash, T. H. (1996). Lichen biology. Cambridge University Press.

Nash, T. H. (ed.) 2008. *Lichen Biology*. 2nd edn. Cambridge University Press, Cambridge.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., & Network, T. S. R. (2007). Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biological conservation, 137(1), 1-19.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S.R., Sipman, H. J. M., & Obregon, A. et al. (2010). Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators, 10, 1111–1118.

Nöske, N. M., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J., & Gradstein, S. R. (2008). Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. Basic and Applied Ecology, 9(1), 4-12.

Ochoa-Jiménez, D. A., Cueva-Agila, A., Prieto, M., Aragón, G. & Benitez, A. (2015). Changes in the epiphytic lichen composition related with air quality in the city of Loja (Ecuador). Caldasia, 37(2), 333-343.

Oishi, Y. (2009). A survey method for evaluating drought-sensitive bryophytes in fragmented forests: a bryophyte life-form based approach. Biological conservation, 142(12), 2854-2861.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. et al. 2013 Vegan: Community Ecology Package.

Pardow, A., & Lakatos, M. (2013). Desiccation tolerance and global change: implications for tropical bryophytes in lowland forests. Biotropica, 45(1), 27-36.

Pardow, A., Gehrig-Downie, C., Gradstein, R., & Lakatos, M. (2012). Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. Biodiversity and Conservation, 21(14), 3637-3655.

Pennington, R., Prado, D. E., & Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography, 27(2), 261-273.

Perhans, K., Gustafsson, L., Jonsson, F., Nordin, U., & Weibull, H. (2007). Bryophytes and lichens in different types of forest set-asides in boreal Sweden. Forest ecology and management, 242(2), 374-390.

Pharo, E. J., & Beattie, A. J. (1997). Bryophyte and lichen diversity: a comparative study. *Australian Journal of Ecology*, *22*(2), 151-162.

Pinheiro, J. C., D. M. Bates, S. DebRoy, and D. Sarkar. 2008. nlme: Linear and nonlinear mixed effects models. R package version 3.1-87.

Pinho, P., Bergamini, A., Carvalho, P., Branquinho, C., Stofer, S., Scheidegger, C., & Maguas, C. (2012). Lichen functional groups as ecological indicators of the effects of land-use in Mediterranean ecosystems. Ecological indicators, 15(1), 36-42.

Proctor, M. C., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., & Mishler, B. D. (2007). Desiccation-tolerance in bryophytes: a review. *The Bryologist*, *110*(4), 595-621.

Ranius, T., Johansson, P., Berg, N., & Niklasson, M. (2008). The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. Journal of vegetation science, 19(5), 653-662.

Richter, M. (2008). Tropical mountain forests – distribution and general features. In: Gradstein, S.R. et al. (eds.): The Tropical Mountain forest – Patterns and Processes in a Biodiversity Hotspot. Biodiversity and Ecology Series 2, 7-24.

Rosabal, D., Burgaz, A. R., & Reyes, O. J. (2013). Substrate preferences and phorophyte specificity of corticolous lichens on five tree species of the montane rainforest of Gran Piedra, Santiago de Cuba. The Bryologist, 116(2), 113-121.

Rosa-Manzano, E., Andrade, J. L., Zotz, G., & Reyes-García, C. (2014). Epiphytic orchids in tropical dry forests of Yucatan, Mexico–Species occurrence, abundance and correlations with host tree characteristics and environmental conditions. Flora-Morphology, Distribution, Functional Ecology of Plants, 209(2), 100-109.

Ruthemberg, H. (1980), Farming systems in the tropics. New York: Oxford University Press. 424 pp.

Sabatini, F. M., Burton, J. I., Scheller, R. M., Amatangelo, K. L., & Mladenoff, D. J. (2014). Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. Applied vegetation science, 17(3), 398-407.

Sanchez, O., Aguirre, Z., Kvist, L.P. 2006. Timber and non-timber uses of dry forests in Loja Province. Lyonia 10:73- 82.

Sanchez-Azofeifa, G. A., Portillo-Quintero, C. 2011. Extent and Drivers of Change of Neotropical Seasonally Dry Tropical Forests. En: Dirzo, R., Mooney, H., Ceballos, G., Young, H. (eds.). Seasonally Dry Tropical Forests: Ecology and Corservation, pp. 45-57. Island Press. Washington, DC 20009, USA.

Sillett, S. C., & Antoine, M. E. (2004). Lichens and bryophytes in forest canopies. Forest Canopies. Elseiver Academic Press, MA, 151-174.

Sipman, H.J.M. and Harris, R.C. (1989). Lichens. In: Tropical Rain Forest Ecosystems. Lieth, H. and Werger, M.J.A. (eds). Elsevier, Amsterdam, pp. 303–309.

Sodhi, N. S. (2002). A comparison of bird communities of two fragmented and two continuous Southeast Asian rainforests. Biodiversity & Conservation, 11(6), 1105-1119.

Soto-Medina, E., Lücking, R., & Bolaños Rojas, A. (2012). Phorophyte specificity and microenvironmental preferences of corticolous lichens in five phorophyte species from premontane forest of Finca Zíngara, Cali, Colombia). Revista de Biología Tropical, 60(2), 843-856.

Sporn, S. G. (2009). *Epiphytic bryophytes in natural forests and cacao agroforests of Central Sulawesi, Indonesia*. Georg-August-Univ.

Sporn, S. G., Bos, M. M., Hoffstätter-Müncheberg, M., Kessler, M., & Gradstein, S. R. (2009). Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia. Functional Plant Biology, 36(2), 171-179.

Stofer, S., Bergamini, A., Aragon, G., Carvalho, P., Coppins, B. J., Davey, S. & Lökös, L. (2006). Species richness of lichen functional groups in relation to land use intensity. The Lichenologist, 38(04), 331-353.

Szövényi, P., Hock, Z. S., & Tóth, Z. (2004). Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. Journal of Bryology, 26(2), 137-146.

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., & Peres, C. A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biological Conservation*, *143*(10), 2328-2340.

Tapia-Armijos, M. F., Homeier, J., Espinosa, C. I., Leuschner, C., & de la Cruz, M. (2015). Deforestation and Forest Fragmentation in South Ecuador since the 1970s–Losing a Hotspot of Biodiversity. PLoS one, 10(9), e0133701.

Trejo, I., & Dirzo, R. (2002). Floristic diversity of Mexican seasonally dry tropical forests. Biodiversity & conservation, 11(11), 2063-2084.

Vergara-Torres, C. A., Pacheco-Álvarez, M. C., & Flores-Palacios, A. (2010). Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. Journal of Tropical Ecology, 26(06), 563-570.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. Oikos, 116(5), 882-892.

Vitousek, P. M. (1994). Beyond global warming: ecology and global change. Ecology, 75(7), 1861-1876.

Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters, 13(3), 267-283.

Werner, F. A., & Gradstein, S. R. (2009). Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science, 20(1), 59-68.

Werner, F.A. (2008). Effects of human disturbance on epiphyte assemblages in the Andes of Ecuador. Ph.D. diss., Univ. Göttingen, Germany.

Will-Wolf, S., Geiser, L. H., Neitlich, P., & Reis, A. H. (2006). Forest lichen communities and environment—how consistent are relationships across scales?. Journal of Vegetation Science, 17(2), 171-184.

Wolseley, P. A., & Aguirre-Hudson, B. (1997). The ecology and distribution of lichens in tropical deciduous and evergreen forests of northern Thailand. Journal of biogeography, 24(3), 327-343.

Yeaton, R. I., & Gladstone, D. E. (1982). The pattern of colonization of epiphytes on Calabash Trees (Crescentia alata HBK.) in Guanacaste Province, Costa Rica. *Biotropica*, 137-140.

Ziemmeck, F. (2011). CDF Checklist of Galapagos Bryophytes - FCD Lista de especies de Briofitas de Galápagos. *In*: Bungartz, F., Herrera, H., Jaramillo, P., Tirado, N., Jiménez-Uzcátegui, G., Ruiz, D., Guézou, A. & Ziemmeck, F. (eds.). Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin.

CAPÍTULOS / CHAPTERS

CAPÍTULO I / CHAPTER I

Effects of tropical montane forest disturbance on epiphytic macrolichens

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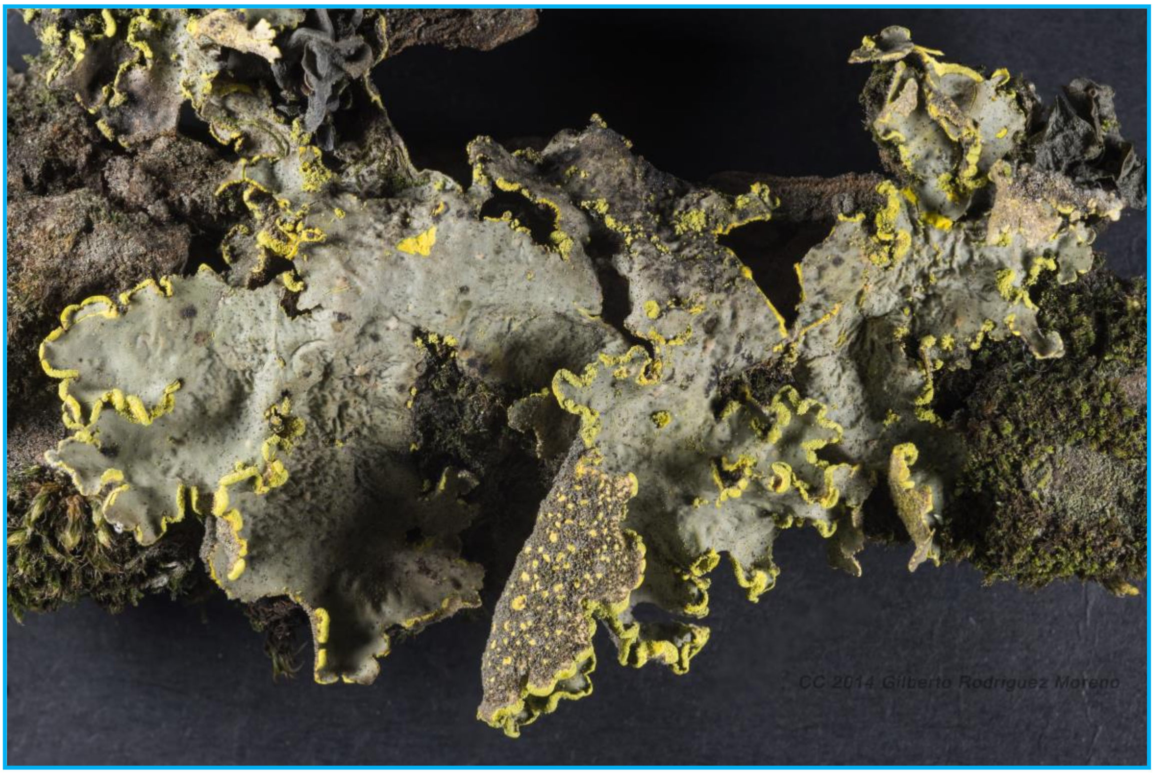
Benítez, Á., Prieto, M., González, Y., & Aragón, G. (2012).
***Science of the Total Environment*, 441, 169-175.**



Pseudocyphellaria aurata (Ach.) Vain

Abstract

The high diversity of epiphytes typical of undisturbed montane tropical forests has been negatively affected by continuous deforestation and forest conversion to secondary vegetation. Macrolichens are an important component of these epiphytes. Because their physiology is strongly coupled to humidity and solar radiation, we hypothesized that microclimatic changes derived from forest clearing and logging can affect the diversity of these poikilohydric organisms. In southern Ecuador, we examined three types of forests according to a disturbance gradient (primary forests, secondary forests, and monospecific forests of *Alnus acuminata*) for the presence/absence and coverage of epiphytic macrolichens that we identified on 240 trees. We found that total richness tended to decrease when the range of the disturbance increased. The impoverishment was particularly drastic for “shade-adapted lichens”, while the richness of “heliophytic lichens” increased in the drier conditions of secondary growth. Epiphytic composition also differed significantly among the three types of forests, and the similarity decreased when the range of the disturbance was greater. We concluded that a span of 40 years of recovery by secondary vegetation was not enough to regenerate the diversity of epiphytic macrolichens that was lost due to forest disturbances.

Keywords: Ecuador, diversity, epiphytic macrolichens, disturbance, tropical montane forest.

1. Introduction

Montane tropical rain forests have been recognized as one of the most diverse ecosystems, being simultaneously one of the most threatened habitats in the world (Henderson et al., 1991; Gentry, 1995; Brummit and Nic Lughadha, 2003; Barthlott et al., 2005). Montane rain forests are disappearing at an incredibly high rate and currently cover a tiny fraction of their historical distributions (Henderson et al., 1991; Bruijnzeel and Hamilton, 2000; Wright, 2005; Laurance and Peres, 2006; Gibbs et al., 2010). Many natural forests have been reduced to small isolated remnants by deforestation and subsequent agricultural or livestock activities (Churchill et al., 1995; Asner et al., 2005; Gibbs et al., 2010). This scenario of forest alteration from logging and different land uses has serious consequences for epiphytes (Barthlott et al., 2001; Wolf., 2005; Nöske et al., 2008), which are important components of the diversity within montane rain forests (Barthlott et al., 2001; Nadkarni et al., 2001; Gradstein et al., 2003; Gradstein, 2008) and have important roles in the total biomass, water balance and nutrient cycling of the ecosystems (see Holz and Gradstein, 2005).

As a general pattern, epiphyte diversity tends to be higher in primary than in secondary vegetation (Barthlott et al., 2001; Gradstein, 2008). This matter has been recently studied in montane forests, but the results have been rather controversial; some studies supported the higher diversity in primary vegetation (Kapelle et al., 1995; Nöske et al., 2008), while others have found no relationship (Hietz, 1998; Holz and Gradstein, 2005; Nöske et al., 2008). This variation in the patterns observed might be related to differences in the studied taxa, the level of disturbance, the diversity of the host tree species, or the age of the secondary vegetation (Hietz et al., 2006; Gradstein, 2008). In addition to the epiphytic richness, forest disturbance also affects species composition of the epiphytes (Hietz et al., 2006). For instance, epiphytes characteristic of a shaded understory declined in more open vegetation than in primary forests, whilst “sun epiphytes” were lacking from the shady canopy strata of natural forests (Hietz et al., 2006; Gradstein, 2008).

Macrolichens (foliose and fruticose lichen species) are important epiphytic organisms in montane rain forest (Mandl et al., 2010), and the diversity and composition of the communities depend mainly on microclimatic factors associated with forest structure (tree age, canopy cover, management intensity, tree diversity) (Aragón et al., 2010). The physiology of macrolichens is strongly coupled to humidity, solar radiation and temperature conditions (Green et al., 2008), so their distributions at a local level are expected to be determined by changes in forest structure derived from natural or human disturbance of the forests (Bergamini et al., 2005; Werth et al., 2005; Nascimbene et al., 2007; Aragón et al., 2010). Within macrolichens, certain groups without cortical pigments (e.g., peltigeralean species) are more sensitive to environmental changes, because they suffer photoinhibition in excessive radiation and are strongly dependent on atmospheric moisture (Lange at al., 2004; Kranner et al., 2008). In this sense, we expect drastic changes in macrolichen composition between the natural rain forest and the more disturbed environment of secondary vegetation. In addition to microclimatic changes caused by the reduction in canopy in disturbed forests, forest logging also causes a loss in diversity of host tree species. This fact may affect the epiphytic diversity and composition because the establishment of a particular species of lichens is determined by several factors related to the host tree species such as bark roughness and pH and tree size (Fritz et al., 2008; Ranius et al., 2008; Belinchón et al., 2009; Aragón et al., 2010). Thus, we expect to find a higher diversity of epiphytic macrolichens in primary forests than in the young secondary vegetation, where the diversity of host tree species is lower and trees are younger.

Our main goal was to analyze differences in species richness and diversity of epiphytic macrolichens in relation with forest disturbance in tropical montane forests. The forest disturbance level considered included remnants of natural forests (primary forests), secondary forests that developed after selective logging of primary forest, and secondary vegetation that consisted of a monospecific forest of *Alnus acuminata*. We hypothesized that the reduction in canopy, the fewer species of host trees and the younger secondary vegetation with respect to primary forests would affect the diversity of the epiphytic macrolichens. Specifically, we addressed the following questions: Do the macrolichen communities suffer an impoverishment when forest disturbance is increased? Which species contribute most to differences among the three forests disturbance levels?

2. Materials and methods

2.1. Study area

The study areas included six tropical montane forests located in southern Ecuador (Loja Province; 2200-2800 m asl) (Fig. 1). The climate is humid tropical with a mean annual temperature of 20ºC, annual rainfall of *ca*. 1900 mm, and relative humidity of *ca*. 80% (Instituto Nacional de Meteorología e Hidrología, INAMI).

In this study, we distinguished three types of vegetation according to a disturbance gradient: (1) Relicts of primary forest area (PF) of evergreen montane tropical vegetation. The PFs are characterized by a dense canopy layer (ca. 80-85% coverage) with large trees (35-40 m tall). The upper canopy is composed of *Cinchona macrocalyx* Pav. ex DC., *Clusia elliptica* Kunth, *Myrica pubescens* Humb. and Bonpl. *ex* Willd, *Podocarpus oleifolius* D. Don and *Weinmannia pubescens* HBK. (2) Secondary forests (SF) that have regrown after selective or total logging events on primary vegetation that took place some 40 years ago (Brown and Lugo, 1990; Holz, 2003). The canopy layer is ca. 60-70% in coverage, mainly composed of species in the *Melastomataceae* and *Lauraceae*, up to 25-30 m tall. (3) Secondary vegetation dominated by young, monospecific forests (MF) of *Alnus acuminata* Kunth, a pioneer native species of the Andes. The MFs were characterized by a very uniform structure, absence of understorey, a canopy layer of *ca*. 50% coverage and trees up to 20 m tall.

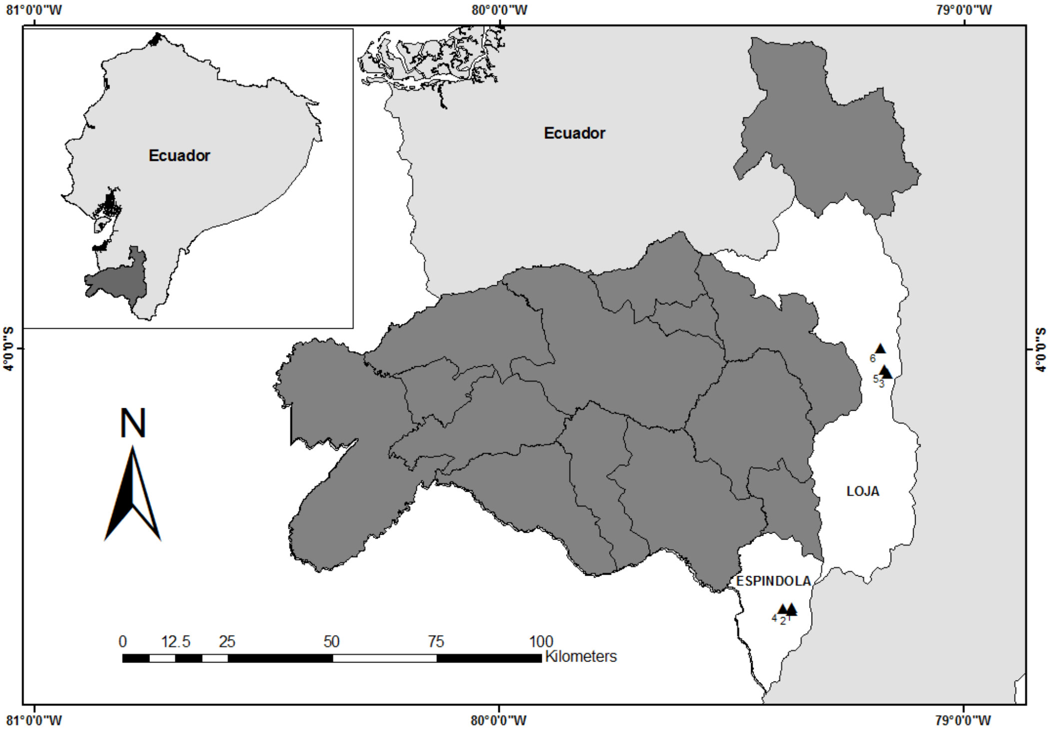


Fig. 1. Study area in Loja Province of southern Ecuador showing the location of the six tropical montane forest sites: 1 and 2, primary forests (PF); 3 and 4, secondary forests (SF); 5 and 6, monospecific forests of *Alnus acuminata* (MF).

2.2. Experimental design

Six forests were selected to span the disturbance gradient considered (2 PFs, 2 SFs and 2 MFs) (Fig. 1). Ten plots (5 x 5 m) at different elevations and orientations were selected within each forest, and four trees were sampled within the 10 plots. The distance between plots within a forest was over 50 m. Trees with the greatest and the smallest diameter and two other trees with a diameter at breast height (dbh) that was closest to the mean dbh within the plot were selected for a reliable representation of the epiphytic macrolichens of the stand. Additionally, we measured the elevation (m asl), slope (º), aspect (cosine transformed), and the canopy cover (%) at plot level, and the dbh of all trees (cm) within each plot. These variables are summarized in Appendix B.

We determined the species richness and composition of epiphytic macrolichens on 240 trees (40 in each forest). On the basis of our field experience in this type of community, we used 20 x 30 cm grids on the bark of each selected tree as monitoring units (Aragón et al., 2012). Six positions were chosen: three heights (0-50 cm, 51-150 cm, 151-200 cm) on the north and on the south aspects to obtain a good representation of the species growing in the different microenvironments of the tree trunks. We calculated the means of two data sets (macrolichen composition and species richness) for a given sample position. The total species richness was defined as the total number of species found in the six sites per tree. For the lichen composition, we calculated the mean estimated cover of each species (% of the site area) for the six sample sites. We calculated the total species cover per tree (as percentage of the grids) using the same methods.

2.3. Data analyses

The effects of microclimatic variables (slope, aspect, elevation, canopy cover, dbh) on the epiphytic richness at the tree and plot level was modelled by fitting Generalised Linear Mixed Models (GLMMs) (McCullagh and Nelder, 1989). This modelling approach was chosen because our data had a hierarchical structure with trees nested within plots, plots nested within forests and forests nested within disturbance level. We analyzed the data using a multilevel approach and, when necessary, considered plots and forests as random factors and applied mixed modelling (Verbeke and Molenberghs, 1997). Disturbance level was also initially included in the models, but none of the response variables were significantly related to it, so it was removed from the models to be as parsimonious as possible. Predictors were included as explanatory variables (fixed factors), and plot and forest were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT).

To test whether the three levels of disturbance had significantly different compositions of epiphytic species and to detect the effects of forest and plot variability, we performed a three-factor permutational multivariate analysis of variance (PERMANOVA) on the cover data (Anderson et al., 2008). In this analysis, the experimental design included three factors: disturbance level (three levels, fixed factor), forest (two levels, random factor nested within disturbance) and plot (10 levels, random nested within forest), with four replicate trees for each plot. The cover data (percentage cover by each macrolichen per tree) were $\log_{10}$ (x + 1)-transformed to account for contributions by both rare and abundant taxa. We used the Bray-Curtis distance measure. To assess species similarity among the different disturbance levels, we performed additional pairwise PERMANOVA tests (Anderson et al., 2008). We also computed a non-metric MDS (multidimensional scaling) ordination from the species cover values to reveal the degree of similarity among levels of disturbance. To identify the species that contributed most to the similarity and dissimilarity among the different disturbances levels, we used the SIMPER statistical routine (Clarke and Warwick, 1998). For all tests, we allowed 9999 random permutations under the reduced model.

3. Results

3.1 Species richness

We recorded a total of 119 species of epiphytic macrolichens on 240 trees. Results showed that the total number of macrolichens increased when forest disturbance decreased (Fig. 2). A total of 82 species were found in primary forests (PF), 64 species in secondary forests (SF) and 49 species in monospecific forests of *Alnus acuminata* (MF) (Appendix A). Moreover, species richness of the Peltigerales decreased when forest disturbance was higher (Appendix A). We found 36 exclusive species in PFs, but only 8 and 17 exclusive species in SFs and MFs, respectively (Appendix A).

Results of the mixed models showed that the most relevant predictors of the epiphytic communities at plot and tree levels were canopy cover and tree diameter (Table 1). The random variable forest was not significant in any case (Table 1).

3.2 Species composition

Multivariate statistical analyses showed that epiphytic composition was structured according to the different spatial scales, and a large component of variation was associated with the disturbance level (Table 2). The non-metric MDS ordination showed a clear separation between trees in the different disturbance levels (Fig. 3). The subsequent pairwise test revealed significant differences in epiphytic composition between all three disturbance levels (Table 3). Results of the PERMANOVA test showed that the highest similarity values for species composition within a disturbance level were associated with the highest disturbance: PF (29.35%), SF (35.44%) and MF (41.59%). The SIMPER routine revealed that not all species contribute equally to establish the differences in the disturbance gradient. We observed that the largest contributions are due to differences in species cover of the genus *Sticta* (*S.* aff. *canariensis*, *S. tomentosa*) (Table 4).

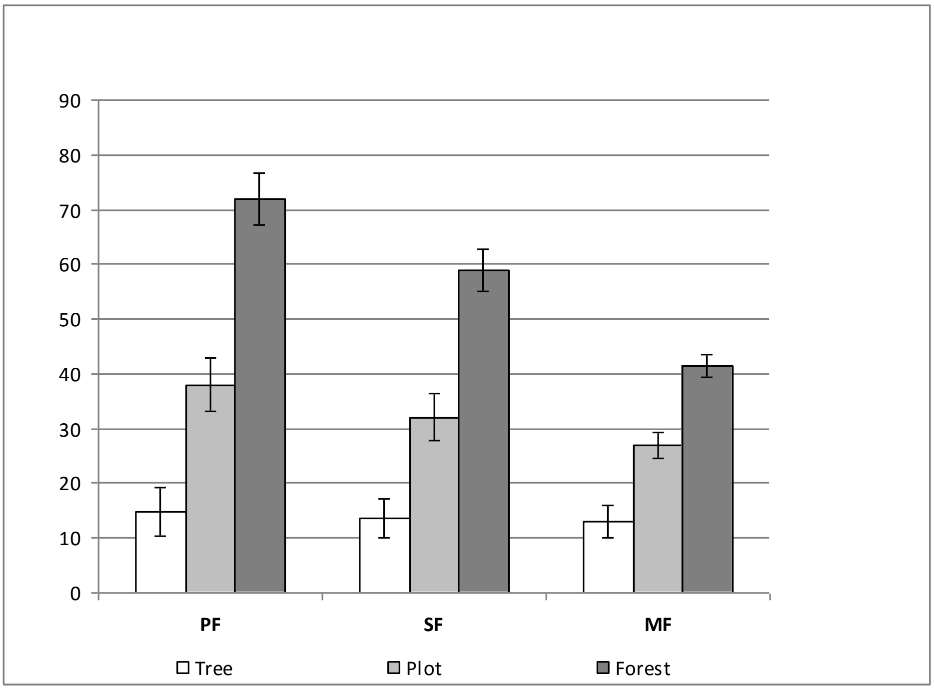


Fig. 2. Species richness of epiphytic macrolichens in the three types of vegetation (PF, SF and MF) at tree, plot and forest levels. Values represent means (±SD).

Table 1. Results of the Generalised Mixed Linear Models on some community traits. Coef.: coefficient of the variable in the model. S.E.: standard error. The random

variable forest was non-significant in both cases, while plot variable at tree level was significant (Z-value=2.67, Prob. Z=0.0038). Tree diameter (cm) was at tree level, while elevation (masl), slope (º), aspect (cosine transformed), canopy cover (%) and mean tree diameter (cm) were at plot level.

Richness	Coef. (S.E.)	F-value	P-value
Tree level			
Tree diameter	0.061(0.022)	6.82	**0.0056**
Elevation	0.002(0.001)	2.84	0.0969
Slope	-0.0085(0.019)	0.19	0.6607
Aspect	0.289(0.319)	0.82	0.3685
Canopy cover	0.052(0.017)	8.73	**0.0031**
Plot level			
Mean tree diameter	0.231(0.049)	21.52	**<0.0001**
Elevation	0.003(0.002)	1.20	0.2783
Slope	-0.010(0.021)	0.23	0.6325
Aspect	0.208 (0.371)	0.31	0.5781
Canopy cover	0.341(0.0472)	46.72	**<0.0001**

4. Discussion

Our results demonstrated that deforestation in tropical montane rainforests resulted in major loss in the species diversity of epiphytic macrolichens. Secondary forests (SF and MF) had on average 25-45% fewer species than in the neighboring primary forests (PF). Similarly, Gradstein (2008) pointed out that deforestation is a major cause in the loss of all epiphytic species, especially those of the shaded understory of the forest, the so-called "shade epiphytes". In our case, the impoverishment of epiphytic macrolichens in the more disturbed forests was mainly due to the severe loss of the more shade-adapted species (Peltigerales). The most plausible explanation could be related to the efficiency in the physiological activity and the degree of desiccation tolerance in the latter group (Lange et al., 1993; Jovan and McCune, 2004; Kranner et al., 2008). The Peltigerales is composed mainly of lichens without cortical pigments that protect the thallus when is exposed to excessive irradiation, and many of them possess cyanobacteria as the photobiont, which are strongly dependent on the amount of atmospheric moisture (Lange et al., 1993; Jovan and McCune, 2004; Kranner et al., 2008; Marini et al., 2011) because they need liquid water to activate photosynthesis (Lange et al., 1993).

Environmental conditions inside primary forests are optimal for the development of shade-adapted lichens because the high canopy cover favours the presence of more light-sheltered sites in the understory layer and a permanently moist environment where the air is constantly saturated (Sipman and Harris, 1989; Gradstein, 2008). On the contrary, the open canopy and stronger radiation in disturbed forests (SF and MF) create a drier microclimate than in natural forests (PF) (Gradstein, 2008). The consequent lower humidity negatively affects the shade-adapted lichens. When desiccation stress was induced for some macrolichens species, photosynthesis, respiration, morphology and growth were negatively affected, and the effects were greater for shade species (included in *Collema*, *Lobaria, Peltigera*, *Sticta*) growing in moist habitats (tropical climate) than for species adapted to more exposed areas and drier environments (see Kranner et al., 2008).

Table 2. Results of three-factor PERMANOVA analysis of species composition by disturbance gradient, forest and plot.

Source	**df**	**MS**	**Pseudo-*F***	***P***	**CV (%)**
Disturbance	2	1.1345	8.9826	0.0001	35.504
Forest (Disturbance)	3	12633	3.9021	0.0001	15.326
Plot (Forest (Disturbance))	54	3237.4	1.9495	0.0001	19.833
Error	180	1664			40.793

However, heliophytic species (with green algae and cortical pigments, mainly included in Lecanorales, Caliciales and Teloschistales) were 13-16% more numerous in more disturbed forests than in the primary forests and were especially abundant in the monospecific forests of *Alnus acuminata*, representing 85% of the total species. The decrease in “shade-adapted lichens” vs. the increase in “heliophytic lichens” in the more disturbed forests provides a negative balance in the total number of the species and therefore an impoverishment of the macrolichen communities linked to the increased forest disturbance. Holz and Gradstein (2005) found a similar pattern in montane forests in Costa Rica, while Nöske et al. (2008) found that the number of epiphytic lichen species increased in secondary forests, suggesting that the number of species along a disturbance gradient does not follow a uniform pattern over time and that community composition might provide a more sensitive indicator of the human impact than species richness.

In addition to the changes in microclimate caused by the more or less open canopy, the impoverishment of epiphytic macrolichens in more disturbed forests might be explained by several factors related to differences in forest structure among the three types of vegetation considered (Fritz et al., 2008; Aragón et al., 2010; Soto-Medina et al., 2011). First, the larger tree size in primary forests involves more bark surface, formation of age-related specialized substrates and longer periods for colonization (Fritz et al., 2008; Ranius et al., 2008; Johansson et al., 2009). Second, since the establishment of lichens is linked to bark roughness and pH (e.g., Coppins and Wolseley, 2002; Rosabal et al., 2010), the species richness will decrease in secondary forests where trees have rather smooth bark and are more architecturally uniform than in primary forests (Gradstein, 2008). However, this trend might be mitigated by the high species diversity in the tropics, by the great water availability or by the interactions between other epiphytic organisms (angiosperms, mosses and ferns) (Cáceres et al., 2007; Soto-Medina et al., 2011). Third, the presence of a dense bryophyte cover provides a suitable substrate for the establishment of the biggest and the most shade macrolichens (several species of *Lobaria* and *Sticta*) (Kranner et al., 2008; Belinchón et al., 2009).

Table 3. Results of pairwise PERMANOVA test between types of vegetation according to disturbance gradient to show dissimilarity (%, according to Bray-Curtis index) and level of significance.

Source	**Dissimilarity (%)**	***P***
PF vs SF	76.94	0.0006
PF vs MF	91.43	0.0007
SF vs MF	82.15	0.0007

Notes: PF: primary forests; SF: secondary forests; MF: monospecific forests of *Alnus acuminata*.

Table 4. Results of the SIMPER analyses

	CA			**CA**			**CA**		
Species	PF	SF	**CD**	PF	MF	**CD**	SF	MF	**CD**
Bulbothrix coronata				0.00	1.18	1.21	0.00	1.18	1.42
Coccocarpia palmicola	0.13	1.14	1.29						
Heterodermia aff. diademata				0.00	1.76	1.77	0.00	1.76	2.07
Heterodermia aff. galactophylla	0.00	2.11	1.96				2.11	0.22	2.42
Heterodermia galactophylla				0.00	1.03	1.05			
Heterodermia isidiophora	0.74	0.96	1.51	0.74	0.92	1.25	0.96	0.92	1.62
Heterodermia japonica	0.73	1.51	1.90	0.73	2.00	2.13	1.51	2.00	2.81
Heterodermia leucomela	0.90	1.15	1.54	0.90	2.38	2.09	1.15	2.38	2.67
Heterodermia spathulifera				0.00	3.30	3.10	0.48	3.30	3.56
Hypotrachyna revoluta	0.58	4.12	3.65	0.58	8.06	7.24	4.12	8.06	8.38
Hypotrachyna rocky				0.00	2.02	1.98	0.45	2.02	2.43
Leptogium azureum	1.64	3.00	3.50	1.64	0.31	1.69	3.00	0.31	3.44
Leptogium cochleatum	0.82	0.44	1.21						
Lobaria subdissecta	4.05	2.54	4.97	4.05	0.00	4.03	2.54	0.00	2.80
Parmeliella ecuadorense	0.38	0.90	1.23						
Parmotrema aff. exquisitum				0.00	1.28	1.33	0.29	1.28	1.69
Parmotrema aff. peralbidum	0.13	3.03	3.32				3.03	0.13	3.39

Parmotrema arnodii	1.60	4.13	4.92	1.60	0.28	1.67	4.13	0.28	4.69
Parmotrema rampoddense				0.45	6.39	6.14	0.40	6.39	7.07
Parmotrema zollongeri	0.00	1.67	1.92	0.00	1.41	1.22	1.67	1.41	2.64
Pseudocyphellaria aurata	0.51	0.86	1.21						
Punctelia aff. crispa	1.76	2.65	3.60	1.76	0.31	1.61	2.65	0.31	2.66
Punctelia aff. reddenda							0.62	1.09	1.50
Sticta aff. canariensis	13.47	3.21	14.05	13.47	0.00	11.66	3.21	0.00	3.26
Sticta andensis	2.13	0.38	2.11	2.13	0.00	1.98			
Sticta ferax	1.24	0.31	1.42						
Sticta humboltii	1.26	0.00	1.39	1.26	0.00	1.21			
Sticta laciniata	1.04	0.00	1.15	1.04	1.03	1.00			
Sticta tomentosa	11.16	4.83	10.56	11.16	0.00	10.28	4.83	0.00	5.40
Sticta sp.1	2.48	0.00	2.74	2.48	0.00	2.39			
Sticta sp.2	1.33	0.00	1.38	1.33	0.00	1.20			
Usnea sp. 1				0.36	7.19	6.23	0.80	7.19	7.08

Notes: CA: mean cover (%); CD: Contribution of each species to the dissimilarity (%).

Differences among management types are also corroborated by results on species composition. However, a large part of the variability in species composition is associated with forest, plot and trees, indicating that local factors contribute to shape lichen communities, independently by management regime. The differences between primary forests and the rest of the disturbed forests (SF and MP) were mainly attributed to the coverage of more shaded-adapted species (e.g., *Sticta* spp.). These species drastically reduced their presence and coverage with disturbance level. Similarly, Rivas Plata et al. (2008) showed that some genera of microlichens had preferences for undisturbed primary forests, fully shaded microhabitat and bark of mature trees. However, in the absence of shade lichens in drier habitats, the increased coverage by the more heliophytic lichens (e.g., *Heterodermia* spp., *Hypotrachyna* spp.) will be responsible for the dissimilarity.

The differences in species composition between the primary and secondary forests (SF and MF), which were not managed during the last 40 years since the last selective or total logging, might indicate that the epiphyte macrolichens had regenerated. Similarly, Gradstein (2008) found that the epiphytic composition in the natural forest was very different than in forests that had 50 years to recover, citing differences in the main variables that determine the response of the epiphytic organisms to habitat disturbance as possible causes: host tree characteristics, openness of the canopy and the microclimate in the forests (Gradstein, 2008; Nöske et al., 2008). In the same way, Holz and Gradstein (2005) suggested that at least 100 years are needed for the complete recovery of the floristic and community composition.

We therefore concluded that tropical forest disturbance significantly and drastically reduces macrolichen diversity. Disruption of the canopy leads to microclimatic changes that affect species richness of epiphytic macrolichens. Species loss is most severe for the “shade-adapted lichens” (included in Peltigerales) because in the disturbed habitats these epiphytes were not able to tolerate the high irradiation; therefore, these species may be useful indicators of forest conservation. In addition, change in the tree species composition and host tree characteristics play an important role. Actually, in this study there was evidence that in secondary forests lichen diversity of native forests was not regenerated; consequently, only the protection of remnants of primary tropical forest might help to preserve a rich and diverse community of epiphytic macrolichens.

Acknowledgments

Financial support for this study was received by the University Técnica Particular de Loja, Secretaria Nacional de Educación Superior, Ciencia, Tecnología e Innovación of Ecuador and the Ministerio de Ciencia e Innovación (proyect EPICON, CGL2010-22049) of Spain. We thank G. Cevallos for fieldwork help and C. Aguirre and A. Gonzaga, who kindly provided access to the study areas.

Appendix A

Number of trees on which each species appears in three types of vegetation according to a disturbance gradient. PF: primary forests, SF: secondary forests, MF: monospecific forests of *Alnus acuminate*

Taxa	**PF**	**SF**	**MF**
Lecanorales			
Alectoria ochroleuca (Hoffm.) A. Massal.	9*		
Anzia parasitica (Fée) Zahlbr.	4*		
Bryoria sp.	1*		
Bulbothrix apophysata (Hale & Kurok.) Hale			6*
Bulbothrix coronata (Fée) Hale			45*
Bulbothrix isidiza (Nyl.) Hale		16*	
Bulbothrix suffixa (Stirton) Hale		14*	
Canomaculina cristobalii (L.I.Ferraro & Elix) Elix		3	14
Canomaculina pilosa (Stizenb.) Elix & Hale	1	1	
Cladonia coniocraea (Flörke) Sprengel	7	13	
Cladonia subradiata (Vainio) S&st.	8	15	
Everniastrum cirrhatum (Fr.) Hale ex Sipman	7	2	
Everniastrum vexans (Zahlbr. ex W.L. Culb. & C.F.Culb.) Hale ex Sipman	5	4	2
Flavopunctelia flaventior (Stirt.) Hale			3*
Hypotrachyna aff. *degelii* (Hale) Hale	16	1	

Hypotrachyna bogotensis (Vain.) Hale	4*		
Hypotrachyna costaricensis (Nyl.) Hale	5	21	9
Hypotrachyna densirhizinata (Kurok.) Hale		6*	
Hypotrachyna eitenii (Hale) Hale			8*
Hypotrachyna rachista (Hale) Hale		4*	
Hypotrachyna revoluta (Flörke) Hale	14	46	64
Hypotrachyna reducens (Nyl.) Hale			9*
Hypotrachyna rockii (Zahlbr.) Hale		15	44
Hypotrachyna sp.			28*
Parmelinopsis miniarum (Vain.) Elix & Hale	5*		
Parmotrema aff. *exquisitum* (Kurok.) DePriest & B.W.Hale		8	31
Parmotrema aff. *peralbidum* (Hale) Hale	3	5	3
Parmotrema arnoldii (Du Rietz) Hale	27	55	8
Parmotrema austrosinense (Zahlbr.) Hale			9*
Parmotrema cristiferum (Taylor) Hale			17*
Parmotrema exquisitum (Kurok.) DePriest & B.W.Hale			12*
Parmotrema internexum (Nyl.) Hale ex DePriest & B.W. Hale.		9	9
Parmotrema mellisii (Dodge) Hale.	8*		
Parmotrema rampoddense (Nyl.) Hale	1	1	61
Parmotrema zollingeri (Hepp) Hale.		31	26
Punctelia aff. *crispa* Marcelli, Jungbluth & Elix	39	34	
Punctelia aff. *reddenda* (Stirt.) Krog		17	27
Ramalina celastri (Spreng.) Krog & Swinscow			26*
Ramalina cochlearis Zahlbr.	2		2
Ramalina peruviana Ach.			2*
Ramalina sp.		5	25
Relicina abstrusa (Vainio) Hale.	7*		
Rimelia subisidiosa (Müll. ARg.) Hale & A. Fletcher	2*		
Rimelia succinreticulata Eliasaro & Adler	5*		
Usnea sp. 1	16	3	65
Usnea sp. 2	1		17
Usnea sp. 3	3*		
Usnea sp. 4	2	1	
Peltigerales			
Coccocapia dissecta Swinscow & Krog	4*		
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	6	6	
Coccocarpia filiformis Arv.	4*		
Coccocarpia guimarana (Vain.) Swinscow & Krog	2*		
Coccocarpia microphyllina Lücking & Aptroot	7*		
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway	8	39	
Coccocarpia pellita (Ach.) Müll. Arg.	12*		
Coccocarpia prostrata Lücking, Aptroot & Sipman	7	5	
Coccocarpia sp.	22*		
Coccocarpia stellata Tuck.	12	16	21
Leioderma glabrum D. J. Galloway & P. M. Jørg.		13*	
Leptogium austroamericanum (Malme) C. W. Dodge	6	4	
Leptogium azureum (Sw.) Mont.	49	32	12
Leptogium burgesii (L.) Mont.	7	17	
Leptogium burnetii Dodge	6*		

Leptogium chloromelum (Ach.) Nyl.	2		5
Leptogium cochleatum (Dicks.) P.M. Jørg. & P. James	28	14	
Leptogium coralloideum (Meyen & Flot.) Vain.	2	3	22
Leptogium corticola (Taylor) Tuck.	9	7	
Leptogium cyanescens (Rabh.) Körb.	13*		
Leptogium diaphanum (Sw.) Nyl.	3*		
Leptogium laceroides B. de Lesd.	5	2	
Leptogium marginellum (Sw.) Gray	4*		
Leptogium millegranum Sierk	6*		
Leptogium olivaceum (Hook.) Zahlbr.		8*	
Leptogium phyllocarpum (Pers.) Mont.	17	1	
Lobaria dissecta (Sw.) Raeusch.	8*		
Lobaria erosa (Eschw.) Nyl.	3	4	
Lobaria subdissecta (Nyl.) Vain.	51	39	
Lobaria tenuis Vain.	1*		
Lobariella crenulata (Hook. in Kunth) Yoshim.	8	7	8
Lobariella exornata (Zahlbr.) Yoshim.	3*		
Lobariella pallida (Hook.) Yoshim.	6	7	
Pannaria conoplea (Ach.) Bory	9	24	
Pannaria mosenii C.W. Dodge	6*		
Pannaria prolificans Vain.	1*		
Parmeliella andina P. M. Jorg. & Sipman	22*		
Parmeliella delicata P. M. Jørg. & Arv.	23*		
Parmeliella miradorensis Vain.	13*		
Parmeliella sp.	17	31	
Peltigera sp.	1*		
Pseudocyphellaria aurata (Ach.) Vain.	2	3	23
Pseudocyphellaria crocata (L.) Vain.	1	3	
Sticta aff. *canariensis* (Ach.) Bory ex Delise	47	28	
Sticta andensis (Nyl.) Trevis.	14	11	
Sticta ferax Müll. Arg.	5	7	
Sticta fuliginosa (Dicks.) Ach.	7*		
Sticta humboltii Hook. f.	11*		
Sticta laciniata (Sw.) Ach.	12*		
Sticta tomentosa (Sw.) Ach.	61	51	
Sticta sp. 1	9*		
Sticta sp. 2	13*		
Caliciales			
Heterodermia aff. *diademata* (Taylor) D.D. Awasthi			54*
Heterodermia aff. *galactophylla* (Tuck.) W.L. Culb.		47	9
Heterodermia comosa (Eschw.) Follmann & Redón		1*	
Heterodermia corallophora (Taylor) Skorepa		9	11
Heterodermia galactophylla (Tuck.) W.L. Culb.		5	48
Heterodermia hypochraea (Vain.) Swinscow & Krog			9*
Heterodermia hypoleuca (Mühl.) Trevis.		2	25
Heterodermia isidiophora (Nyl.) D.D. Awasthi	25	28	32
Heterodermia japonica (M. Satô) Swinscow & Krog	23	39	46
Heterodermia leucomela (L.) Poelt	43	38	61
Heterodermia microphylla (Kurok.) Swins. & Krog	1*		
Heterodermia palpebrata (Taylor) Trass		2*	
Heterodermia sitchensis Goward & Noble		7*	
Heterodermia spathulifera Moberg & Purvis		15	54

Heterodermia subcitrina Moberg			3*
Heterodermia sp.	2	8*	
Phaeophyscia aff. *limbata* (Poelt) Kashiw.			12*
Teloschistales			
Teloschistes flavicans (Sw.) Norman			41*

References

Anderson MJ, Gorley RN, Clarke KR. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth, UK:PRIMER-E;2008.

Aragón G, Martínez I, García A. loss of epiphytic diversity along a latitudinal gradient in southern Europe. Sci Total Environ 2012;426:188–95.

Aragón G, Martínez I, Izquierdo P, Belinchón R, Escudero A. Effects of forestmanagement on epiphytic lichen diversity in Mediterranean forests. Appl Veg Sci 2010;13:183–94.

Asner GP, Knapp D, Broadbent E, Oliveira P, Keller M, Silva J. Selective logging in the Brazilian Amazon. Science 2005;310:480–482.

Barthlott W, Schmitt-Neuerburg V, Nieder J, Engwald S. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol 2001;152:145–156.

Barthlott W, Mutke J, Rafiqpoor MD, Kier G, Kreft H. Global centres of vascular plant diversity. Nova Act Lc 2005;342:61–83.

Belinchón R, Martínez I, Otálora MAG, Aragón G, Dimas J, Escudero A. Fragment quality and matrix affect epiphytic performance in a Mediterranean forest landscape. Am J Bot 2009;96:1974–1982.

Bergamini A, Scheidegger C, Stofer S, Carvalho P, Davey S, Dietrich M, et al. Performance of macrolichens and lichen genera as indicators of lichen species richness and composition. Conserv Biol 2005;19:1051–62.

Brown S, Lugo AE. Tropical secondary forests. J Trop Ecol 1990;6:1–32.

Bruijnzeel LA, Hamilton LS. Decision time for cloud forests. IHP Humid Tropical Programme Series 2000;13:1–40.

Brummit N, Nic Lughadha E. Biodiversity. Where’s hot and where’s not. Conserv Biol 2003;17:1442–1448.

Cáceres MS, Lücking R, Rambold G. Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycol Prog 2007;10:190–210.

Churchill SP, Balslev H, Forero E, Luteyn JL. Biodiversity and Conservation of Neotropical Montane Forests. New York: New York Botanical Garden; 1995.

Clarke KR, Warwick RM. Quantifying structural redundancy in ecological communities. Oecologia 1998;113:278–89.

Coppins BJ, Wolseley P. Lichens of tropical forests. In: Watling R, Frankland JC, Ainsworth AM, Isaac S, Robinson CH, editors. Tropical Mycology: Micromycetes. Wallingford: CABI Publishing; 2002. p. 113-131.

Fritz Ö, Niklasson M, Churski M. Tree age is a factor for the conservation of epiphytic lichens and bryophytes beech forest. Appl Veg Sci 2008;12:93–106.

Gentry AH. Patterns of diversity and floristic composition in neotropical montane forests. In: Churchill SP, Balslev H, Forero E, Luteyn J L, editors. Biodiversity and conservation of neotropical montane forests. New York: New York Botanical Garden Bronx; 1995. p. 103–126.

Gibbs HK, Reusch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA. Tropical forests were the primary sources of new agricultural lands in the 1980s and 1990s. Proc Nat Acad Sci 2010;107:16732–16737.

Gradstein SR, Nadkarni NM, Krömer T, Holz I, Nöske N. A protocol for rapid and representative sampling of epiphyte diversity of tropical rain forests. Selbyana 2003;24:87–93.

Gradstein SR. Epiphytes of tropical montane forests—impact of deforestation and climate change. In: Gradstein SR, Homeier J, Gansert, D, editors. The tropical mountain forest. Patterns and Processes in a Biodiversity Hotspot. Göttingen: University Press; 2008. p. 51–65.

Green TGA, Nash III TH, Lange OL. Physiological ecology of carbon dioxide exchange, In: Nash III, TH, editor. Lichen Biology. Cambridge: Cambridge University Press UK; 2008. p. 152–81.

Henderson A, Churchill SP, Luteyn JL. Neotropical plant diversity. Nature 1991;351:21–22.

Hietz P. Diversity and conservation of epiphytes in a changing environment. Pure Appl Chem 1998;70:2114–2125.

Hietz P, Buchberger G, Winkler M. Effect of forest disturbance on abundance and distribution of epiphytic bromeliads and orchids. Ecotropica 2006;12:103–112.

Holz I. Diversity and Ecology of Bryophytes and Macrolichens in Primary and Secondary Montane Quercus Forests, Cordillera de Talamanca, Costa Rica. Dissertation. Universität Göttingen; 2003.

Holz I, Gradstein SR. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica, species richness, community composition and ecology. Plant Ecol 2005;178:89–109.

Johansson V, Bergman KO, Lättman H, Milberg P. Tree and site quality preferences of six epiphytic lichens growing on oaks in southeastern Sweden. Ann Bot Fenn 2009;46:496–506.

Jovan S, McCune B. Regional variation in epiphytic macrolichen communities in northern and central California forest. Bryologist 2004;104:328–339.

Kappelle M, Kennis PAF, Vries RAJ. Changes in diversity along a successional gradient in a Costa Rica upper montane Quercus forest. J Trop Ecol 1995;12:681–698.

Kranner I, Beckett R, Hochman A, Nash TH III. Desiccation-Tolerance in Lichens: A Review. Bryologist 2008;111:576–593.

Lange O, Büdel A, Meyer A, Kilian E. Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. Lichenologist 1993;25:175–189.

Lange OL, Burkhard B, Meyer A, Zellner H, Zotz G. Lichen carbon gain under tropical conditions: water realtions and CO_2 exchange of Lobariaceae species of a lower montane rainforest in Panama. Lichenologist 2004;36:329–342.

Laurance WF, Peres CA. Emerging Threats to Tropical Forests. Chicago: Chicago University Press; 2006.

Mandl N, Lehnert M, Kessler M, Gradstein SR. A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. Biodivers Conserv 2010;19:2359–2369.

Marini L, Nascimbene J, Nimis PL. Large-scale patterns of species richness of epiphytic lichens: exploring the role of human, climate, and forest structure. Sci Total Environ 2011;409:4381–4386.

Nadkarni NM, Merwin MC, Nieder J. Forest canopies: plant diversity. In: Levin S, editor. Encyclopedia of Biodiversity. San Diego California USA: Academic Press; 2001. p. 27-40.

Nascimbene J, Marini L, Nimis PL. Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. Forest Ecol Manag 2007;247:43–7.

Nöske N, Hilt N, Werner FA, Brehm G, Fiedler K, Sipman HJ, Gradstein SR. Disturbance effects on diversity of epiphytes and moths in a montane forest of Ecuador. Basic Appl Ecol 2008;9:4–12.

Ranius T, Johansson P, Berg N, Niklasson M. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. J Veg Sci 2008;19:653–662.

Rivas Plata E, Lücking R, Lumbsch HT. When family matters: na analysis of Thelotremataceae (Lichenized Ascomycota: Ostropales) a bioindicators of ecological continuity in tropical forests. Biovivers Conserv 2008;17:1319-51.

Rosabal D, Burgaz AR, De la Masa R. Diversity and distribution of epiphytic macroliches on tree trunks in two slopes of the montane rainforest of Gran Piedra, Santiago de Cuba. Bryologist 2010;113:313–321.

Sipman HJM, Harris RC. Lichens. In: Lieth H, Werger MJA, editors. Tropical Rain Forest Ecosystems. Amsterdam: Elsevier; 1989. p. 303–309.

Soto-Medina E, Lücking R, Bolaños-Rojas A. Especificidad de forófito y preferencias microambientales de los líquenes cortícolas en cinco especies de forófitos en el bosque premontano de la finca Zíngara (Cali, Colombia). Rev Biol Trop 2011;59(4).

Verbeke G, Molenberghs G. Linear mixed models in practice. A SAS-oriented approach. Springer, New York; 1997.

Werth S, Tømmervik H, Elvebakk A. Epiphytic macrolichen communities along regional gradients in northern Norway. J Veg Sci 2005;16:199–208.

Wolf JHD. The response of epiphytes to anthropogenic disturbance of pine oak forests in the highlands of Chiapas, Mexico. Forest Ecol Manag 2005;212:376–393.

Wright SJ. Tropical forests in a changing environment. Trends Ecol Evol 2005;20:553–560.

CAPÍTULO II / CHAPTER II

Large trees and dense canopies: key factorsformaintaininghigh epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests

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Benítez, Á., Prieto, M., & Aragón, G. (2015).
***Forestry*, 88, 521–527.**

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Abstract

The high richness of epiphytes in moist tropical montane forests is continuously decreasing due to deforestation and habitat loss. Lichens and bryophytes are important components of epiphyte diversity on trunk bases and play an important role in the water balance and nutrient cycling of tropical montane forests. As lichens and bryophytes are very sensitive to microclimatic changes, we hypothesized that their species richness and composition would change with forest alteration. We also expected their response patterns to be different given the capability of lichens to photosynthetize using water vapour. In this study, we assessed the richness and composition of epiphytes (lichens and bryophytes) on the trunk bases of 240 trees in primary and secondary forests of southern Ecuador. We found that diversity was higher in primary forests and lower in monospecific secondary forest stands. Total diversity was negatively affected by habitat loss and by the reduction of canopy cover for bryophytes. Shade epiphytes were replaced by sun epiphytes in open secondary forests. We conclude that lichen and bryophyte diversity of tropical montane forests are negatively affected by the removal of large trees and canopy disruption. The different species compositions of primary and secondary forests and the high number of species exclusive to primary forests indicate that secondary forests are of limited importance in compensating for the loss of non-vascular epiphyte species associated with primary forests.

Keywords: non-vascular epiphytic communities, lichens, bryophytes, logging, secondary forests, tropical montane forest, Ecuador

Introduction

Neotropical montane rain forests are considered "hot spots" of global biodiversity and are a high conservation priority (Gentry, 1995; Myers *et al*., 2000; Dirzo and Raven, 2003). Epiphytes constitute an important floristic, structural and functional component in these forests (Barthlott *et al.*, 2001; Gradstein, 2008; Köster *et al*., 2009); however, this exceptional diversity is threatened by continued deforestation and habitat loss (Churchill *et al.*, 1995; Bruijnzeel and Hamilton, 2000; Gibbs *et al*., 2010). Forest conversion produces changes which directly influence epiphyte diversity: abiotic conditions are altered, habitat complexity (i.e. tree size, tree species and canopy structure) is reduced, and dispersal is constrained (Werner *et al*., 2005, 2011; Hietz *et al*., 2006). In fact, several authors have found a loss of epiphytic diversity (including vascular plants, bryophytes and lichens) in secondary forests and a higher diversity in primary forests (Barthlott *et al*., 2001; Acebey *et al*., 2003; Krömer and Gradstein 2003; Wolf, 2005; Gradstein 2008; Gradstein and Sporn, 2010).

Non-vascular epiphytes (i.e. bryophytes and lichens) constitute an important fraction of epiphytic organisms in tropical montane forests in terms of diversity, biomass and nutrient cycling (Pócs, 1982; Sipman, 1995; Holz and Gradstein, 2005; Mandl *et al*., 2010; Gehrig-Downie *et al*., 2011). Due to their poikilohydric nature, these organisms are tolerant to desiccation (Pardow and Lakatos, 2013), even though their degree of desiccation tolerance varies greatly among species (Proctor *et al*., 2007; Kranner *et al*., 2008). In particular, lichens and bryophytes in humid sites in tropical forests, mainly the forest understory and inner parts of the canopy, are highly sensitive to desiccation (Kranner *et al*., 2008; Pardow and Lakatos, 2013) and may experience photoinhibition when exposed to a small rise in solar radiation (Sillett and Antoine, 2004; Green *et al*., 2008; Pardow and Lakatos, 2013). As the physiology of these organisms is strongly linked to ambient moisture, solar radiation and temperature (Gignac, 2001; Sillett and Antoine, 2004; Green *et al*., 2008), forest logging and land use may greatly affect the diversity of non-vascular epiphytic communities.

The canopy disruption caused by forest logging can affect the humidity, temperature, and light conditions inside forests, making them unsuitable sites for shade-adapted species (Gradstein, 2008; Gradstein and Sporn, 2010; Norman *et al*., 2010; Benítez *et al*., 2012). Open forests are generally drier, warmer and windier compared to closed forests, where moisture content is higher and less variable (Gradstein, 2008). However, these microclimate changes do not necessarily involve a decrease in species richness, but rather a replacement in community composition (Holz and Gradstein, 2005; Nöske *et al.*, 2008). The more shade-adapted lichens and bryophytes that are intolerant to desiccation are often replaced by heliophytic species (Ariyanti *et al*., 2008; Gradstein, 2008; Gradstein and Sporn, 2010; Benítez *et al*., 2012).

Forest logging may also have immediate negative effects on the persistence of bryophytes and lichens due to the removal of host tree species (Gradstein, 2008). Host tree characteristics, especially tree size, play an important role in lichen and bryophyte colonization (Benítez *et al*., 2012; Rosabal *et al.*, 2013), probably due to greater bark surface available for colonization on large trees and the creation of additional microhabitats (Fritz *et al*., 2008; Ranius *et al*., 2008). Epiphytic diversity may also be influenced by bark roughness, humus and moss cover on the bark surface, stochastic effects of species dispersion, and to lesser extent, bark pH (Sipman and Harris, 1989; Cáceres *et al.*, 2007; Gradstein and Culmsee, 2010; Soto *et al*., 2012).

As a result of human activities in Ecuador, primary forests have often been replaced by secondary vegetation, creating forests with a less developed canopy structure, smaller trees, and less tree diversity. Benítez *et al*. (2012) found that the diversity of "shade epiphytes" decreased drastically as a result of such forest disturbance. This could be due to the high percentage of the macrolichen species belonging to the order Peltigerales (ca. 50%), as these species are adapted to within forest conditions, have high water demands and are sensitive to high solar radiation. However, as macrolichens represent less than one-third of all poikilohydric epiphytic species in tropical montane forests, these results should be interpreted with caution when considering epiphytic communities as a whole (bryophytes and lichens). Knowledge of the differences in epiphytic diversity in primary and secondary forests is crucial to evaluate the conservation status of these forests and to design conservation strategies.

The goal of this study was to explore the response of the non-vascular epiphytic community to forest logging in tropical montane rain forests. We hypothesized that differences in species diversity and community composition would be related to differences in forest structure and microclimate caused by the intensity of forest logging. Another objective was to compare the response patterns between bryophytes and lichens, as lichens prefer relatively high light levels (excluding some cyanolichens) (Sillett and Antoine, 2004; Green *et al*., 2008; Normann *et al.*, 2010) and are generally less negatively affected by drought than bryophytes (Perhans *et al*., 2009).

Materials and methods

Study area

This study was carried out at two sites in southern Ecuador and included six remnants of tropical montane forests along a disturbance gradient (Table 1). The climate is humid tropical with a mean annual temperature of 20°C, an annual rainfall of approximately 1900 mm and a relative humidity of approximately 80% (National Institute of Meteorology and Hydrology, INAMI). The altitude of the studied plots ranged from 2200 to 2800 m a.s.l.

Field work was carried out in three types of forest vegetation varying in age, species composition and tree cover: (1) Remnant primary forest fragments (PF) of evergreen tropical montane forests characterized by a dense canopy layer (ca. 75-85% cover) and large trees (35-40 m tall). The main canopy trees were *Cinchona macrocalyx* Pav. ex DC., *Clusia elliptica* Kunth, *Myrica pubescens* Humb. & Bonpl. ex Willd., *Podocarpus oleifolius* D. Don ex Lamb. and *Weinmannia pubescens* Kunth. (2) Secondary mixed forest fragments (SF) regrown after selective logging events which took place ca. 40 years earlier (Brown and Lugo, 1990; Holz, 2003). Canopy cover was ca. 60-70%, and the main canopy trees were *Melastomataceae* and *Lauraceae* species (25-30 m tall). (3) Secondary monospecific forests of *Alnus acuminata* Kunth (MF; 35-40 y old) regrown by natural regeneration after forest clearing (Hofstede and Aguirre, 1999). This tree is a pioneer and native species of the Andes. Monospecific forests are characterized by their uniform structure, absence of understory plants, approximately 50% canopy cover and trees up to 20 m tall. Logging and firewood extraction were the main contemporary human activities in MF, while there were no human activities in PF and SF.

Species identification

For species identification we used more than 200 taxonomic and floristic papers (e.g. Gradstein *et al.,* 2001; Gradstein and Costa, 2003; Frisch *et al.*, 2006; Cáceres, 2007; Aptroot *et al.*, 2008; Timdal, 2008; Lücking, 2009; Moncada *et al.*, 2013). For species nomenclature we followed mainly Tropicos.org for bryophytes and MycoBank for lichens.

Experimental design

We sampled two stands of each forest type (PF, SF and MF). We established ten 5×5 m plots in each stand for a total of 60 plots. The distance between the plots in each forest stand was >50 m. In each plot, epiphytic lichens and bryophytes were sampled on the bases of 4 mature trees (240 trees total) using 20 × 30 cm grids. Samples were taken on each tree at three different heights (0–50, 51–150, 151–200 cm) on the northern and southern exposure for a total of six samples per tree. Species richness was defined as the total number of species found in each plot. For epiphytic composition, we estimated the mean cover of each species (% of grid area) per tree and per plot (as the percentage of four trees). We also measured the following variables at the plot level: canopy cover (%), elevation (m a.s.l.), slope (º), aspect (cosine transformed) and mean tree DBH (cm) of the 4 trees analyzed per plot as a proxy for stand structure.

Table 1 Means of the environmental variables in the studied primary and secondary montane forests (2 stands of each forest type) in Ecuador. PF, primary forest; SF, mixed secondary forest; MF, monospecific secondary forest of *Alnus acuminata*.

Forest	Location	Canopy cover (%)	Tree diameter (cm)	Elevation (masl)	Slope (º)	Aspect
PF1	4°33’27”S, 79°22’9”W	78.0	33.1	2848	26.6	E-SW
PF2	4°33’54”S, 79°22’13”W	76.5	34.4	2586	32.8	SW-N
SF1	4°3’9”S, 79°9’55”W	67.5	28.2	2688	38.2	NW-NE
SF2	4°33’35”S, 79°23’21”W	66.0	26.5	2393	32.6	E-SW
MF1	4°2’36”S, 79°10’20”W	51.5	16.2	2377	26.4	E-SW
MF2	3°59’53”S, 79°10’46”W	54.0	19.6	2196	18.1	NE-SW

Data analyses

Richness and diversity

We determined the effect of the environmental variables (canopy cover, mean DBH, elevation, aspect and slope) on the following community traits: total species richness, lichen richness, bryophyte richness and species diversity (Simpson inverse and Shannon indices). The Simpson and Shannon indices allow data on species richness and relative abundance to be combined (Gorelick, 2006). The Simpson index was determined by the predominant species, and the Shannon index was based on the assumption that individuals were randomly selected and that all species were represented in the sample (Magurran, 2004). Although host trees have a great influence on epiphyte diversity in temperate regions, the effect of host tree was not explored, as host-specificity does not seem to play an important role in tropical forests with a relatively high diversity of tree species (Sipman & Harris, 1989; Cáceres *et al*., 2007; Rosabal *et al*., 2013).

The effects of slope, aspect, elevation, canopy cover and mean tree diameter on species richness, the Shannon index and Simpson inverse index were analyzed at the plot level using generalized linear mixed models (GLMMs) (McCullagh and Nelder, 1989; Verbeke and Molenberghs, 1997). Because forest stands were quite far apart (Benítez *et al*., 2012), stand distance was initially included in the models, but it was later removed as no significant differences were detected. Predictors were included as explanatory variables (fixed factors), and forest and plot were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. We fitted the mixed models using a normal distribution with an “identity” link function. All GLMM computations were performed using SAS (GLIMMIX ver. 8 for SAS/STAT).

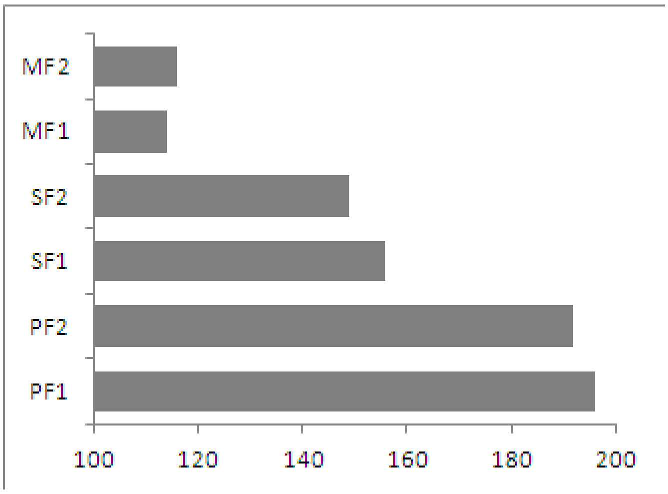

Figure 1 Species richness of epiphytic lichens and bryophytes in primary and secondary montane forests in Ecuador. PF, primary forest; SF, Mixed secondary forest; MF, monospecific secondary forest of *Alnus acuminata*. Axis X, epiphytic species richness; Axis Y, forest types.

We measured total species richness, lichen richness and bryophyte richness at the forest level, as the total species identified on 40 trees in each forest. Sampling completeness at the forest level was estimated with *Chao2* species richness estimator, using EstimateS 9.1.0 (Colwell, 2013).

Species composition and community structure

Non-metric multidimensional scaling (NMDS) ordination was performed to detect the main factors influencing epiphytic composition. NMDS analyses were carried out using CRAN software R (R Core Team 2013) with vegan package (Oksanen *et al*., 2013). For the NMDS analyses, the Bray-Curtis distance was used, as it is one of the most effective measures for community data (McCune *et al*., 2002). The coefficients of determination (r^2) for the predictor variables were calculated with ordination axes to interpret the relationships between the variables and community composition (1000 permutations).

Bray-Curtis dissimilarity between plots within a forest was calculated as a measure of species replacement. A pairwise PERMANOVA test using Bray-Curtis distance was also performed to assess species similarity among the three types of forest vegetation. Statistical analysis was performed using version 6.1.11 of PRIMER multivariate statistical analysis software (Anderson *et al*., 2008), allowing 9999 random permutations under the reduced model.

Results

Richness and diversity

A total of 374 epiphytic species (307 lichens, 67 bryophytes) were collected in the 60 plots (Supplementary data). The highest number of species was observed in primary forests (PF) with 234 species, followed by secondary mixed forests (SF) with 191 species and monospecific secondary forests with 134 species (Figure 1; Table 2). A similar pattern was observed for the richness estimator (*Chao* 2), confirming the occurrence of the highest species richness in PF (Table 2). Fifty-four species were exclusive to PF, exceeding the number of species exclusive to SF (Supplementary data). Species replacement (as a measure of dissimilarity) was also higher in PF for both lichens and bryophytes (Table 2). Analysis of environmental variables showed that tree diameter was the most relevant predictor of species richness at the plot level

(Table 3). Canopy cover had a significant effect on bryophyte richness. The random variable forest was non-significant in all cases.

Table 2 Species richness and dissimilarity of bryophytes and lichens at the forest level. Chao2 estimates of total richness are shown in brackets. SE: standard error. PF, primary forest; SF, Mixed secondary forest; MF, monospecific secondary forest of *Alnus acuminata*.

	Bryophytes		**Lichens**	
	Observed species (*Chao 2*; *SE*)	Bray Curtis Dissimilarity (%)	Observed species (*Chao 2*; *SE*)	Bray Curtis Dissimilarity (%)
PF1	44 (46; 3.42)	70.79	152 (173; 9.25)	76.53
PF2	42 (44; 2.53)	72.51	150 (157; 5.16)	73.26
SF1	35 (36; 1.17)	67.83	121 (128; 5.05)	68.79
SF2	31 (32; 2.13)	69.22	118 (132; 7.71)	67.41
MF1	23 (23: 0.04)	58.04	91 (93: 2.06)	57.85
MF2	26 (27; 2.04)	49.8	86 (92; 3.86)	59.34

Table 3 Results of the Generalized Mixed Linear Models on community traits at the plot level including beta coefficients (Coef) and associated standard errors (SE).

Plot level	Coef. (SE)	*F*-value	*P*-value
Total Richness			
Mean tree diameter	0.009(0.002)	14.46	**0.001**
Canopy cover	0.002(0.002)	1.45	0.235
Elevation	0.032(0.016)	3.95	0.054
Slope	<-0.001(0.001)	0.09	0.771
Aspect	<0.001 (0.000)	2.04	0.179
Bryophytes Richness			
Mean tree diameter	0.208(0.070)	8.74	**0.005**
Canopy cover	0.146(0.062)	5.62	**0.021**
Elevation	0.121(0.501)	0.06	0.811
Slope	0.018(0.027)	0.42	0.522
Aspect	0.002(0.004)	0.30	0.591
Lichen Richness			
Mean tree diameter	0.430(0.137)	9.88	**0.003**
Canopy cover	-0.039(0.113)	0.12	0.732
Elevation	0.061(0.053)	3.60	0.052
Slope	-0.019(0.051)	0.13	0.721
Aspect	0.005(0.004)	1.63	0.207
Shannon index			
Mean tree diameter	0.017(0.006)	7.54	**0.008**
Canopy cover	<-0.001(0.005)	0.01	0.934
Elevation	0.046(0.042)	1.17	0.285
Slope	<0.001(0.002)	0.02	0.901
Aspect	<-0.001(0.000)	0.01	0.922
Simpson inverse index			
Mean tree diameter	0.445(0.173)	6.60	**0.013**
Canopy cover	0.008(0.151)	0.01	0.957
Elevation	1.252(1.230)	1.04	0.313

Slope	0.027(0.067)	0.16	0.690
Aspect	-0.007(0.008)	0.73	0.406

Species composition and community structure

NMDS ordination resulted in a two-dimensional pattern with an average stress of 13.22 and showed a clear separation of the three different forest types. Most of the variability was explained by axis 1 (r^2=0.69), followed by axis 2 (r^2=0.12, Fig. 2). Axis 1 was associated with changes in canopy cover (Axis 1=-0.926, Axes 2=+0.378, r^2=0.712, p=0.001) and tree diameter (Axis 1=-0.8333, Axis 3=+0.553, r^2=0.539, p=0.001). The pairwise test revealed significant differences in epiphytic composition between the three types of forest vegetation: PF vs SF (66.40% dissimilarity, *p*=0.025), SF vs MF (75.00% diss., *p*=0.034) and PF vs MF (84.18% diss., *p*=0.015). *Herbertus divergens*, *Coccocarpia filiformis*, *C. pellita*, *Coenogonium eximium* and *Cryptothecia exilis* correlated with a dense canopy and large trees as found in PF, whereas *Frullania brasiliensis*, *F. gibbosa*, *Metzgeria lechleri*, *Graphis anfractuosa*, *G. cinerea*, *Heterodermia diademata* and *H. hypochraea* correlated with a more open canopy and smaller trees, characteristic of SF and MF (Supplementary data).

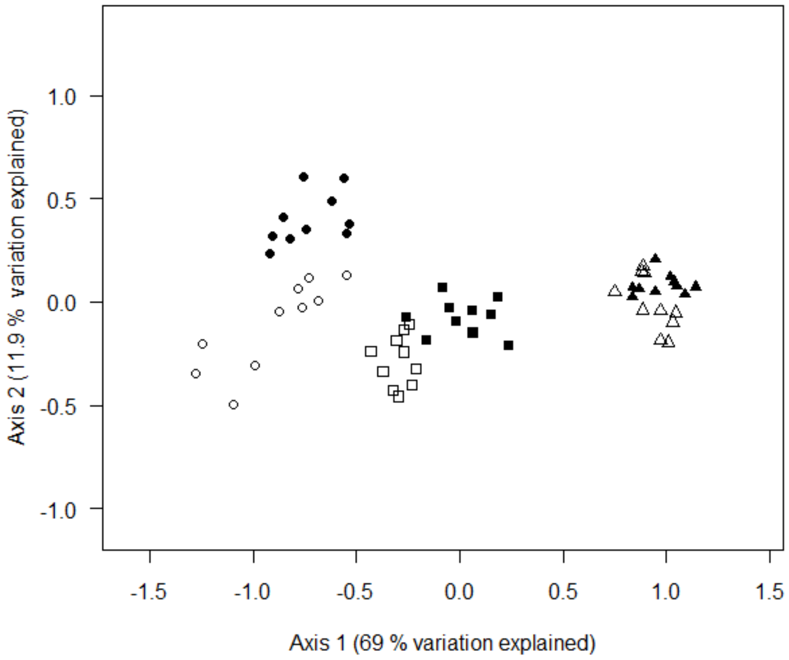

Figure 2 Non-metric multidimensional scaling (NMDS) analysis of species composition for the samples (plots) in the studied primary and secondary montane forests (2 stands of each forest type) in Ecuador. PF, primary forest (circle); SF, Mixed secondary forest (square); MF, monospecific secondary forest of *Alnus acuminate* (triangle).

Discussion

Our results showed significant changes in non-vascular epiphytic diversity (lichens and bryophytes) related to forest alteration in montane tropical forests. Major shifts in species diversity were caused by changes in canopy cover and tree size. Thus, epiphytic diversity was higher in primary forests (PF) than in the forests with more altered vegetation. In these two forest types, diversity was higher in mixed (SF) than in monospecific (MF) secondary forests. These results are consistent with other studies on epiphyte diversity in tropical montane forests (e.g. Acebey *et al*., 2003; Wolf, 2005; Werner and Gradstein, 2009) and support the notion that forest alteration leads to species loss in these communities. These data further indicate that species loss is related to the degree of forest alteration (i.e. selective logging, clear-cut, plantation) (Ariyanti *et al.*, 2008; Sporn *et al.*, 2009; Gradstein and Sporn, 2010) and the time since disturbance (Holz and Gradstein, 2005; Gradstein, 2008). As at least one hundred years are needed for the complete recovery of epiphyte diversity in montane forests (Holz and Gradstein, 2005), the maintenance of primary forests is crucial in the conservation of tropical rain forest biodiversity (Gibson *et al*., 2011).

We also found that lichens and bryophytes responded differently to forest disturbance. Species loss in lichens mainly correlated with reduced tree size, while species loss in bryophytes was also significantly related to climatic changes (i.e. increase in solar radiation, decrease in air humidity) induced by lower canopy cover in SF and MF. A high, dense canopy promotes optimal climatic conditions inside forests for the growth of shade epiphytes which have higher water demands and are very sensitive to solar radiation (Sillett and Antoine, 2004; Gradstein, 2008; Benítez *et al*., 2012; Pardow and Lakatos, 2013). The irradiation in closed forests is converted into heat at the interface of the atmosphere and the canopy, maintaining moist and cool conditions in the forest understory (Hohnwald, 1999, cited in Werner and Gradstein, 2009). Canopy disruption caused by selective logging produces small openings in the canopy (5-10%), which can significantly affect ambient moisture (Zimmerman and Kormos, 2012) and lead to a decrease in the diversity of shade epiphytes, adapted to the moist, shaded interior of the forest (Sipman and Harris, 1989; Acebey *et al*., 2003; Gradstein, 2008; Gradstein and Sporn, 2010). However, while bryophytes experienced species loss due to high irradiation and evaporation stress in more open habitats (Perhans *et al*., 2009), total lichen richness was not reduced by these factors. This may be because some of the more shade-adapted species (shade epiphytes) were replaced by light-demanding species (sun epiphytes) especially in MF where canopy openness was the highest (ca.

50%). Thus, open secondary montane forests can support a high richness of epiphytic lichens, even though there are fewer shade epiphytes (Hietz *et al*., 2006; Nöske *et al*., 2008).

Species composition of both bryophytes and lichens was severely altered by the increase in canopy openness, indicating that community composition is a more sensitive indicator of human impact than species richness (Nöske *et al.*, 2008). In general, shade epiphytes are more sensitive to environmental changes, because they are strongly dependent on atmospheric moisture and experience photoinhibition when exposed to greater sunlight than in their normal environment (Gauslaa *et al*., 2001; Green *et al*., 2008; Kranner *et al*., 2008). Ariyanti *et al*. (2008) found that microclimatic changes related to the loss of shaded cover were responsible for shifts in bryophyte composition. In our study, differences in species composition between the three forest types were particularly noticeable in the higher number of species of the liverwort genus *Plagiochila* and the lichen genera *Coccocarpia*, *Coenogonium*, *Herpothallon*, *Leptogium* and *Sticta* in primary forests versus species of the lichen genera *Graphis, Heterodermia* or *Parmotrema* in secondary forests. Biological characteristics of lichens exclusive to primary forests are the predominance of the photobiont with a reduction of the mycobiont (*Coenogonium*) or the presence of cyanobacteria as photobionts, constituting the so-called “cyanolichens” (*Leptogium*, *Coccocarpia*, *Sticta*) (Green *et al*., 2008; Benítez *et al*., 2012). However, some cyanolichen species (e.g. *Coccocarpia stellata*, *Leptogium azureum*, *L. chloromelum*, *Sticta weigelii*) may also occur in open, relatively dry habitats (Normann *et al.*, 2010; Rosabal *et al.*, 2010). In this sense, and focusing on these cyanolichens, we observed a contrasted vertical and horizontal zonation along the trunks. In the drier and more open sites along our gradient (*Alnus acuminata* forests), these species were more common on tree bases (below 50 cm) and on northern exposures where light incidence was lower. However, these species in primary forests were located at higher elevations (151-200 cm) on both exposures (north and south).

One of the major problems faced by tropical forests is the harvesting of large, long-lived and slow-growing trees (Zimmerman and Kormos, 2012), as they have the greatest bark surface area and the greatest formation of specialized aged bark substrates (e.g. Fritz *et al*., 2008; Johansson *et al*., 2009; Király *et al*., 2013). We suggest that these features, which are absent on younger, smaller trees, are preferred by epiphyte species, which might explain the high species replacement (measured as dissimilarity) between PF and MF.

Conclusion

Species diversity of non-vascular epiphytes (lichens and bryophytes) growing on the trunk bases of tropical montane forests is negatively affected by forest alteration in two ways: (1) removal of hosts, especially large trees and (2) environmental changes caused by canopy disruption. Opposite to Dent and Wright (2009), who pointed the importance of secondary forests in terms of supporting tropical biodiversity, our analyses showed different species composition of primary and secondary forests and a high number of species found exclusively in primary forests, thus suggesting that secondary forests are of limited importance in compensating for the loss of epiphytic species in primary forests. Although this study contributes to the knowledge of these organisms and their dynamics in tropical ecosystems, we should consider the constraints related to the number of replicates per forest type. Since the response of lichens and bryophytes to new environmental conditions caused by the increase in canopy openness is related to their morphological and anatomical characteristics (e.g. growth form, thallus thickness, type of photobiont, cortical pigments), more studies on the functional traits of epiphytes are needed to better understand their response to forest disturbance.

Supplementarydata: Number of trees on which each species appears in the six forests. Primary forests (PF1 and PF2); Mixed secondary forest (SF1 and SF2); Monospecific secondary forest of *Alnus acuminata* (MF1 and MF2). *: The species only occurs in one forest. Axis coordinates from each species (NMDS).

Taxa	PF1	PF2	SF1	SF2	MF1	MF2	AXIS 1	AXIS 2
Bryophytes								
Adelanthus decipiens (Hook.) Mitt.	12	6	4	3	4	2	-0,8806	-0,1233
Adelothecium bogotense (Hampe) Mitt.			6*				-0,6396	-1,2754
Anoplolejeunea conferta (C. F. W. Meissn. *ex* Spreng.) A. Evans	1	9	6	17	12	14	0,5922	0,1117
Bazzania falcata (Lindenb.) Trevis.			1*				-0,3388	-1,1763
Bazzania longistipula (Lindenb.) Trevis.		1*					-1,2057	1,3783
Campylopus asperifolius Mitt.	1	1		1			-0,5886	-1,111
Cheilolejeunea aff. *inflexa* (Hampe *ex* Lehm. & Lindenb.) Grolle			3*				-0,9523	0,3445
Cheilolejeunea rigidula (Mont.) R .M. Schust.	9	1	6		19	27	1,0725	0,1309
Cryphaea sp.						9*	1,636	0,26
Diplasiolejeunea pauckertii Steph.	4	26			2		-1,2192	0,7959
Drepanolejeunea granatensis (J.B. Jack & Steph.) Bischl.	11	3	1	18			-0,4291	-0,3909

Frullania apiculata (Reinw., Blume & Nees) Dumort.				1*			0,0123	-0,2796
Frullania brasiliensis Raddi					35	4	1,4713	0,3144
Frullania convoluta Lindenb. & Hampe	31	17					-1,2687	0,26
Frullania ericoides (Nees) Mont.					5	6	1,3659	0,1361
Frullania gibbosa Nees					28	32	1,5766	0,1331
Frullania kunzei Lehm. & Lindenb.	5	17	5	23			-0,3944	0,0513
Frullania aff. *convoluta* Lindenb. & Hampe		2*					-1,1658	1,0656
Frullania sp.	3	2		2			-0,3785	0,2191
Groutiella apiculata (Hook.) H.A. Crum & Steere	3	1					-1,6131	-0,0775
Herbertus divergens (Steph.) Herzog	4	2					-1,453	0,116
Lejeunea laetevirens Nees & Mont.	16	14	22	8			-0,6847	-1,4407
Lejeunea cerina (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees			3*				-1,024	-0,1167
Lepicolea pruinosa (Taylor) Spruce			4*				-0,4618	-1,1732
Lepidozia incurvata Lindenb.	1*						-1,6345	-0,6363
Lepidozia sp.					6	4	1,5034	-0,2125
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) A. Evans					3	3	1,5313	-0,1618
Leptotheca boliviana Herzog	8*						-1,0157	0,2777
Leucobryum antillarum Schimp. *ex* Besch.	2	1					-1,5925	-0,1864
Lophocolea bidentata (L.) Dumort.		1				1	0,0118	0,8879
Lophocolea muricata (Lehm.) Nees	2	2	14				-0,7531	-0,5369
Macromitrium podocarpi Müll. Hal.	5	17	4	3	7	13	-0,0082	-0,2191
Macromitrium sp.					7	4	1,5799	0,0269
Marchesinia brachiata (Sw.) Schiffner	2	3			8	1	-0,3575	-0,0858
Mastigolejeunea auriculata (Wils. & Hook.) Schiffn*..*					3	1	1,4547	0,3706
Metzgeria lechleri Steph.					17	12	1,5485	0,2301
Metzgeria consanguinea Schiffner			3*				-0,5035	-0,8275
Metzgeria leptoneura Spruce	13	18					-1,2511	0,7176
Metzgeria polytricha Spruce	3	1	3	24			-0,4642	-0,2919
Metzgeria sp.	1*						-1,184	0,1744
Microlejeunea bullata (Taylor) Steph.	3	4	6	7	5	2	0,0726	-0,3778
Neckera scabridens Müll. Hal.	8	6	9	9	2		-0,6236	-0,321
Omphalanthus filiformis (Sw.) Nees	6	5	3		3	2	-0,4513	0,2517
Plagiochila aerea Taylor	16	8	3	1			-0,6786	-0,6061
Plagiochila bifaria (Sw.) Lindenb.	1	7	8	6	8	2	-0,5775	0,1657
Plagiochila bryopterioides Spruce	17	1	17	1	13	5	-0,3885	-0,356
Plagiochila cristata (Sw.) Dumort			5*				-0,4141	-1,0033
Plagiochila diversifolia Lindenb. & Gottsche	4	3	21	4			-0,5598	-0,841
Plagiochila longispina Lindenb. & Gottsche			6*				-0,547	-1,2991
Plagiochila pachyloma Taylor	4	2					-1,5531	-0,4221
Plagiochila raddiana Lindenb.	2	13	22	5	1		-0,8582	-0,1441
Plagiochila sp.	9*						-1,6774	-0,318
Porella brachiata (Taylor) Spruce	5	3			3		-0,9673	0,2635
Porella swartziana (F. Weber) Trev.	1	6	11				-0,7335	-0,4148

Porotrichodendron superbum (Taylor) Broth.	24	13	31	7			-0,5923	-0,7584
Porotrichum longirostre (Hook.) Mitt.	7	4	14	3			-0,8877	-0,4846
Porotrichum sp.	3	6		1			-0,8845	0,2942
Prionodon densus (Sw. ex Hedw.) Müll. Hal.	26	26	18	13			-0,9516	-0,032
Radula javanica Gottsche	7	2	11	3			-0,858	-0,6694
Radula quadrata Gottsche	5			2			-0,3612	0,0687
Radula voluta Taylor *ex* Gottsche, Lindenb. & Nees	5	4	15				-0,8225	-0,2877
Rhizogonium novae-hollandiae (Brid.) Brid.				3*			0,1985	-0,0533
Sematophyllum cuspidiferum Mitt.	1	13	2	6			-0,8296	0,1853
Squamidium nigricans (Hook.) Broth.	2	4	5	1			-0,4524	-0,294
Syrrhopodon gaudichaudii Mont.		3		4			-0,5329	0,0379
Trichocolea tomentosa (Sw.) Gottsche			2*				-0,3388	-1,1763
Thuidium tomentosum Schimp.	1		9		14	3	-0,0315	-0,5061
Lichens								
Agonimia sp.		1*					-1,007	1,0341
Alectoria ochroleuca (Hoffm.) A. Massal.	3	6					-1,0661	0,8524
Amandinea sp.					6*		1,4873	-0,5609
Amandinea submontana Marbach			2	1			-0,5563	-0,9939
Anthracothecium macrosporum (Hepp) Müll. Arg.		1*					-1,8372	0,666
Anzia parasitica (Fée) Zahlbr.	3	1					-1,3543	-0,0716
Arthonia cinnabarina (DC.) Wallr.	2	1	2	2	12	2	1,2159	0,2052
Arthonia sp.1			1*				-1,1558	-0,0643
Arthonia sp.2			2*				-0,9316	-1,1498
Arthonia sp.3	1*						-0,6423	-1,1003
Arthothelium sp.			1*				-0,7022	-1,5286
Bacidia sp.1			6	14			-1,3999	0,3915
Bacidia sp.2					9	2	1,5742	0,3114
Bacidia sp.3				1		2	0,2081	-0,5939
Bacidia sp.4	4	3	1	1	11		0,2692	0,4478
Bacidia sp.5				3	6	18	1,0125	0,068
Bacidia sp.6	1	2					-0,1282	-0,3867
Bacidia sp.7				4*			1,2931	0,3245
Baculifera remensa (Stirt.) Marbach					5*		1,5112	-0,5295
Badimia sp.	2	1	1	3			-0,2905	-0,3788
Brigantiaea leucoxantha (Spreng.) R. Sant. & Hafellner	9	5	4	4			-0,868	-0,2585
Bryoria sp.		1*					-1,2057	1,3783
Buellia rhombispora Marbach					2	32	1,7057	0,2325
Bulbothrix apophysata (Hale & Kurok.) Hale					3	3	1,5052	0,3666
Bulbothrix coronata (Fée) Hale					22	22	1,6021	0,2371
Bulbothrix isidiza (Nyl.) Hale			1	6			-0,249	-0,6858
Bulbothrix suffixa (Stirton) Hale			1	4			-0,4039	-0,751
Byssoloma subdiscordans (Nyl.) P. James	3	4	2	3			-0,8092	0,4612
Canomaculina cristobalii (L.I. Ferraro & Elix) Elix				3	1	13	1,3869	0,2056

Canomaculina pilosa (Stizenb.) Elix & Hale		1	7	3			-0,443	-0,854
Chiodecton sphaerale Ach.	4*						-1,0637	0,0808
Chrysothrix chrysophtalma (P. James) P. James & J. R. Laundon					29	31	1,6105	0,2127
Cladonia coniocraea (Flörke) Sprengel	1	6	8	5			-0,4683	0,0071
Cladonia subradiata (Vainio) Sandst.	2	6	1	5			-0,6137	-0,2632
Coccocarpia dissecta Swinscow & Krog	1	3					-1,4545	0,5895
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	2	4	2	4			-0,5518	0,0897
Coccocarpia filiformis Arv.	3	1					-1,4627	0,0117
Coccocarpia guimarana (Vain.) Swinscow & Krog	2*						-0,9731	0,4409
Coccocarpia microphyllina Lücking & Aptroot	2	5					-1,3902	0,3248
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway	7	1	19	2			-0,3463	-0,5133
Coccocarpia pellita (Ach.) Müll. Arg.	7	5					-1,3329	0,2654
Coccocarpia prostrata Lücking, Aptroot & Sipman	7		4	3			-0,8401	-0,4684
Coccocarpia stellata Tuck.	8	4	1	6	1	11	0,4314	-0,1792
Coccocarpia sp.	11	11					-1,2153	0,6801
Coenogonium aff. frederici (Kalb) Kalb & Lücking					1	12	1,4801	-0,0627
Coenogonium aff. kawanae (H. Harada & Vezda) H. Harada & Lumbsch	2*						-0,7834	0,511
Coenogonium bacilliferum (Malme) Lücking, Aptroot & Sipman		6*					-1,2271	1,1342
Coenogonium epiphyllum Vain.	1	6	6				-0,981	-0,3999
Coenogonium eximium (Nyl.) Kalb & Lücking	2*						-1,5293	-0,1674
Coenogonium isidiosum (Breuss) Rivas Plata, Lücking, Umaña & Chavez	1*						-1,3272	-0,1434
Coenogonium kalbii Aptroot, Lücking & Umaña	5	6		3			-0,9037	0,7113
Coenogonium leprieurii (Mont.) Nyl.	22	3	11	6			-0,956	0,4233
Coenogonium linkii Ehrenb.		2					0,7082	0,2875
Coenogonium luteolum (Kalb) Kalb & Lücking					5	5	1,5664	0,0334
Coenogonium lutescens (Vezda & Malcolm) Malcolm	1*						-1,184	0,1744
Coenogonium magdalenae Rivas Plata, Lücking & Lizano	5	5	1	8			-0,541	-0,2207
Coenogonium moniliforme Tuck.	2*						-1,2319	-0,0994
Coenogonium nepalense (G. Thor & Vezda) Lücking, Aptroot & Sipman	2			3	9	1	1,1265	0,2659
Coenogonium pertenue (Stirt.) Kalb & Lücking					14	13	1,517	0,0193
Coenogonium pineti (Ach.) Lücking & Lumbsch	5*						-1,175	0,1835
Coenogonium roumeguerianum (Müll. Arg.) Kalb		8*					-1,1939	1,1009
Coenogonium sp.		1*					-1,0703	0,9772
Cresponea leprieurii (Mont.) Egea & Torrente	7	7	7	12			-0,5408	-0,1737
Cresponea melanocheloides (Vain.)	1	9					-1,314	0,8368

Egea & Torrente								
Cryptothecia effusa (Müll. Arg.) R. Sant.		3					-1,3764	1,0547
Cryptothecia exilis G. Thor		1*					-1,007	1,0341
Cryptothecia punctisorediata Sparrius & Saipunkaew	1	2					-1,0045	0,6169
Cryptothecia striata Thor		2*					-1,0145	1,0274
Dichosporidium boschianum (Mont.) G. Thor	9		5	12	5	1	-0,1013	-0,2464
Diplolabia sp.	1			1			-0,8179	-0,3639
Echinoplaca sp.			1*				-0,3533	-0,9345
Everniastrum cirrhatum (Fr.) Hale ex Sipman		7		2			-0,7383	0,3994
Everniastrum vexans (Zahlbr. *ex* W.L. Culb. & C.F. Culb.) Hale *ex* Sipman	5		4		2		-0,3775	-0,1356
Fellhanera sp.		2*					-1,2445	0,8858
Fissurina sp.1				2*			-1,1558	-0,0643
Fissurina sp.2	1*						-0,0376	-0,6453
Fissurina triticea (Nyl.) Staiger			4*				-0,497	-0,9976
Flakea papillata O. E. Erikss					2*		1,401	0,5822
Flavopunctelia flaventior (Stirt.) Hale					1	2	1,618	0,3208
Glyphis cicatricosa Ach.					3	1	1,5292	0,2996
Glyphis scyphulifera (Ach.) Staiger	2	1	3	1			-0,6771	-1,3547
Graphis aff. bettinae Lücking, Umaña, Chaves & Sipman					11*		1,4247	0,4261
Graphis aff. striatula (Ach.) Spreng.	2		1	1	4		0,2337	0,058
Graphis anfractuosa (Eschw.) Eschw.						1*	1,7075	0,51
Graphis bettinae Lücking, Umaña, Chaves & Sipman					8	4	1,5424	-0,0708
Graphis cinerea (Zahlbr.) M. Nakan.						1*	1,7075	0,51
Graphis conferta Zenker	7	2	5	3			-0,6723	-0,5718
Graphis elixiana A.W. Archer				1*			-0,0541	-0,315
Graphis elongatoradians Fink.						2*	1,3517	0,2038
Graphis leptoclada Müll. Arg.					9	33	1,6171	0,1889
Graphis leptogramma Nyl.					2*		1,536	-0,4967
Graphis myrtacea (Müll. Arg.) Lücking					1	1	1,3503	0,2594
Graphis pinicola Zahlbr.					15	3	1,4635	0,2551
Graphis ruiziana (Fée) A. Massal.			4	18	11	11	0,4229	-0,3777
Graphis scaphella (Fée) A. Massal.	1*						-1,0612	0,3792
Graphis sitiana Vain.					2*		1,5849	-0,2582
Graphis streblocarpa (Bél.) Nyl.	3	8	2	4			-0,5498	0,1027
Graphis subcontorta (Müll. Arg.) Lücking & Chaves				1*			-0,0422	-0,5722
Graphis subserpentina Nyl.			1*				-0,9316	-1,1498
Graphis sp.		2				15	1,4612	0,3829
Gyalecta sp.		1*					-1,3	0,6871
Haematomma africanum (J. Steiner) C.W. Dodge						2*	1,6596	0,2471
Haematomma flexuosum Hillm.			3*				-0,5915	-0,7196
Herpothallon aff. roseocinctum (Fr.) Aptroot, Lücking & G. Thor	17	9	27	7			-0,769	-0,4589
Herpothallon confusum G. Thor		1*					-1,4671	0,7689

Herpothallon granulare (Sipman) Aptroot & Lücking	4	5	19	4			-0,6154	-0,4568
Herpothallon hypoprotocetraricum G. Thor			4*				-0,4746	-1,1639
Herpothallon rubrocinctum (Ehrenb.) Aptroot & Lücking	11	9					-1,4285	-0,0456
Herpothallon sp.1	4	19					-1,3725	0,871
Herpothallon sp.2	5	7					-1,1465	0,7531
Herpothallon sp.3						2*	1,3018	0,1484
Heterodermia aff. galactophylla (Tuck.) W.L. Culb.			24	23	3	6	-0,0654	-0,6285
Heterodermia comosa (Eschw.) Follmann & Redón			1*				-0,6423	-1,1003
Heterodermia corallophora (Taylor) Skorepa			4	5	9	2	0,781	-0,2206
Heterodermia diademata (Taylor) D.D. Awasthi					19	35	1,5283	0,3
Heterodermia galactophylla (Tuck.) W.L. Culb.				5	18	3	1,7187	0,0015
Heterodermia hypochraea (Vain.) Swinscow & Krog					4	5	1,3343	0,2494
Heterodermia hypoleuca (Mühl.) Trevis.				2	15	1	1,494	0,4144
Heterodermia isidiophora (Nyl.) D.D. Awasthi	13	12	9	19	16	16	1,3937	0,0589
Heterodermia japonica (M. Satô) Swinscow & Krog	16	7	12	28	25	21	0,2681	-0,0198
Heterodermia leucomela (L.) Poelt	26	17	13	25	32	29	0,5412	-0,1458
Heterodermia microphylla (Kurok.) Swinscow & Krog	1*						0,5862	0,0647
Heterodermia palpebrata (Taylor) Trass			2*				-1,184	0,1744
Heterodermia sitchensis Goward & W.J.Noble			4	3			-0,5865	-1,028
Heterodermia spathulifera Moberg & Purvis			1	14	3	24	-0,3342	-0,6207
Heterodermia subcitrina Moberg					2	1	1,2919	-0,001
Heterodermia sp.			4	4			1,542	0,402
Hypoflavia velloziae (Kalb) Marbach					1	1	-0,2796	-0,7694
Hypotrachyna aff. degelii (Hale) Hale	5	11		1			1,5369	0,4694
Hypotrachyna bogotensis (Vain.) Hale	1	3					-0,6393	0,3855
Hypotrachyna costaricensis (Nyl.) Hale	1	4	8	13	4	5	-0,9266	0,8906
Hypotrachyna densirhizinata (Kurok.) Hale			5	1			0,1294	-0,3628
Hypotrachyna eitenii (Hale) Hale					3	5	-0,5114	-1,0864
Hypotrachyna rachista (Hale) Hale			4*				1,5884	-0,2125
Hypotrachyna reducens (Nyl.) Hale					9*		-0,6167	-0,9068
Hypotrachyna revoluta (Flörke) Hale	12	2	15	31	37	27	0,8866	0,0306
Hypotrachyna rockii (Zahlbr.) Hale			5	1	18	26	1,2943	0,0298
Hypotrachyna sp.					7	21	1,4744	0,3758
Lecanora caesiorubella Ach.			3	5	19		1,079	-0,3585
Lecanora chlarothera Nyl.				1*			0,0123	-0,2796
Lecanora flavidomarginata B. de Lesd.					7	3	1,498	0,0314
Lecanora helva Stizenb.				4	11	3	1,4972	0,2189
Lecanora neonashii Lumbsch						3*	1,82	0,2477
Lecanora varia (Hoffm.) Ach.			8		14	23	1,5102	0,0186

Lecanora sp.			1*				-0,6423	-1,1003
Leioderma glabrum D. J. Galloway & P. M. Jørg.	3	2	8	5			-0,5149	-0,4356
Leiorreuma exaltatum (Mont. & Bosch) Staiger	2*						-1,6519	-0,2581
Lepraria sp.1	1	6	1	1			-0,9357	0,7633
Lepraria sp.2	5	12	6	25	12	27	0,1457	0,1321
Leptogium austroamericanum (Malme) C.W. Dodge	3	3	1	3			-0,634	-0,1728
Leptogium azureum (Sw.) Mont.	18	31	32	17	4	8	-0,5409	-0,1842
Leptogium burgesii (L.) Mont.		7	5	12			-0,309	-0,1619
Leptogium burnetii Dodge	4	2					-1,0501	0,7487
Leptogium chloromelum (Ach.) Nyl.	1	1			5		0,6812	0,5368
Leptogium cochleatum (Dicks.) P.M. Jørg. & P. James	21	7	4	1			-0,7821	-0,0333
Leptogium coralloideum (Meyen & Flot.) Vain.		2	3		2	2	1,1646	0,0582
Leptogium corticola (Taylor) Tuck.	2	7		7			-0,6028	0,5347
Leptogium cyanescens (Pers.) Körb.	5	8					-1,2088	0,7393
Leptogium diaphanum (Sw.) Mont.	1	2					-1,786	0,3105
Leptogium laceroides B. de Lesd.	2	3	1	1			-0,7462	0,2195
Leptogium marginellum (Sw.) Gray	4*						-1,2556	-0,1122
Leptogium millegranum Sierk	4	2					-1,1936	0,4798
Leptogium olivaceum (Hook.) Zahlbr.		1	5	3			-0,5723	0,134
Leptogium phyllocarpum (Pers.) Mont.	12	5	1				-1,2789	0,1754
Lithothelium sp.1						2*	1,7359	0,2611
Lithothelium sp.2					6*		1,336	0,5494
Lobaria erosa (Eschw.) Nyl.	1	2	2	2			-0,787	0,236
Lobaria tenuis Vain.	7	3					-1,2943	0,5182
Lobariella crenulata (Hook.) Yoshim.	5	3	3	4		8	0,2208	-0,0127
Lobariella exornata (Zahlbr.) Yoshim.		3*					-1,0712	1,3234
Lobariella pallida (Hook.) Yoshim.	1	5	5	2			-0,8498	0,601
Lopezaria versicolor (Fée) Kalb & Hafellner				2*			0,2324	-0,6873
Malcolmiella fuscella (Müll. Arg.) M. Cáceres & Lücking	2	3	2				-1,1519	0,1391
Malcolmiella gyalectoides (Vain.) Cáceres & Lücking						3*	1,5703	0,1335
Malcolmiella sp.	1*						-1,6345	-0,6363
Malmidea aff. rhodopis (Tuck.) Kalb, Rivas Plata & Lumbsch	1*						-1,1558	-0,0643
Maronea constans (Nyl.) Hepp		2			2		-0,8666	0,8381
Maronina multifera (Nyl.) Hafellner & R. W. Rogers			4		2	3	0,7004	-0,146
Megalaria sp.1	3*						-0,97	0,3554
Megalaria sp.2				1	4		1,1695	-0,0349
Megalospora admixta (Nyl.) Sipman				1*			0,0123	-0,2796
Megalospora melanodermia (Müll. Arg.) Zahlbr.		3*					-1,0923	1,2976
Megalospora sulphurata var. nigricans (Müll. Arg.) Riddle			5	4			-0,8839	0,4491
Megalospora sulphurata var. sulphurata Meyen	1	17	1	5			-0,4594	-0,7728

Megalospora tuberculosa (Fee) Sipman	3	2	6	1			-1,6039	-0,1529
Megalospora sp.	1*						-1,1486	0,0576
Micarea sp.1			2*				-0,5368	-0,7096
Micarea sp.2		1*					-0,7335	1,2553
Micarea sp.3		3*					-1,0807	1,0486
Mycomicrothelia subfallens (Mull. Arg.) D. Hawksw.	1	2					-1,301	0,8097
Myeloconis sp.	1	3	2	3	4	3	0,0118	0,1335
Normandina pulchella (Borrer) Nyl.				1*			-0,0422	-0,5722
Ocellularia sp.	1	3					-1,5481	0,6371
Ochrolechia pseudopallescens Brodo			2	2	5	1	1,1984	-0,5536
Ochrolechia sp.			2*				-0,6118	-1,1694
Opegrapha sp.		2*					-0,9664	1,1009
Pannaria conoplea (Ach.) Bory	9		15	9			-0,7063	-0,7166
Pannaria mosenii C.W. Dodge	1	5					-1,0884	0,9477
Pannaria prolificans Vain.	5	5					-1,2221	0,5428
Parmeliella andina P.M. Jørg. & Sipman	13	9					-1,3356	0,2264
Parmeliella delicata P.M. Jørg. & Arv.	4	19					-1,2274	0,834
Parmeliella miradorensis Vain.	1	3					-1,4304	0,2241
Parmeliella sp.	9	8	13	18			-0,4191	-0,2604
Parmelinopsis miniarum (Vain.) Elix & Hale		5*					-1,062	1,0211
Parmotrema aff. exquisitum (Kurok.) DePriest & B.W. Hale			6	2		31	1,3446	0,0975
Parmotrema arnoldii (Du Rietz) Hale	16	11	28	27	6	2	-0,3355	-0,4273
Parmotrema austrosinense (Zahlbr.) Hale						9*	1,7904	0,2772
Parmotrema cristiferum (Taylor) Hale					7	1	1,5321	-0,0827
Parmotrema exquisitum (Kurok.) DePriest & B.W. Hale						12*	1,3685	0,1334
Parmotrema internexum (Nyl.) Hale *ex* DePriest & B.W. Hale			2	7	4	5	0,4636	-0,3918
Parmotrema mellisii (Dodge) Hale	4	4					-1,0672	0,5633
Parmotrema peralbidum (Hale) Hale	3		24	26	3		-0,2027	-0,6252
Parmotrema rampoddense (Nyl.) Hale		1	7	3	28	33	1,2701	0,3603
Parmotrema zollingeri (Hepp) Hale			2	11	25	1	0,5037	-0,5411
Peltigera sp.		1*					-1,8372	0,666
Pertusaria aff. papillata (Ach.) Tuck	1	2					-1,515	0,1989
Pertusaria excludens Nyl.						8*	1,3647	0,1468
Pertusaria hypothamnolica Dibben	4	5	3	6			-0,7168	0,1153
Pertusaria multipunctoides Dibben	2		6				-0,9067	-0,5836
Pertusaria ventosa Malme	11	3	4	17	27	28	0,738	-0,0391
Pertusaria sp.1	5	3					-1,0722	0,5085
Pertusaria sp.2	1	3	2	3	4	3	0,5472	-0,0897
Pertusaria sp.3		1*					-1,3791	1,108
Pertusaria sp.4				2*			-0,2558	-0,6171
Phaeographis "scalpturatilla"					16*		1,4959	0,0916
Phaeographis brasiliensis (A. Massal.) Kalb & Matthes-Leicht					1*		1,4608	-0,5959
Phaeographis brevinigra Sipman					39	26	1,4793	0,1472
Phaeographis dendritica (Ach.) Müll. Arg.					16*		1,4318	0,247

Phaeographis inconspicua (Fée) Müll. Arg.				2	5		1,1246	-0,1838
Phaeographis scalpturata (Ach.) Staiger					1	5	1,5351	0,0772
Phaeographis sp.				1*			-0,2919	-0,7499
Phaeophyscia aff. limbata (Poelt) Kashiw.					7	5	1,5567	0,2712
Phlyctella sp.1	4	2	2	1			-0,7646	-0,0091
Phlyctella sp.2				2*			-0,0404	-0,1907
Phyllopsora chlorophaea (Müll. Arg.) Zahlbr.	3	3					-1,1483	0,5473
Phyllopsora fendleri (Tuck. & Mont.) Müll. Arg.	2*						-1,6345	-0,6363
Phyllopsora furfuracea (Pers.) Zahlbr.	8	11	23	1			-0,7688	-0,4082
Phyllopsora glaucescens Timdal	3*						-1,213	0,0762
Phyllopsora hispaniolae Timdal	12*						-1,2439	-0,0023
Phyllopsora isidiotyla (Vain.) Riddle	4	2	2				-0,8789	0,144
Phyllopsora parvifolia (Pers.) Mull. Arg.	4	18	3	4			-1,0004	0,5831
Phyllopsora parvifoliella (Nyl.) Mull. Arg.	4	3	2				-1,0343	0,3376
Phyllopsora santensis (Tuck.) Swinscow & Krog		16	3	5			-0,9029	0,555
Phyllopsora sp.	8	3					-1,1977	0,4783
Porina aff. nucula Ach.	1*						-1,1558	-0,0643
Porina imitatrix Müll. Arg.	4	1		2	1	13	0,6997	0,1008
Porina internigrans (Nyl.) Müll. Arg.	2	2					-1,1794	0,3026
Porina nucula Ach.	3	3	3	4			-0,5258	-0,1096
Porina sp.						1*	1,535	0,1373
Pseudocyphellaria aurata (Ach.) Vain.	13	7	11	19	1	13	0,2159	-0,0709
Pseudocyphellaria crocata (L.) Vain.	2	8	2	1			-0,8822	0,8298
Punctelia crispa Marcelli, Jungbluth & Elix	17	22	16	18			-0,4374	-0,0934
Punctelia reddenda (Stirt.) Krog			9	8	15	12	0,8994	-0,1634
Pyrenula aff. falsaria (Zahlbr.) R. C. Harris					4*		1,4543	0,1358
Pyrenula aff. mamillana (Ach.) Trevisan	4*						-1,2795	-0,1625
Pyrenula andina Aptroot			4*				1,3907	0,1015
Pyrenula cf. nitidula (Bresadola) R. C. Harris	1*						-0,4426	-1,1124
Pyrenula macrocarpa A. Massal.	3	2	4	1			-1,6039	-0,1529
Pyrenula mastophoroides (Nyl.) Zahlbr.						2*	-0,5168	-0,6307
Pyrenula microcarpa Mull. Arg.	1*						-1,1558	-0,0643
Pyrenula microtheca R. C. Harris					2*		1,3514	0,5177
Pyrenula tenuisepta R. C. Harris	2	3	6	2			-1,0722	-0,3004
Pyrenula sp.1		1	1	2			-1,3162	0,8481
Pyrenula sp.2				3*			-0,5711	-0,687
Pyrenula sp.3		2*					-0,0934	-0,4638
Pyrenula sp.4			2*				-0,2919	-0,7499
Pyrgillus sp.	2*						-1,1418	0,2448
Ramalina celastri (Spreng.) Krog & Swinscow					14	12	1,5686	-0,2905
Ramalina cochlearis Zahlbr.					2*		1,536	-0,4967
Ramalina peruviana Ach.					1	1	1,4106	0,1351
Ramalina sp.			2	3	15	1	1,3995	-0,0279

Ramonia sp.	3*						-1,1011	0,1681
Relicina abstrusa (Vain.) Hale	1	6					-0,8971	0,7665
Rimelia subisidiosa (Müll. Arg.) Hale & A. Fletcher	2	2					-1,3145	0,455
Rimelia succinreticulata Eliasaro & Adler		5*					-0,92	1,1038
Rinodina sp.1			1*				1,4248	0,116
Rinodina sp.2						2*	-0,7022	-1,5286
Sarcographa fenicis (Vain.) Zahlbr.			2*				-0,7022	-1,5286
Squamacidia janeirensis (Müll. Arg.) Brako	2	1					-0,9462	0,6957
Squamacidia sp.	2*						-1,2633	0,0511
Sticta andensis (Nyl.) Trevis.	5	9	5	6			-0,9478	0,6402
Sticta ferax Müll. Arg.	4	1	3	4			-1,1416	-0,1886
Sticta fuliginosa (Dicks.) Ach.	1	6					-1,3363	0,8404
Sticta humboldtii Hook.	6	5					-1,3583	0,4085
Sticta laciniata (Sw.) Ach.	1	2					-1,4922	0,1865
Sticta lobarioides Moncada & Coca	17	16	13	8			-1,1698	0,0346
Sticta neolinita Gyeln*.*	4	5	4	3			-1,2162	0,3314
Sticta neopulmonarioides Moncada & Coca	3	2					-1,1825	0,5873
Sticta tomentosa (Sw.) Ach.	32	29	26	25			-0,9183	0,1525
Sticta weigelii (Ach.) Vain.	14	22	31	33	14	13	-0,3603	-0,1973
Sticta sp. 1	3	6					-1,1985	0,8257
Sticta sp. 2	7	6					-1,1464	0,6384
Teloschistes flavicans (Sw.) Norman					16	25	1,5933	0,2311
Tephromela atra (Hudson) Hafellner					1	9	1,5344	0,3259
Thelotrema aff. hawaiense (Hale) Hale		2*					0,1985	-0,0533
Thelotrema hawaiense (Hale) Hale				1*			-1,1977	1,1608
Thelotrema sp.1	1	1					-1,52	0,5488
Thelotrema sp.2		4		3			-0,5899	0,3467
Thelotrema sp.3		2	1				-1,067	-0,012
Trichothelium horridulum (Mull. Arg.) R. Sant.	2	4					-1,1325	1,1111
Trypethelium sp.	5	8	8				-0,9668	-0,061
Usnea sp. 1	5	11	13	17	37	28	1,3266	-0,1165
Usnea sp. 2		1			12	5	1,4927	0,3923
Usnea sp. 3	1	2					-1,271	0,5039
Usnea sp. 4	1	1	1				-0,6119	-0,3519
Yoshimuriella dissecta (Sw.)B. Moncada & Lücking	5	3					-0,8001	0,2356
Yoshimuriella subdissecta (Nyl.)B. Moncada & Lücking	19	32	22	17			-1,3911	0,3002

Acknowledgments

The authors thank X. Yadira González for field assistance, Dr. S. Robbert Gradstein, Dr. Chris Johnson and anonymous reviewers for their valuable comments, corrections and suggestions which help us to improve de manuscript, and Lori De Hond for English revision and comments.

Funding

Financial support for this study was received from the Universidad Técnica Particular de Loja, the Secretaria Nacional de Educación Superior, Ciencia, Tecnología e Innovación of Ecuador and the Ministerio de Ciencia e Innovación of Spain (project EPICON, CGL2010-22049).

References

Acebey, A., Gradstein, S.R. and Krömer, T. 2003 Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* **19**, 9–18.

Anderson, M.J., Gorley, R.N. and Clarke, K.R. 2008 *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth, UK: PRIMER-E.

Aptroot, A., Lücking, R., Sipman, H.J.M., Umaña, L. and Chaves, J.L. 2008 Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. *Bibl. Lichenol.* **97**, 1–162.

Ariyanti, N.S., Bos, M.M., Kartawiniata, K., Tjitrosoedirdjo, S.S., Guhadja, E. and. Gradstein, S.R. 2008 Bryophytes on tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. *Biol. Conserv*. **141**, 2516–2527.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J. and Engwald, S. 2001 Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Pl. Ecol.* **152,** 145–156.

Benitez, A.R., Prieto, M., González, X.Y. and Aragón, G. 2012 Effects of tropical montane forest disturbance on epiphytic macrolichens. *Sci. Tot. Environ*. **441**, 169–175.

Brown, S. and Lugo, A.E. 1990 Tropical secondary forests. *J. Trop. Ecol*. **6**,1–32.

Bruijnzeel, L.A. and Hamilton, L.S. 2000 Decision time for cloud forests. *IHP Humid Trop. Progr. Ser.* **13**, 1–40.

Cáceres, M.E.S. 2007 Corticolous and microfoliose lichens of northeastern Brazil. *Libri Bot*. **22**, I–168.

Cáceres, M.E.S., Lücking, R. and Rambold, G. 2007 Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. *Mycol Progress* **10**, 190–210.

Churchill, S.P., Balslev, H., Forero, E. and Luteyn, J.L. 1995 *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden Bronx, New York.

Colwell, R.K. 2013 *Statistical estimation of species richness and share species from samples*. http://viceroy.eeb.uconn.edu/estimates/.

Dent, D.H. and Wright, S.J. 2009 The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv*. **142**, 2833–2843.

Dirzo, R. and Raven, P.H. 2003 Global State of Biodiversity and Loss. *Ann. Rev. Environ. Resour*. **28**, 137–167.

Frisch, A., Kalb, K. and Grube, M. 2006 Contributions towards a new systematics of the lichen family Thelotremataceae. *Bibl. Lichenol*. **92**, 3–556.

Fritz, Ö., Niklasson, M. and Churski, M. 2008 Tree age is a factor for the conservation of epiphytic lichens and bryophytes beech forest. *Appl. Veg. Sci*. **12**, 93–106.

Gauslaa, Y., Ohlson, M., Solhaug, K.A., Bilger, W. and Nybakken, L. 2001 Aspect-dependent high-irradiance damage in two transplanted foliose forest lichens, *Lobaria pulmonaria* and *Parmelia sulcata. Can. J. For. Research* **31**, 1639–1649.

Gehrig-Downie, Ch., Obregón, A., Bendix, J. and Gradstein, S.R. 2011 Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana. *Biotropica* **43**, 591–596.

Gentry, A.H. 1995 Patterns of diversity and floristic composition in neotropical montane forests. In: *Biodiversity and conservation of neotropical montane forests*. Churchill, S.P., Balslev, H., Forero, E. and Luteyn, J.L. (eds). New York Botanical Garden Bronx, pp. 103–126.

Gibbs, H.K., Reusch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N. *et al.* 2010 Tropical forests were the primary sources of new agricultural lands in the 1980s and 1990s. *Proc. Natl. Acad. Sci.* **107**, 16732–16737.

Gignac, L.D. 2001 Bryophytes as indicators of climate change. *Bryologist* **104**, 410-420.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J. *et al.* 2011 Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381.

Gorelick, R. 2006 Combining richness and abundance into a single diversity index using matrix analogues of Shannon's and Simpson's indices. *Ecography* **29**, 525–530.

Gradstein, S.R. 2008 Epiphytes of tropical montane forests—impact of deforestation and climate change. In: *The tropical mountain forest. Patterns and Processes in a Biodiversity Hotspot*. Gradstein, S.R., Homeier, J. and Gansert, D. (eds). University Press, Göttingen, pp. 51–65.

Gradstein, S.R. and Costa, D.P. 2003 The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York botanical Garden* **87**, 1–317.

Gradstein, S.R. and Culmsee, H. 2010 Bryophyte diversity on tree trunks in montane forests of Central Sulawesi. *Trop. Bryol.* **31**, 95–105.

Gradstein, S.R. and Sporn, S.G. 2010 Land-use change and epiphytic bryophyte diversity in the Tropics. *Nova Hedwigia* **138**, 309–321.

Gradstein, S.R., Churchill, S.P. and Salzar, N. 2001 Guide to the Bryophytes of tropical America. *Memoirs of the New York botanical Garden* **86**, 1–577.

Green, T.G.A., Nash III, T.H. and Lange, O.L. 2008 Physiological ecology of carbon dioxide exchange. In: *Lichen Biology*. Nash III, T.H. (ed). Cambridge University Press, Cambridge, UK, pp. 152–181.

Hietz, P., Buchberger, G. and Winkler, M. 2006 Effect of forest disturbance on abundance and distribution of epiphytic bromeliads and orchids. *Ecotropica* **12**, 103–112.

Holz, I. 2003 *Diversity and Ecology of Bryophytes and Macrolichens in Primary and Secondary Montane Quercus Forests, Cordillera de Talamanca, Costa Rica*. PhD Thesis, University of Göttingen, Göttingen.

Holz, I. and Gradstein, R.S. 2005 Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. *Pl. Ecol*. **178**, 89–109.

Hofstede, R. and Aguirre, N. 1999 Biomasa y dinámica del carbono en relación con las actividades forestales en la Sierra del Ecuador. In: *El páramo como espacio de mitigación de carbono atmosférico*. Medina, G. and Mena, P. (eds). Quito, pp. 29–51.

Hohnwald, S. 1999 Beiträge zum Mikroklima interandiner Trockentäler Boliviens. *Geoökodynamik* **20**, 221-229.

Johansson, V., Bergman, K.O., Lättman, H. and Milberg, P. 2009 Tree and site quality preferences of six epiphytic lichens growing on oaks in southeastern Sweden. *Ann. Bot. Fenn*. **46**, 496–506.

Király, I., Nascimbene, J., Tinya, F. and Ódor, P. 2013 Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiver. Conserv*. **22**, 209–223.

Köster, N., Friedrich, K., Nieder, N. and Barthlott, W. 2009 Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conserv. Biol*. **23**, 911–919.

Kranner, I., Beckett, R., Hochman, A. and Nash III, T.H. 2008 Desiccation-Tolerance in Lichens: A Review. *Bryologist* **111**, 576–593.

Krömer, T. and Gradstein, S.R. 2003 Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana* **25**, 190–195.

Lücking, R. 2009 The taxonomy of the genus *Graphis* Staiger (Ascomycota: Ostropales: Graphidaceae). *Lichenologist* **41**, 319–362.

Magurran, A. 2004 *Measuring biological diversity*. Backwell Publishing. Oxford.

Mandl, N., Lehnert, M., Kessler, M. and Gradstein, S.R. 2010 A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. *Biodivers. Conserv*. **19**, 2359–2369.

McCune, B., Grace, J.B. and Urban, D.L. 2002 *Analyses of ecological communities*. MjM software design Gleneden Beach, Oregon.

McCullagh, P. and Nelder, J.A. 1989 *Generalized linear models*. Second Edition. Monographs on statistics and applied probability **37**. Chapman and Hall/CRC, New York, USA.

Moncada, B., Coca, F. and Lücking, R. 2013 Neotropical members of *Sticta* (lichenized Ascomycota: Lobariaceae) forming photosymbiodemes, with the description of seven new species. *Bryologist* **116**, 169–200.

Myers, N., Mittermeler, R.A., Mittermeler, C.G., Fonseca, G.A.B. and Kent, J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S.R., Sipman, H. J. M., Obregon, A. *et al.* 2010 Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. *Ecol. Indic*. **10**, 1111–1118.

Nöske, N.M., Hilt, N., Werner, F.A., Brehm, G., Fiedler, K., Sipman, H.J.M. *et al.* 2008 Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. *Basic Appl. Ecol.* **9**, 4–12.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* 2013 *Vegan: Community Ecology Package*.

Pardow, A. and Lakatos, M. 2013 Desiccation tolerance and global change: implications for tropical bryophytes in lowland forests. *Biotropica* **45**, 27–36.

Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Söderström, B. and Gustafsson, L. 2009 Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biol. Conserv*. **145**, 1125–1133.

Pócs, T. 1982 Tropical forest bryophytes. In: Bryophyte ecology. Smith, A. J. E. (ed). Champman and Hall, London, pp. 59–105.

Proctor, M.C.F., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Cleavitt, N.L. *et al*. 2007. Desiccation-Tolerance in Bryophytes: A Review. *Bryologist* **110**, 595–621.

Ranius, T., Johansson, P., Berg, N. and Niklasson, M. 2008 The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *J. Veg. Sci*. **19**, 653–662.

Rosabal, D., Burgaz, A.R. and de la Masa, R. 2010 Diversity and distribution of epiphytic macrolichens on tree trunks in two slopes of the montane rainforest of Gran Piedra, Santiago de Cuba. *Bryologist* **113**, 313–321.

Rosabal, D., Burgaz, A.R. and Reyes, O.J. 2013 Substrate preferences and phorophyte specificity of corticolous lichens on five tree species of the montane rainforest of Gran Piedra, Santiago de Cuba. *Bryologist* **116**, 113–121.

Sillett, S.C. and Antoine, M. 2004 Lichens and bryophytes in forest canopies. In: *Forest canopies*. Lowman, M.D. and Rinker, H.B. (eds). Elsevier Academic Press, pp. 151–174.

Sipman, H.J.M. 1995 Preliminary review of the lichen biodiversity of the Colombian Montane Forests. In: *Biodiversity and Conservation on neotropical Montane Forests*. Churchill, A.P., Balslev, H., Forero, E. and Luteyn, J.L. (eds). New York Botanical Garden, New York, pp. 313–320.

Sipman, H.J.M. and Harris, R.C. 1989 Lichens. In: *Tropical Rain Forest Ecosystems.* Lieth, H. and Werger, M.J.A. (eds). Elsevier, Amsterdam, pp. 303–309.

Soto, E., Lücking, R. and Bolaños, A. 2012 Especificidad de forófito y preferencias microambientales de los líquenes cortícolas en cinco forófitos del bosque premontano de finca Zíngara, Cali, Colombia. *Rev. Bio. Trop.* **60**, 843–856.

Sporn, S.G., Bos, M.M., Hoffstätter-Müncheberg, M., Kessler, M. and Gradstein, S.R. 2009 Microclimate determines community composition but not richness of epiphytic understorey bryophytes of rainforest and cacao agroforests in Indonesia. *Funct. Plant Biol*. **36**, 171–179.

Timdal, E. 2008 Studies on the *Phyllopsora* (Ramalinaceae) in Peru. *Lichenologist* **40**, 337–362.

Verbeke, G. and Molenberghs, G. 1997 *Linear mixed models in practice. A SAS-oriented approach*. Springer-Verlag, New York.

Werner, F.A. and Gradstein, S.R. 2009 Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. *J. Veg. Sci*. **20**, 59–68.

Werner, F.A., Homeier, J. and Gradstein, S.R. 2005 Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. *Ecotropica* **11**, 21–40.

Werner, F.A., Homeier, J., Oesker, M. and Boy, J. 2011 Epiphytic biomass of a tropical montane forest varies with topography. *J. Trop. Ecol.* **28**, 23–31.

Wolf, J.H.D. 2005 The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *For. Ecol. Manage.* **212**, 376-393.

Zimmerman, B. and Kormos, C. 2012 Prospects for Sustainable Logging in Tropical Forests. *BioScience* **62**, 479–487.

CAPÍTULO III / CHAPTER III

Functional traits of epiphytic lichens as indicators of forest disturbance level and predictors of total richness and diversity of epiphytic lichens

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Abstract

Deforestation affects tropical montane forest producing loss on biodiversity and alteration of ecological processes. In order to manage and preserve biodiversity, understand ecosystem functioning and the effect of forest disturbance of these complex systems it is important to study the functional diversity. However, most studies are focused on plants, while the information related with lichen functional traits remains largely unknown. Epiphytic lichens are poikilohydric organisms, sensitive to climatic changes due its physiological characteristics making them good ecological indicators. In this study we aim to use functional groups of epiphytic lichens to detect forest disturbance and to infer total species richness and diversity. Thus, we evaluated changes in functional diversity in a gradient of disturbance of tropical montane forests. To do this, we assessed nine different traits related with photobiont type, growth form, reproductive strategy and chemistry of epiphytic lichens on the trunk bases of 240 trees on three types of forests according to a disturbance gradient (primary forests and secondary vegetation). Most functional traits of the lichen communities were related to structural changes along a forest disturbance gradient and mostly related with canopy cover and tree diameter. Several trait categories (e.g. cyanobacterial lichens, filamentose species, lirellate species) were suitable to be used as indicators of forest disturbance level and growth forms were useful indicators for total lichen richness and diversity in montane tropical forests. As a tool and a complement for conservation studies and management we propose here the use of lichen functional traits to infer disturbance level of tropical montane forests and to infer total species richness of epiphytic lichens.

Keywords: conservation, community weighted mean **(**CWM), Ecuador, indicator species, growth forms, photobiont, reproductive strategy, tropical montane forest.

Introduction

Despite tropical montane rain forests are among the richest biologically and ecologically complex ecosystems in the world, they are disappearing at alarming rates due to anthropogenic threats (Myers et al., 2000; Laurance et al., 2006; Laurance 2007; Gardner et al., 2009; Laurance et al., 2011; Gibson et al., 2011). A large proportion of the original landscapes of montane rain forests have been transformed into secondary vegetation, croplands or grasslands in order to satisfy human needs related with food, fiber, timber, and other ecosystem goods (Dirzo & Raven 2003, Foley et al., 2005; Wright et al., 2005; Chazdon 2008; Gibbs et al., 2010; Gibson et al., 2011). Consequently, this scenario of rapid deforestation and forest conversion has caused the decline and disappearance of numerous species populating these habitats (Lawton et al., 1998; Sillet & Antoine 2004; Kessler et al., 2005, Barlow et al., 2007; Gray et al., 2007, Nöske et al., 2008), among which lichens are a significant part in terms of diversity, biomass and nutrient cycling (Holz & Gradstein 2005)

Numerous studies have used the species richness and diversity to understand the impact of forest disturbance on communities, but sometimes these data are not sufficient to fully understand the ecological processes shaping these communities (Lawton et al., 1998; Schulze et al., 2004; Nöske et al., 2008; Larrea & Werner 2010; Aragón et al., 2010; Gradstein & Sporn 2010; Benitez et al., 2015). An alternative approximation to understand the mechanisms of community assembly and thus, how communities will respond to rapid environmental changes (e.g. forest disturbance) is to consider functional traits, as they are directly related to biotic and abiotic factors (Díaz et al., 2007; Webb et al., 2010; Pinho et al.,2012). In vascular plants, functional traits have been broadly used to study the response to forest disturbance, providing suitable information for biodiversity conservation and ecosystem functioning (Díaz et al., 1999; 2002, 2004; Mabry & Fraterrigo 2009; Laliberte et al., 2010; Sabatini et al., 2014; Carreño-Rocabado et al., 2016). The use of functional traits is very efficient and provides more information on ecosystem functioning than taxonomic diversity that explains very little variation in ecosystem processes (Díaz et al., 1999; Díaz & Cabido 2001; Mokany et al., 2008; Bässler et al., 2015). Thus, forest disturbance effects can be detected by functional trait analysis much more easily than by using approaches based on floristic information only.

Generally, lichens are sensitive indicators of climatic conditions, because their poikilohydric physiology depends directly on water availability, surrounding temperature and light received (Nash 1996; Green et al., 2008; Kranner et al., 2008; Aragón et al., 2010; Marini et al., 2011). Forests conversion and logging alter microclimatic conditions related with moisture and light. Lichens present functional strategies related with photobiont partner, growth forms, reproduction strategies, presence of cortical pigments and secondary metabolites which depends on the environmental conditions and provide (dis)-advantages to them (Kranner et al., 2008; Marini et al., 2011; Giordani et al., 2012; Hauck et al., 2013). Previous studies have shown that several functional traits (photobiont type, growth forms, reproductive structure and chemistry), are directly related to microclimatic factors associated with forest structure (e.g. canopy cover, and tree age) and environmental conditions as humidity, temperature and light availability (Ellis & Coppins 2006; Marini et al., 2011; Pinho et al.,2012; Li et al., 2013). A measure to characterize the community structure from a functional perspective (Ricotta & Moretti 2011) is the community weighted mean (CWM), which describes the trait averages over a community (de Bello et al., 2007). This measure reflects the dominant trait in a given community (Garnier et al., 2004; Lepš et al., 2006; Violle et al., 2007; Lavorel et al., 2008) and is a good indicator to understand how species respond to the environment changes (Diaz & Cabido 1997; Vandewalle et al., 2010; Concostrina-Zubiri et al., 2014).

Forest logging and deforestation significantly and drastically reduces epiphytic lichen diversity (Gradstein 2008; Nöske et al., 2008; Aragón et al., 2010; Benitez et al., 2012, 2015). Therefore, it is essential to use indicator species in conservation strategies as a valid approach for a quick measure in diversity surveys (Giordani et al., 2009; Aragón et al., 2013). A promising approach is to use growth forms as an indicator for total richness (Aragón et al., 2016), instead of using species, genera or families due to that their identification and sampling requires considerable effort (Bergamini et al., 2005; 2007; Aragón et al., 2013). Several studies related with non-vascular epiphytes (bryophytes and lichens) suggest that the richness of life-forms or growth forms is a robust estimator for detection of species richness of bryophytes and lichens in biodiversity hotspots as tropical forests and Mediterranean forests (Oishi 2009; Pardow et al., 2012; Aragón et al., 2016). Therefore, from a conservation perspective, the use of easily recognizable growth forms in lichens could be used to detect areas of high lichen biodiversity.

Our main goal was to evaluate changes in lichen functional traits in relation with a gradient of disturbance in tropical montane rainforests. We hypothesized that forest structure, in particular, canopy cover, would affect the individual species traits and the community weighted mean (CWM). Second, we suspect that the richness of growth forms would be an indicator of total species richness and diversity of lichens. Specifically, we addressed the following questions: 1) how do the richness of each functional trait category and the CWM respond to forests disturbance? 2) which lichen functional trait category is the best indicator of forest disturbance?, and 3) could the total lichen species richness and diversity be predicted by the richness of growth forms alone?.

Methods

Study area

Experimental design and details of the geographical location of the six forest remnants is detailed in Benitez et al. (2012; 2015), and only a brief summary is included here. The study was conducted in tropical montane forests of southern Ecuador. The climate is humid tropical with a mean annual temperature of 20 °C, annual rainfall of ca. 1900 mm and relative humidity of ca. 80% (data from INAMI).

Field work was carried out in six remnants of tropical montane forest between April 2010 and December 2010. The altitude of the studied remnants ranged from 2200 to 2800 m a.s.l. These forests were chosen to cover a disturbance gradient, with the following three categories: (1) remnant primary forest fragments (PF) of evergreen montane tropical vegetation characterized by a dense canopy layer and large trees. (2) Secondary forest fragments (SF) that have regrown after selective logging events which took place some 40 years ago. (3) Secondary monospecific vegetation (MF) dominated by *Alnus acuminata* Kunth which have re-grown after a total logging of the original forest, and are characterized by a more open canopy cover and young trees.

Sampling design and data collection

Two forests were studied per disturbance category. Within each forest, we established 10 plots, 5 m x 5 m each. In each plot, four trees were selected to estimate the occurrence of epiphytic lichens. For these trees, lichen frequency and coverage were estimated visually on six 20×30 cm grids located at three heights (0–50 cm, 51–150 cm, 151–200 cm), and on the north and south aspects. In addition, the following variables were measured at plot level: canopy cover (%), elevation (m a.s.l.), slope (º), aspect (cosine transformed) and mean tree DBH (cm) of the 4 trees analyzed per plot as a proxy to the stand forest structure.

For species identification, we used general and specific taxonomic and floristic papers (e.g. Brako 1991; Egea & Torrente 1993; Brodo et al., 2001; Nash et al., 2002, 2004; Rivas-Plata et al., 2006; Nash et al., 2007; Lücking et al., 2008, 2009; Brodo et al., 2008; Timdal 2008; Aptroot *et al.*, 2008, 2009; Aptroot 2012; Moncada 2012, Moncada et al., 2013).

Functional traits

For each lichen species found in the study area, nine traits were assessed to perform the functional analysis: (1) Photobiont type; (2) Growth form; (3) Size; (4) Reproduction type; (5) Type of reproductive structure; (6) Ascospores septation; (7) Ascospores size; (8) Thallus colour; and (9) Chemistry (Table 1).

Table 1. Functional traits categories and codes.

Functional trait	Categories
Photobiont type	C=Chlorococcoid; CY=Cyanobacteria; T=Trentepholia
Growth form	C= Crustose; CP=Crustose with prothallus; FB= Foliose broad lobed; FN= Foliose narrow lobed; FP= Foliose placodiod; FL=Filamentose; F=Fruticose, G=Gelatinose; S=Squamulose
Size	M=Macrolichens; MC=Microlichens
Reproduction type	A=Asexual; S=Sexual; AS=Asexual and sexual; N=None
Reproductive structure	A=Apothecia; I=Isidia; L=Lirellae; P=Perithecia; S=Soredia
Ascospores septation	S=Simple; S=Septate; M=Muriform
Ascospores size*	S=Small (<100 µm); M=Medium (>100 µm); L=Large (>500 µm)
Thallus colour	D=Dark; L=Light
Chemistry**	A=Acids; O = Other compounds; N= No compounds

*Ascospore size was calculated as the product of the length and width (µm^2).

**Acids correspond to atranorin, parietin, furmarprotocetraric, stictic, norstictic and usnic. Other compounds include exclusive compounds of several species, for example chiodectonic acid of *Herpothallon rubrocinctum* and lecanoric acid *Ochrolechia pseudopallescens.*

The information related to these traits was obtained from specific taxonomic literature (cited above), observed directly from the specimen collected and the Database for the Rapid Identification of Lichens (http://liaslight.lias.net/). The functional traits with all the used categories (states) are detailed in Table 1. Functional traits categories of each species are detailed in Appendix 1.

The functional traits were selected based on previous studies, due to that provide key information for understanding of ecosystems functioning (Ellis & Coppins 2006; Stofer et al., 2006, Johansson et al., 2007; Marini et al., 2011; Giordani et al., 2012; Pinho et al., 2012; Li et al., 2013). Specifically, photobiont type is related with light, temperature and water requirements for the photosynthesis and respiration processes (Lange et al., 1986; Lakatos et al., 2006; Marini et al., 2011). Growth forms (thallus morphology) are related with water uptake and loss (Lakatos et al., 2006; Büdel & Scheidegger 2008). Secondary metabolites (e.g. usnic acid) contribute to protect lichens from solar irradiation and herbivory (Cocchietto et al., 2002; Hauck et al., 2007, 2009). Finally, the reproductive strategy is related with dispersion ability and establishment (Stofer et al., 2006; Koch et al., 2013).

We propose the use functional morphological characters (e.g. life-forms or growth forms) as indicators of species richness in these highly diverse habitats, due to that they have been previously used for other ecosystems (Oishi 2009; Pardow et al., 2012; Aragón et al., 2016). Thus, they might be a helpful surrogate of species richness to detect conservation priority areas in biodiversity hotspots.

Data analysis

We calculated species richness as the total number of different lichen species occurring in a plot. Species diversity was calculated with compared by calculating the Simpson´s and Shannon´s indices (Magurran 2004). The Simpson´s index was determined by the predominant species, and the Shannon´s index was based on the assumption that individuals were randomly selected and that all species were represented in the sample (Magurran, 2004). These diversity indices were calculated for each plot with PRIMER v 6.1.11 software. In addition, we calculated floristic similarities using Sørensen's and Bray-Curtis similarity indices (Chao et al., 2005), using EstimateS 9.1.0 (Colwell 2013).

The total species richness of each functional trait category was calculated as the total number of species with each trait category found in the four trees per plot. Community weighted means, considering a continuous trait, represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al., 2008).

For multinomial traits, we have calculated it as the sum of the cover of all species sharing a trait divided by the total species cover, representing the proportion of each individual trait-category per community (i.e. mean trait values weighted with the abundance). The effect of environmental variables (canopy cover, elevation, slope, aspect and mean tree diameter per plot) on richness and CWM of the different lichen functional trait categories was modelled by fitting Generalized Linear Mixed Models (GLMMs) (McCullagh & Nelder 1989). The richness and CWM models of each functional trait category were fitted with Poisson errors. Significance was estimated by means of deviance analysis (Guisan et al., 2002). All GLMMs computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT).

Analyses were carried to determine which lichen functional trait category were associated with the forest type, in order to identify them as indicator traits. To do this we used an analysis of indicator traits (Koch et al., 2013) based on the indicator species analysis developed by Dufrêne & Legendre (1997). This analysis calculates an indicator value for each trait category based on the mean cover of each functional trait category per forest, which results from multiplying the relative abundance for each trait category by the frequency for each trait category in each forest. The indval function with the labdsv package was used for this purpose (Roberts 2012). The indicator value ranges from 0 (when one species trait was absent from one forest type) to 100 (when one species trait occurred in all plots of one forest type and was absent from other plots). The significance was tested using a Monte Carlo permutation with 1000 replicates.

To determine whether a single functional category could be used as predictor for the total species richness of lichens, we used Pearson’s linear correlation coefficients to explore the relationships between the species richness per growth forms (pairwise tests) and the total species richness and diversity indices. When testing correlation, the number of species of each growth forms was subtracted to the total richness of lichens to avoid biases produced by differences in species abundance. To keep a reasonable test-wide Type I error, the alpha values were divided by the number of correlations (nine correlations) (Sebastião & Grelle 2009).

Results

A total of 307 epiphytic lichen species were recorded in 60 plots; for which nine functional traits were assessed (Appendix 1). The richness of most functional traits categories decreased along the gradient of disturbance (Figs 1 - 4). Thus, lichen species with Cyanobacteria and *Trentepohlia* decreased with increasing forest disturbance (Figure 1).

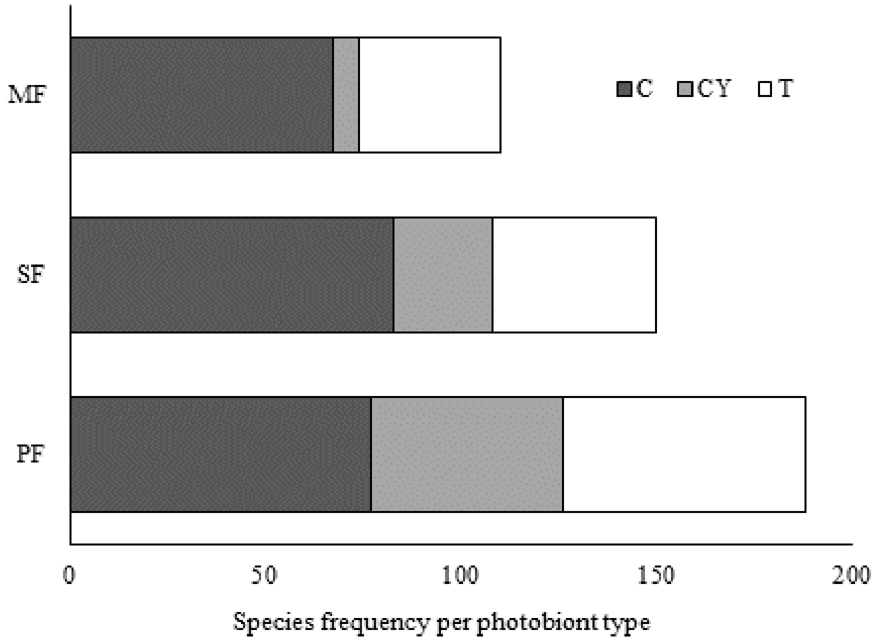

Figure 1. Richness of each photobiont type by type of forest (PF=primary forest; SF=mixed secondary forest; MF=monoespecific secondary forest of *Alnus acuminata*). C=Chlorococcoid. CY= Cyanobacteria. T=*Trentepohlia.*

A similar pattern was found in the growth form categories, where crustose species with prothallus, foliose broadly lobed, filamentose and gelatinose species decreased in secondary forests (Figure 2), with the disappearance of foliose placoidiod and squamulose species in the more disturbed forests.

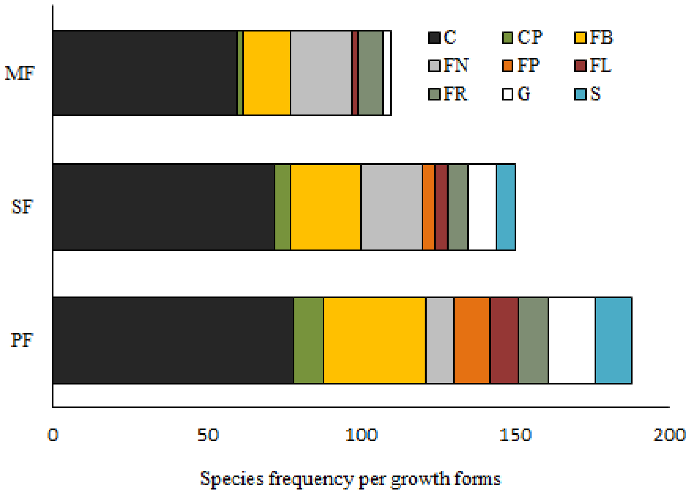

Figure 2. Richness of each growth form per type of forest (PF=primary forest; SF=mixed secondary forest; MF=monoespecific secondary forest of *A. acuminata*). C= Crustose; CP=Crustose with prothallus; FB= Foliose broad lobed; FN= Foliose narrow lobed; FP= Foliose placodiod; FL=Filamentose; F=Fruticose, G=Gelatinose; S=Squamulose.

Species with apothecia and isidia also decreased in monospecific forests (Figures 2 and 3). In contrast, foliose species with narrow lobes and those species with lirellate apothecia increased along the disturbance gradient (Figuress 2 and 3).

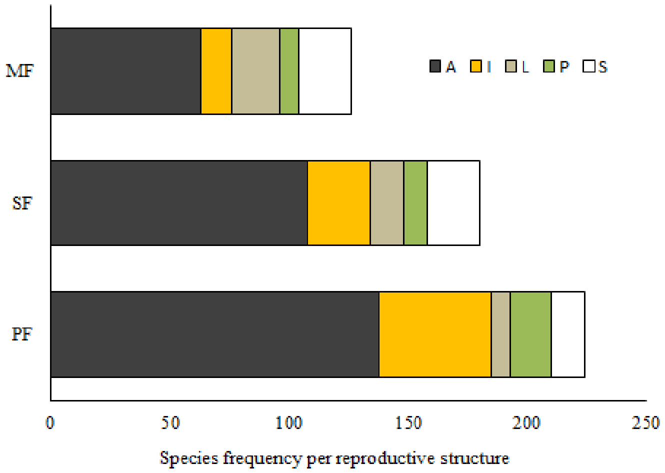

Figure 3. Richness of reproductive structures per type of forest (PF=primary forest; SF=mixed secondary forest; MF=monoespecific secondary forest of *A. acuminata*). A=Apothecia; I=Isidia; L=Lirellae; P=Perithecia; S=Soredia.

In addition, lichens with acids as secondary compounds (atranorin, atrachinones, stictic and usnic acid) were most frequent in secondary forest, while lichens without acids (or with other compounds) increased in primary forests (Figure 4).

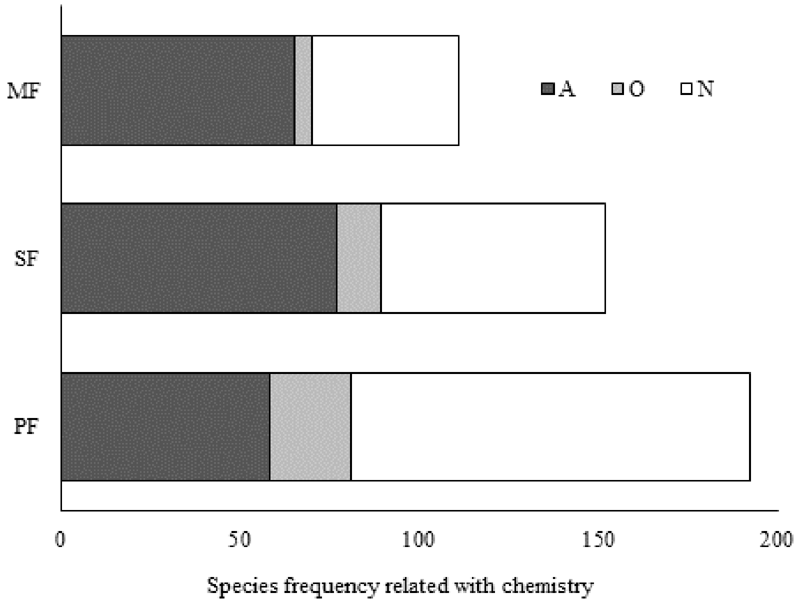

Figure 4. Richness of different secondary compounds per type of forest (PF=primary forest; SF=mixed secondary forest; MF=monoespecific secondary forest of *A. acuminata*). A=Acids; O = Other compounds; N= No compounds.

The most relevant predictors for the richness of functional traits and CWM of epiphytic lichens were canopy cover and tree diameter, followed by altitude; aspect and slope had influence on very few traits (Table 2). Canopy cover had a significant and positive effect on cyanolichens, crustose species with prothallus, foliose placodioid, gelatinose species and lichens without secondary metabolites. Tree diameter had the same effect on *Chroococcoid* species, foliose with broad lobes, fruticose, squamulose and isidiate species. On the other hand, canopy cover had a negative effect on the species with *Trentepohlia*, foliose lichens with narrow lobes, species with lirellae, with soredia and with acids as secondary metabolites (Table 2).

Table 2. Results of the Generalised Linear Mixed Models of plot-scale variables on the richness and CWM of the considered functional trait categories of epiphytic lichens. Coefficients of the variables in the model and *P*-value (between parentheses) are

indicated. DBH=mean tree diameter, CWM= community weighted means of trait values.

	Richness					**CWM**				
	Canopy cover	**DBH**	**Altitude**	**Aspect**	**Slope**	**Canopy cover**	**DBH**	**Altitude**	**Aspect**	**Slope**
Photobiont										
Chlorococcoid		+13.69 (0.0006)								
Cyanobacteria	+7.95 (0.0080)		+8.09 (0.0074)			+11.41 (0.0014)				
Trentepholia						-25.92 (0.0001)				+4.35 (0.0456)
Size										
Macrolichens										
Microlichens										
Growth form										
Crustose										
Crustose with prothallus	+11.56 (0.0013)					+8.54 (0.0075)				
Foliose broad lobed		+7.16 (0.0100)								
Foliose narrow lobed			-6.93 (0.0110)			-6.19 (0.0177)				
Foliose placodioid	+9.23 (0.0037)		+7.14 (0.0155)			+4.55 (0.0378)				
Filamentose			+5.13 (0.0456)			+5.05 (0.0317)				
Fruticose		+8.00 (0.0065)								
Gelatinose	+12.08 (0.0010)		+5.05 (0.0417)			+9.18 (0.0037)				
Squamulose		+5.45 (0.0233)	+4.12 (0.0473)							
Reproduction										
Asexual		+28.50 (<0.0001)					+12.46 (0.0009)			
Sexual							-6.14 (0.0165)			
Asexual and sexual										
None						+4.27 (0.0444)				+4.91 (0.0311)
Reproductive structure										
Apothecia		+9.48 (0.0033)					-7.28 (0.0106)	+4.40 (0.0434)		
Isidia		+18.47 (<0.0001)								
Lirellae					+4.46 (0.0393)	-7.20 (0.0097)				
Perithecia						+6.53 (0.0146)				
Soredia		+15.79 (0.0002)	+3.97 (0.0491)			-7.49 (0.0084)	+5.75 (0.0204)			
Ascospores septation										
continued										

	Richness					CWM				
	Canopy cover	**DBH**	**Altitude**	**Aspect**	**Slope**	**Canopy cover**	**DBH**	**Altitude**	**Aspect**	**Slope**
Simples		+5.44 (0.0235)		+4.81 (0.0381)			+4.07 (0.478)			
Septated										
Muriform								+4.78 (0.0476)		
Ascospores size										
Small		+8.31 (0.0057)							-6.80 (0.0118)	
Medium										
Large										
Tallus colour										
Dark		+13.59 (0.0006)	+10.20 (0.0027)							
Light										
Chemistry										
Acids		+12.96 (0.0007)				-7.62 (0.0079)				
Other compounds										
No compounds	+10.04 (0.0025)		+4.97 (0.0343)			+8.88 (0.0044)				

Species with cyanobacterial photobionts, without secondary compounds, crustose with protallus, foliose placodiod, filamentose, gelatinose and squamulose growth forms, were the best indicators of sheltered habitats of montane undisturbed forests (PF), whereas, fruticose, foliose species with narrow lobes, lirellate and sorediate lichens and species with light thallus colour and acids as secondary compounds were the best indicator of disturbed forest (Table 3).

Table 3. Trait categories of epiphytic lichens with statistical significant values of indication for each forests type, following the indicator species analyses. *P*-values < 0.05 are considered significant. Trait categories with indicator value > 55% are considered as the best indicators.

Functional group	**Forest type**	**Indicator value**	***P-value***
Photobiont			
Chlorococcoid	MF	49.7	0.0001
Cyanobacteria	PF	65.4	0.0001
Trentepohlia	MF	49	0.0001
Size			
Macrolichens	PF	36	0.1332
Microlichens	MF	43.6	0.0001
Growth form			

Crustose	MF	54.8	0.0001
Crustose with prothallus	PF	56.3	0.0001
Foliose broad lobed	PF	50.1	0.0001
Foliose narrow lobed	MF	59.6	0.0001
Foliose placodioid	PF	55.5	0.0001
Filamentose	PF	66	0.0001
Fruticose	MF	76.5	0.0001
Gelatinose	PF	55.4	0.0087
Squamulose	PF	63.9	0.0001
Reproduction			
Asexual	SF	38.4	0.0162
Sexual	MF	35.8	0.1131
Asexual and sexual	MF	38.7	0.0357
None	MF	54.8	0.0094
Reproductive structure			
Apothecia	PF	38.7	0.0003
Isidia	SF	46.3	0.0002
Lirellae	MF	80	0.0001
Perithecia	SF	40.5	0.2162
Soredia	MF	55.5	0.0001
Ascospores type			
Simple	MF	40.3	0.0229
Septate	PF	40.2	0.0005
Muriform	PF	43.6	0.0525
Ascospores size			
Small	MF	43.9	0.0016
Medium	PF	41.6	0.0001
Large	MF	49	0.0002
Thallus colour			
Dark	PF	53.3	0.0001
Light	MF	55.1	0.0001
Chemistry			
Acids	MF	55.5	0.0001
Other compounds	MF	36.6	0.5857
No compounds	PF	59	0.0001

Several trait categories were correlated within the growth forms. Gelatinose was highly and positively correlated with the foliose placodioid, crustose with prothallus and filamentose growth forms whereas foliose species with narrow lobes were negatively correlated with these latter four growth forms (Table 4).

Table 4. Pearson’s correlation of species richness per growth forms of epiphytic lichens. *P*-value with asterisk is indicated. ns= Not significant. *= $P < 0.05$. ** = $P < 0.01$. ***= $P < 0.001$.

Richness	**CP**	**S**	**FI**	**FN**	**FB**	**FP**	**FR**	**G**
C	-0.55***	-0.31*	-0.36**	0.47***	-0.59***	-0.51***	0.34**	-0.44***
CP		0.80***	0.73***	-0.87***	0.70***	0.85***	-0.43***	0.85***

S	0.72***	-0.82***	0.55***	0.83***	-0.37**	0.85***
FI		-0.77***	0.59***	0.70***	-0.25ns	0.69***
FN			-0.61***	-0.89***	0.47***	-0.88***
FB				0.60***	-0.22ns	0.64***
FP					-0.40**	0.85***
FR						-0.40**

Total species richness and diversity of epiphytic lichens were highly and positively correlated with the five growth form categories. The increase in the richness of gelatinose growth forms, filamentous, squamulose, foliose placodiod and crustose with prothallus was highly and significantly correlated with the increase in the total species richness and diversity. On the other hand, the richness of crustose and foliose species with narrow lobes were negatively correlated with the total richness of lichens (Table 5). Most growth forms were negatively correlated with Sørensen's and Bray-Curtis similarity indices except crustose, fruticulose and foliose species with narrow lobes (Table 5).

Table 5. Pearson's correlation coefficients between the total lichen species richness and diversity and growth forms of epiphytic lichens. *P*-value is indicated as ns= Not significant. *= $P < 0.05$. ** = $P < 0.01$. ***= $P < 0.001$.

Traits richness	Total Richness	Shannon index	Simpson inverse index	Sorensen index	Bray Curtis
Crustose	-0.61***	-0.19ns	-0.13ns	0.54***	0.53***
Crustose with prothallus	0.55***	0.40**	0.15ns	-0.77***	-0.73***
Foliose broad lobed	-0.02ns	0.70***	0.53***	-0.68***	-0.78***
Foliose narrow lobed	-0.87***	-0.31*	-0.04ns	0.78***	0.67***
Foliose placodioid	0.56***	0.30*	0.04ns	-0.73***	-0.73***
Filamentose	0.70***	0.30*	0.06ns	-0.68***	-0.63***
Fruticulose	-0.24ns	-0.01ns	0.07ns	0.42***	0.31*
Gelatinose	0.74***	0.44***	0.17ns	-0.73***	-0.76***
Squamulose	0.64***	0.32*	0.02ns	-0.68***	-0.63***

Discussion

Our results demonstrate that lichen traits and the CWM were related to the forest structural changes along a gradient of disturbance and were mainly controlled by factors related with the canopy cover and tree diameter. Several trait categories have high indicator values of the forest conservation status and growth forms are related with the total lichen species richness and diversity in tropical montane forests.

Several studies show that functional traits as growth forms, photobiont type and reproductive structure responds to the forest structural changes (e.g. canopy openness) and environmental conditions (e.g. light and humidity) (Ellis & Coppins 2006; Stofer et al., 2006; Marini et al., 2011; Giordani et al., 2012; Koch et al., 2013; Li et al 2013; Bässler et al., 2015), although they have not been used to infer total richness or diversity as we do here.

In the studied gradient, the changes in functional groups (species with similar trait categories) with disturbance level may be caused by the similarity in the ecological and physiological requirements. Thus, the greater occurrence of three functional groups (i.e. Cyanolichens, species with gelatinose, crustose or foliose placodiod thalli) on primary forests, was mainly due to the presence of a closed canopy. As a general pattern, several studies showed that lichens with cyanobacterial photobiont, gelatinous and foliose placodiod thalli are more abundant in sheltered and humid sites of mature forests, with unaltered forest interior environments (Belinchón et al., 2007; Kranner et al., 2008; Normann et al., 2010; Rosabal et al., 2010; Aragón et al., 2010, Marini et al., 2011; Benitez et al., 2012; Li et al., 2013), due to that they are intolerant to excessive light and need liquid water to activate photosynthesis (Lange et al., 1986; Nash III 1996; Hedenås & Ericson 2000; Sillet & Antoine 2004). This is also suggested for crustose species with prothallus (e.g. *Cryptothecia* and *Herpothallon*), more frequent in primary forest and probably related with their hydrophobic adaptation to repel water excess by the projections of hyphae from the medulla that create a hydrophobic layer, as it has been reported for *Cryptothecia rubrocincta* (Lakatos et al., 2006).

For instance, filamentose lichens (e.g. *Coenogonium*) were related with old-growth and dense primary forests. This group are among the few species in which the lichen morphology is shaped by the filamentous photobiont being restricted to the low light environment of tropical shady understorey (Sipman & Harris 1989, Lücking 1999; Brodo et al., 2001), due to that filamentous arrangement leads to high evaporation rates and rapid desiccation of the thallus (Lakatos 2002). In accordance, previous studies shown that species with this growth form were negatively correlated with shady areas, due to requiring higher light availability and lower humidity condition (Giordani et al., 2012; Koch et al., 2013).

In contrast, we found that foliose species with narrow lobes, lirellate apothecia and those species with acids as secondary metabolites were more abundant in secondary forests and negatively correlated with canopy cover. This could be probably related to a higher luminosity and a lower humidity conditions promoted by canopy disruption. Thus, foliose lichens narrowly lobed (e.g. *Heterodermia* and *Hypotrachyna*) are more heliophytic living in situations with high irradiance levels and water stress characteristic from secondary forests (Aragón et al., 2010; Rosabal et al., 2010; Marini et al., 2011, Benitez et al., 2012; Giordani et al., 2012).

Similarly, lichens with lirellae ascomata (e.g. *Graphis*) are also more abundant in secondary forest. Most of the species found present black and closed lirellae, two characters that have been reported to help in granting protection to high light intensities and to dry and exposed habitats (Kappen 1988; Lücking 1999; Koch et al., 2013) explaining the pattern found here. Besides, lichens that usually produce acids (atranorin, usnic acid and norestictic acid) as secondary compounds were more common in secondary forests. These compounds could confer an effective protection against excessive photosynthetic radiation. In accordance, several studies showed that secondary metabolites in lichens, such as usnic acid may provide effective protection against ultraviolet and visible light on disturbed forests (Cocchietto et al., 2002; Hauck et al., 2007, 2009, 2013).

Our study reveals that with increasing disturbance intensity the importance of Chlorococcoid green algae and *Trentepohlia* as lichen photobiont increased, while it decreased for cyanobacteria. Stofer et al. (2006) found evidence showing that lichens with green algae are better adapted in open and intensively managed forests. They have great capacity to avoid photoinhibition effects and are able to photosynthetize with minimum thallus water content being capable of reactivate photosynthesis from air humidity (Lange et al., 1986; Demmig-Adams et al., 1990; Gauslaa & Solhaug 2004; Hilmo et al., 2005; Ellis & Coppins 2006). Similarly, the greater occurrence of species with fruticose growth forms on secondary forests may be related to a higher luminosity caused by more canopy openness. Fruticulose lichens have a high surface area to mass ratio (Larson and Kershaw 1976), therefore can rehydrate very fast their thallus, giving advantage to these growth forms to live in dryer areas as secondary forests. Thus, ecological success (e.g. gas exchange and photosynthesis) of this group is limited in areas with higher precipitations (Lange et al., 1993; Green et al., 2008).

The analysis for the assessment of indicator traits showed that photobiont type, growth forms, reproductive structure and secondary metabolites can be used as indicators of the conservation status (i.e. disturbance level) in tropical montane rainforests. The indicator species give clues about the state of an ecosystem, due to they indicate the conditions within the local environments (Holz & Gradstein 2005). Thus, indicators (indicator species) are a reliable protocol to monitor forest changes (e.g. forest disturbance) with important ecological implications in several forests (Holz & Gradstein, 2005; Gignac & Dale 2005; Johansson et al., 2006; Nascimbene et al., 2010; Li et al., 2011, 2013; Lundström et al., 2013). However, indicator species analysis (ISA) considered identifying organisms to more specific taxonomic resolution (Bakker 2008). In this context, analysis of indicator traits is more advantageous in conservation studies, that indicator species because traits categories (e.g. growth forms, photobiont, reproductive structure) are easier to recognize than species taxa. Several species of lichens require considerable sampling effort and taxonomic expertise for identification related with anatomical characters (medulla structure and spore size) and thin-layer chromatography analysis of secondary metabolites (Bergamini et al., 2005). Based on analysis of indicator traits of lichens is possible to affirm that twelve trait categories can be used as the best indicators of forest disturbance in mountain forest due to their highly significant indicator value. For instance, lichens crustose with protallus, foliose placodiod, filamentose, gelatinose and squamulose growth forms can be used as indicators of the primary forests. On the other hand, foliose with narrow lobes and fruticose growth forms; and lirellate and sorediate lichens were the best indicators of secondary forests. In accordance Koch et al., 2013 affirm that some traits categories of lichens (e.g. fruticose and foliose growth forms) can be used as indicators of forest succession of tropical ecosystems. Therefore, the application of functional trait categories of lichens as indicators of forest disturbance is a feasible and promising alternative for evaluating and monitoring environmental changes in tropical mountain forests.

On the other hand, our study revealed that the five lichen growth forms can be used to infer species richness and diversity in tropical montane forest. These functional groups are characterized by similar eco-physiological properties related with higher water demands (Lakatos et al., 2006; de Vries & Watling 2008; Kranner et al., 2008). Thus, they are more prevalent in mature and dense forest in which we observed the highest richness values (Benitez et al., 2012).Similarly, studies suggest that the richness of functional life-forms of bryophytes (e.g. thalloid mats and short turfs) and growth forms of lichens (e.g. Crustose inconspicuous, foliose narrow-lobed and gelatinose) are a robust estimator for detection of total species richness (Oishi, 2009; Pardow et al., 2012; Aragón et al., 2016). This method will provide an important step toward the conservation of lichens in fragmented tropical montane forests.

In conclusion, species traits and CWM of lichen communities responded significantly to structural forest changes along disturbance gradient as canopy cover and tree diameter. Photobiont type, growth form, reproductive structure and secondary compounds, are the most suitable functional trait categories to be used as indicators of different forest types. Thus, based on these results, we recommend the use of richness of different growth forms to obtain information about the total epiphytic lichen species richness and diversity in montane tropical forests, which is crucial for forest monitoring and biodiversity conservation. These approaches may be studied in other forests as indicators valuable in the case of rapid diversity surveys, due to that can be applied by non-specialists and they are easier to recognize than species taxa.

Acknowledgments:

Financial support for this study was granted by the “Universidad Técnica Particular de Loja” (PROY_CCNN_941), the “Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación” of Ecuador and the “Ministerio de Ciencia e Innovación of Spain” (project EPICON, CGL2010-22049). We thank A. Arévalo and G. Cevallos for his help with fieldwork and Ministerio del Ambiente del Ecuador by providing access to the study areas.

References

Aptroot, A. (2012) A world key to the species of *Anthracothecium* and *Pyrenula*. *The Lichenologist* 44(1): 5 – 53.

Aptroot, A., Lücking, R., Sipman, H.J.M., Umaña, L. & Chaves, J.L. (2008) Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. *Bibliotheca Lichenologica* 94: 1–191.

Aptroot, A., Thor, G., Lücking, R., Elix, J.A. & Chaves, J.J. (2009) The lichen genus *Herpothallon* reinstated. *Bibliotheca Lichenologica* 99: 19–66.

Aragón, G., Belinchón, R., Martínez, I., & Prieto, M. (2013). Estimating epiphytic lichen richness by single families in Mediterranean forests. *Forest Ecology and Management*, *310*, 187-193.

Aragón, G., Belinchón, R., Martínez, I., & Prieto, M. (2016). A survey method for assessing the richness of epiphytic lichens using growth forms. *Ecological Indicators*, *62*, 101-105.

Aragón, G., Martínez, I., Izquierdo, P., Belinchón, R., & Escudero, A. (2010). Effects of forest management on epiphytic lichen diversity in Mediterranean forests. *Applied*

Vegetation Science, *13*(2), 183-194.

Bakker, J. D. (2008). Increasing the utility of indicator species analysis. *Journal of Applied Ecology*, *45*(6), 1829-1835.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A., & Peres, C. A. (2007). The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology*, *44*(5), 1001-1012.

Bässler, C., Cadotte, M. W., Beudert, B., Heibl, C., Blaschke, M., Bradtka, J. H., & Müller, J. (2015). Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography* 38, 001–0010.

Belinchón, R., Martínez, I., Escudero, A., Aragón, G., & Valladares, F. (2007). Edge effects on epiphytic communities in a Mediterranean Quercus pyrenaica forest. *Journal of Vegetation Science*, *18*(1), 81-90.

Benítez, Á., Prieto, M., & Aragón, G. (2015). Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *Forestry*, *88*(5), 521-527.

Benítez, Á., Prieto, M., González, Y., & Aragón, G. (2012). Effects of tropical montane forest disturbance on epiphytic macrolichens. *Science of the Total Environment*, *441*, 169-175.

Bergamini, A., Scheidegger, C., Stofer, S., Carvalho, P., Davey, S., Dietrich, M., ... & Keller, C. (2005). Performance of macrolichens and lichen genera as indicators of lichen species richness and composition. *Conservation Biology*,*19*(4), 1051-1062.

Brako, L. (1991) *Phyllopsora* (Bacidiaceae). *Flora Neotropica Monograph* 55: 1–66.

Brodo, I. M., Sharnoff, S. D., & Sharnoff, S. (2001). *Lichens of north America*. Yale University Press.

Brodo, I.M., Culberson, W.L. & Culberson Ch. F. (2008) *Haematomma* (Lecanoraceae) in North and Central America, including the West Indies. *The Bryologist* 111: 363–423.

Büdel, B., Scheidegger, C., 2008. Thallus morphology and anatomy. In:Nash III, T.H. (Ed.), Lichen Biology, second ed. Cambridge University Press, Cambridge, pp. 40–68.

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Díaz, S., Quétier, F., Chuviña, J., & Poorter, L. (2016). Land-use intensification effects on functional properties in tropical plant communities. *Ecological Applications* 26(1), 174-189

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology letters, 8(2), 148-159.

Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, *320*(5882), 1458-1460.

Cocchietto, M., Skert, N., Nimis, P.L., Sava, G., 2002. A review on usnic acid, an interesting natural compound. *Naturwissenschaften* 89, 137-146.

Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application.

Concostrina-Zubiri, L., Pescador, D. S., Martínez, I., & Escudero, A. (2014). Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodiversity and conservation, 23(7), 1757-1770.

de Bello, F., Lepš, J., Lavorel, S., & Moretti, M. (2007). Importance of species abundance for assessment of trait composition: an example based on pollinator communities. Community Ecology, 8(2), 163-170.

De Vries, M.C., & Watling, J. R. (2008). Differences in the utilization of water vapour and free water in two co-occurring foliose lichens from semi-arid southern Australia. *Austral Ecology*, *33*(8), 975-985.

Demmig-Adams, B., Máguas, C., Adams III, W. W., Meyer, A., Kilian, E., & Lange, O. L. (1990). Effect of high light on the efficiency of photochemical energy conversion in a variety of lichen species with green and blue-green phycobionts. *Planta*, *180*(3), 400-409.

Díaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. Journal of vegetation Science, 463-474.

Díaz, S., & M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646–655.

Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E., & Araníbar, J. (1999). Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science*, *10*(5), 651-660.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104(52), 20684-20689.

Díaz, S., McIntyre, S., Lavorel, S., & Pausas, J. G. (2002). Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. *New Phytologist*, 154(1), 7-9.

Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, *28*(1), 137-167.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., ... & Band, S. R. (2004). The plant traits that drive ecosystems: evidence from three continents. *Journal of vegetation science*, *15*(3), 295-304.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs*, *67*(3), 345-366.

Egea, J.M & Torrente, P. (1993) *Cresponea*, a new genus of lichenized fungi in the order Arthoniales (Ascomycotina). *Mycotaxon* 48: 301–31.

Ellis, C. J., & Coppins, B. J. (2006). Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography*, *33*(9), 1643-1656.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., & Helkowski, J. H. (2005). Global consequences of land use. *Science*, *309*(5734), 570-574.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology letters*, *12*(6), 561-582.

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., ... & Neill, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. Ecology, 85(9), 2630-2637.

Gauslaa, Y., & Solhaug, K. A. (2004). Photoinhibition in lichens depends on cortical characteristics and hydration. *The Lichenologist*, *36*(2), 133-143.

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, *107*(38), 16732-16737.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*(7369), 378-381.

Gignac, L. D., & Dale, M. R. (2005). Effects of fragment size and habitat heterogeneity on cryptogam diversity in the low-boreal forest of western Canada. *The bryologist*, *108*(1), 50-66.

Giordani, P., Brunialti, G., Bacaro, G., & Nascimbene, J. (2012). Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecological Indicators*, *18*, 413-420.

Giordani, P., Brunialti, G., Benesperi, R., Rizzi, G., Frati, L., & Modenesi, P. (2009). Rapid biodiversity assessment in lichen diversity surveys: implications for quality assurance. *Journal of Environmental Monitoring*, *11*(4), 730-735.

Gradstein, S. R., & Sporn, S. G. (2010). Land-use change and epiphytic bryophyte diversity in the tropics. Cambio en el uso de la tierra y diversidad de briófitas epífitas en los trópicos. *Nova Hedwigia.*, *138*, 311-323.

Gradstein, S.R. (2008). Epiphytes of tropical montane forests—impact of deforestation and climate change. In: *The tropical mountain forest. Patterns and Processes in a Biodiversity Hotspot*. Gradstein, S.R., Homeier, J. and Gansert, D. (eds). University Press, Göttingen, pp. 51–65.

Gray, M. A., Baldauf, S. L., Mayhew, P. J., & Hill, J. K. (2007). The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology*, *21*(1), 133-141.

Green, T.G.A., Nash III, T.H. and Lange, O.L. 2008 Physiological ecology of carbon dioxide exchange. In: *Lichen Biology*. Nash III, T.H. (ed). Cambridge University Press, Cambridge, UK, pp. 152–181.

Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling*, *157*(2), 89-100.

Hauck, M., & Huneck, S. (2007). The putative role of fumarprotocetraric acid in the manganese tolerance of the lichen Lecanora conizaeoides. *The Lichenologist*, *39*(3), 301-304.

Hauck, M., Böning, J., Jacob, M., Dittrich, S., Feussner, I., & Leuschner, C. (2013). Lichen substance concentrations in the lichen Hypogymnia physodes are correlated with heavy metal concentrations in the substratum. *Environmental and Experimental Botany*, *85*, 58-63.

Hauck, M., Willenbruch, K., & Leuschner, C. (2009). Lichen substances prevent lichens from nutrient deficiency. *Journal of chemical ecology*, *35*(1), 71-73.

Hedenås, H., & Ericson, L. (2000). Epiphytic macrolichens as conservation indicators: successional sequence in Populus tremula stands. *Biological conservation*, *93*(1), 43-53.

Hilmo, O., Hytteborn, H., & Holien, H. (2005). Do different logging strategies influence the abundance of epiphytic chlorolichens?. *The Lichenologist*, *37*(6), 543-553.

Holz, I., & Gradstein, R. S. (2005). Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica–species richness, community composition and ecology. *Plant Ecology*, *178*(1), 89-109.

Johansson, P., Wetmore, C. M., Carlson, D. J., Reich, P. B., & Thor, G. (2006). Habitat preference, growth form, vegetative dispersal and population size of lichens along a wildfire severity gradient. *The Bryologist*, *109*(4), 527-540.

Johansson, P., Rydin, H., & Thor, G. (2007). Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience*, *14*(1), 81-91.

Kappen, L. (1988). Ecophysiological relationships in different climatic regions.*Handbook of lichenology*, *2*, 37-100.

Kessler, M., Keßler, P. J., Gradstein, S. R., Bach, K., Schmull, M., & Pitopang, R. (2005). Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. *Biodiversity & Conservation*, *14*(3), 547-560.

Koch, N. M., de Azevedo Martins, S. M., Lucheta, F., & Müller, S. C. (2013). Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. *Ecological indicators*, *34*, 22-30.

Kranner, I., Beckett, R., Hochman, A., & Nash III, T. H. (2008). Desiccation-tolerance in lichens: a review. *The Bryologist*, *111*(4), 576-593.

Lakatos, M. (2002). Ökologische Untersuchungen wuchsformbedingter Verbreitungsmuster von Flechten im tropischen Regenwald.

Lakatos, M., Rascher, U., & Büdel, B. (2006). Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New phytologist*, *172*(4), 679-695.

Laliberte, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., & McNamara, S. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology letters*, 13(1), 76-86.

Laliberte, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., & McNamara, S. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology letters*, 13(1), 76-86.

Lange, O. L., Büdel, B., Meyer, A., & Kilian, E. (1993). Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *The Lichenologist*, 25(2), 175-189.

Lange, O. L., Kilian, E., & Ziegler, H. (1986). Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia*, *71*(1), 104-110.

Larrea, M. L., & Werner, F. A. (2010). Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. *Forest Ecology and Management*, *260*(11), 1950-1955.

Larson, D. W., & Kershaw, K. A. (1975). Measurement of CO2 exchange in lichens: a new method. *Canadian Journal of Botany*, 53(15), 1535-1541.

Laurance, W. F. (2007). Have we overstated the tropical biodiversity crisis?. *Trends in Ecology & Evolution*, *22*(2), 65-70.

Laurance, W. F., Nascimento, H. E., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, *87*(2), 469-482.

Laurance, W. F., Useche, D. C., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., & Hietz, P. (2011). Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, *144*(1), 548-557.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S., Garden, D., Dorrough, J., & Bonis, A. (2008). Assessing functional diversity in the field–methodology matters!. *Functional Ecology*, *22*(1), 134-147.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., & Stork, N. E. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, *391*(6662), 72-76.

Lepš, J., F. de Bello, S. Lavorel, & S. Berman. 2006. Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia* 78:481-501.

Li, S., Liu, W., Wang, L., Ma, W., & Song, L. (2011). Biomass, diversity and composition of epiphytic macrolichens in primary and secondary forests in the subtropical Ailao Mountains, SW China. *Forest Ecology and Management*,*261*(11), 1760-1770.

Li, S., Liu, W. Y., & Li, D. W. (2013). Bole epiphytic lichens as potential indicators of environmental change in subtropical forest ecosystems in southwest China. *Ecological indicators*, *29*, 93-104.

Lundström, J., Jonsson, F., Perhans, K., & Gustafsson, L. (2013). Lichen species richness on retained aspens increases with time since clear-cutting.*Forest Ecology and Management*, *293*, 49-56.

Lücking, R. (1999). Ecology of foliicolous lichens at the ‘Botarrama’trail (Costa Rica), a neotropical rainforest. IV. Species associations, their salient features and their dependence on environmental variables. *The Lichenologist*, *31*(3), 269-289.

Lücking, R., Archer, A.W. & Aptroot, A. (2009) A world-wide key to the genus *Graphis* (Ostropales: Graphidaceae). *The Lichenologist* 41: 363–452

Lücking, R., Chaves, J.L., Sipman, H.J.M., Umaña, L. & Aptroot, A. (2008) A first assessment of the Ticolichen biodiversity inventory in Costa Rica: The genus *Graphis*, with notes on the genus *Hemithecium* (Ascomycota : Ostropales : Graphidaceae). *Fieldiana* 46: 1–130.

Mabry, C. M., & Fraterrigo, J. M. (2009). Species traits as generalized predictors of forest community response to human disturbance. *Forest Ecology and Management*, *257*(2), 723-730.

Magurran, A. E. (2004). Measuring biological diversity. *African Journal of Aquatic Science*, *29*(2), 285-286.

Marini, L., Nascimbene, J., & Nimis, P. L. (2011). Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. *Science of the Total Environment*, *409*(20), 4381-4386.

McCullagh, P. and Nelder, J.A. (1989). Generalized linear models. Second Edition. Monographs on statistics and applied probability 37. Chapman and Hall/CRC, New York, USA.

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, *96*(5), 884-893.

Moncada, B. (2012) *El género Sticta en Colombia: Taxonomía, Ecogeografía e Importancia.* Doctoral thesis, Universidad Nacional de Colombia, Bogotá, 418 pp.

Moncada, B., Coca, L.F. & Lücking, R. (2013) Neotropical members of *Sticta* (lichenized Ascomycota: Lobariaceae) forming photosymbiodemes, with the description of seven new species. *The Bryologist* 116(2): 169–200.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853-858.

Nascimbene, J., Brunialti, G., Ravera, S., Frati, L., & Caniglia, G. (2010). Testing Lobaria pulmonaria (L.) Hoffm. as an indicator of lichen conservation importance of Italian forests. *Ecological Indicators*, *10*(2), 353-360.

Nash III, T. H., Gries, C. & Bungartz, F. (2007) *Lichen Flora of the Greater Sonoran Desert Region*, vol. 3. Lichens Unlimited, Tempe, Arizona, 567 pp.

Nash III, T. H., Ryan, B. D., Gries, C. & Bungartz, F. (2002) *Lichen Flora of the Greater Sonoran Desert Region,* vol. 1. Lichens Unlimited, Tempe, Arizona, 532 pp.

Nash III, T.H., Ryan, B.D., Diederich, P., Gries, C. & Bungartz, F. (2004) *Lichen Flora of the Greater Sonoran Desert Region,* vol. 2. Lichen Unlimited: Tempe, Arizona 742 pp.

Nash, T. H. (1996). *Lichen biology*. Cambridge University Press.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S. R., Sipman, H. J., Obregon, A., & Bendix, J. (2010). Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. *Ecological Indicators*, *10*(6), 1111-1118.

Nöske, N. M., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J., & Gradstein, S. R. (2008). Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. *Basic and Applied Ecology*, *9*(1), 4-12.

Oishi, Y. (2009). A survey method for evaluating drought-sensitive bryophytes in fragmented forests: a bryophyte life-form based approach. *Biological conservation*, *142*(12), 2854-2861.

Pardow, A., Gehrig-Downie, C., Gradstein, R., & Lakatos, M. (2012). Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. *Biodiversity and Conservation*, *21*(14), 3637-3655.

Pinho, P., Bergamini, A., Carvalho, P., Branquinho, C., Stofer, S., Scheidegger, C., & Maguas, C. (2012). Lichen functional groups as ecological indicators of the effects of land-use in Mediterranean ecosystems. *Ecological indicators*, *15*(1), 36-42.

R Development Core Team, (2012). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0 http://www.R-project.org/

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia, 167(1), 181-188.

Rivas-Plata, E., Lücking, R., Aptroot, A., Sipman, H.J.M., Chaves, J.L., Umaña, L. & Lizano, D. (2006) A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (Ostropales: Coenogoniaceae), with a world-wide key and checklist and a phenotype-based cladistic analysis. *Fungal Diversity* 23: 255–321.

Roberts, D.W., (2012). Labdsv: Ordination and Multivariate Analysis for Ecology. Version 1.4-1. http://CRAN.R-project.org/package=labdsv

Rosabal, D., Burgaz, A. R., & De la Masa, R. (2010). Diversity and distribution of epiphytic macrolichens on tree trunks in two slopes of the montane rainforest of Gran Piedra, Santiago de Cuba. *The Bryologist*, *113*(2), 313-321.

Sabatini, F. M., Burton, J. I., Scheller, R. M., Amatangelo, K. L., & Mladenoff, D. J. (2014). Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. *Applied vegetation science*, 17(3), 398-407.

Schulze, C. H., Waltert, M., Kessler, P. J., Pitopang, R., Veddeler, D., Mühlenberg, M., & Tscharntke, T. (2004). Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, *14*(5), 1321-1333.

Sebastião, H., & Grelle, C. E. (2009). Taxon surrogates among Amazonian mammals: Can total species richness be predicted by single orders?. *Ecological indicators*, *9*(1), 160-166.

Sillett, S. C., & Antoine, M. E. (2004). Lichens and bryophytes in forest canopies. *Forest Canopies. Elseiver Academic Press, MA*, 151-174.

Sipman, H.J.M. and Harris, R.C. (1989). Lichens. In: *Tropical Rain Forest Ecosystems.* Lieth, H. and Werger, M.J.A. (eds). Elsevier, Amsterdam, pp. 303–309.

Stofer, S., Bergamini, A., Aragón, G., Carvalho, P., Coppins, B. J., Davey, S., & Lökös, L. (2006). Species richness of lichen functional groups in relation to land use intensity. *The Lichenologist*, *38*(04), 331-353.

Timdal, E. (2008) Studies on *Phyllopsora* (Ramalinaceae) in Peru. *The Lichenologist* 40(4): 337–362.

Vandewalle, M., De Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., ... & Da Silva, P. M. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodiversity and Conservation, 19(10), 2921-2947.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. Oikos, 116(5), 882-892.

Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, *13*(3), 267-283.Wright, S. J. (2005). Tropical forests in a changing environment. Trends in ecology & evolution, 20(10), 553-560.

Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in ecology & evolution*, *20*(10), 553-560.

Appendix A. List of the lichens species with each trait categories. Codes for functional trait categories are described in Table 1.

Species	Photobiont type	Growth form	Size	Reproduction type	Reproductive structure	Ascospore septation	Ascopore size	Thallus colour	Chemistry
Agonimia sp.	C	C	MC	S	P	M	-	D	N
Alectoria ochroleuca (Hoffm.) A. Massal.	C	F	M	N	-	-	-	D	A
Amandinea sp.	C	C	MC	S	A	SP	-	D	N
Amandinea submontana Marbach	C	C	MC	S	A	SP	-	D	N
Anthracothecium macrosporum (Hepp) Müll. Arg.	C	C	MC	S	P	SP	L	D	N
Anzia parasitica (Fée) Zahlbr.	C	FN	M	N	-	-	-	D	A
Arthonia cinnabarina (DC.) Wallr.	T	C	MC	S	A	SP	M	L	A
Arthonia sp.1	T	C	MC	S	A	SP	-	L	A
Arthonia sp.2	T	C	MC	S	A	SP	-	L	A
Arthonia sp.3	T	C	MC	S	A	SP	-	L	A
Arthothelium sp.	T	C	MC	S	L	M	-	L	N
Bacidia sp.1	C	C	MC	S	A	SP	-	L	A
Bacidia sp.2	C	C	MC	S	A	SP	-	L	A
Bacidia sp.3	C	C	MC	S	A	SP	-	L	A
Bacidia sp.4	C	C	MC	S	A	SP	-	L	A
Bacidia sp.5	C	C	MC	S	A	SP	-	L	A
Bacidia sp.6	C	C	MC	S	A	SP	-	L	A
Bacidia sp.7	C	C	MC	S	A	SP	-	L	A
Baculifera remensa (Stirt.) Marbach	C	C	MC	S	A	SP	M	L	A
Badimia sp.	C	C	MC	S	A	SP	-	L	A
Brigantiaea leucoxantha (Spreng.) R. Sant. & Hafellner	C	C	MC	S	A	M	L	L	A
Bryoria sp.	C	F	M	N	-	-	-	D	A
Buellia rhombispora Marbach	C	C	MC	S	A	SP	M	L	A
Bulbothrix apophysata (Hale & Kurok.) Hale	C	FN	M	A	I	-	-	L	A
Bulbothrix coronata (Fée) Hale	C	FN	M	S	A	S	S	L	A

Bulbothrix isidiza (Nyl.) Hale	C	FN	M	AS	A,I	S	S	L	A
Bulbothrix suffixa (Stirton) Hale	C	FN	M	S	A	S	S	L	A
Byssoloma subdiscordans (Nyl.) P. James	C	C	MC	S	A	SP	S	L	N
Canomaculina cristobalii (L.I. Ferraro & Elix) Elix	C	FB	M	A	S	-	-	L	A
Canomaculina pilosa (Stizenb.) Elix & Hale	C	FB	M	A	S	-	-	L	A
Chiodecton sphaerale Ach.	T	C	MC	S	A	SP	-	L	N
Chrysothrix chrysophtalma (P. James) P. James & J. R. Laundon	C	C	MC	S	A	SP	M	D	O
Cladonia coniocraea (Flörke) Sprengel	C	F	M	AS	A,S	S	S	D	A
Cladonia subradiata (Vainio) Sandst.	C	F	M	AS	A,I,S	S	S	L	A
Coccocapia dissecta Swinscow & Krog	CY	FB	M	AS	A,I	S	S	D	N
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	CY	FB	M	S	A	S	S	D	N
Coccocarpia filiformis Arv.	CY	FB	M	S	A	S	S	D	N
Coccocarpia guimarana (Vain.) Swinscow & Krog	CY	FB	M	A	I	-	-	D	N
Coccocarpia microphyllina Lücking & Aptroot	CY	FB	M	AS	A,I	S	S	D	N
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway	CY	FB	M	AS	A,I	S	S	D	N
Coccocarpia pellita (Ach.) Müll. Arg.	CY	FB	M	AS	A,I	S	S	D	N
Coccocarpia prostrata Lücking, Aptroot & Sipman	CY	FB	M	S	A	S	S	D	N
Coccocarpia stellata Tuck.	CY	FB	M	S	A	S	S	D	N
Coccocarpia sp.	CY	FB	M	S	A	S	-	L	N
Coenogonium aff. frederici (Kalb) Kalb & Lücking	T	C	MC	S	A	SP	-	D	N
Coenogonium aff. kawanae (H. Harada & Vezda) H. Harada & Lumbsch	T	C	MC	S	A	SP	-	D	N
Coenogonium bacilliferum (Malme) Lücking, Aptroot & Sipman	T	C	MC	S	A	SP	S	D	N
Coenogonium epiphyllum Vain.	T	FL	MC	S	A	SP	-	D	N

Coenogonium eximium (Nyl.) Kalb & Lücking	T	FL	MC	S	A	SP	S	D	N
Coenogonium isidiosum (Breuss) Rivas Plata, Lücking, Umaña & Chavez	T	C	MC	AS	A,I	SP	S	D	N
Coenogonium kalbii Aptroot, Lücking & Umaña	T	C	MC	S	A	SP	S	D	N
Coenogonium leprieurii (Mont.) Nyl.	T	FL	MC	S	A	SP	S	D	N
Coenogonium linkii Ehrenb.	T	FL	MC	S	A	SP	S	D	N
Coenogonium luteolum (Kalb) Kalb & Lücking	T	FL	MC	S	A	SP	S	D	N
Coenogonium lutescens (Vezda & Malcolm) Malcolm	T	C	MC	S	A	SP	S	D	N
Coenogonium magdalenae Rivas Plata, Lücking & Lizano	T	C	MC	S	A	SP	S	D	N
Coenogonium moniliforme Tuck.	T	FL	MC	S	A	SP	S	D	N
Coenogonium nepalense (G. Thor & Vezda) Lücking, Aptroot & Sipman	T	C	MC	S	A	SP	-	D	N
Coenogonium pertenue (Stirt.) Kalb & Lücking	T	C	MC	S	A	SP	S	D	N
Coenogonium pineti (Ach.) Lücking & Lumbsch	T	FL	MC	S	A	SP	S	D	N
Coenogonium roumeguerianum (Müll. Arg.) Kalb	T	C	MC	S	A	SP	-	D	N
Coenogonium sp.	T	C	MC	S	A	SP	-	D	N
Cresponea leprieurii (Mont.) Egea & Torrente	T	C	MC	S	A	SP	M	D	N
Cresponea melanocheloides (Vain.) Egea & Torrente	T	C	MC	S	A	SP	M	D	N
Cryptothecia effusa (Müll. Arg.) R. Sant.	T	CP	MC	S	A	M	L	L	O
Cryptothecia exilis G. Thor	T	CP	MC	S	A	M	L	D	O
Cryptothecia punctisorediata Sparrius & Saipunkaew	T	CP	MC	AS	A,S	M	L	D	O
Cryptothecia striata Thor	T	CP	MC	S	A	M	L	D	A
Dichosporidium boschianum (Mont.) G. Thor	T	CP	MC	S	A	SP	-	D	N
Diplolabia sp.	T	C	MC	S	L	SP	-	D	O

Echinoplaca sp.	C	C	MC	S	A	SP	-	L	N
Everniastrum cirrhatum (Fr.) Hale ex Sipman	C	F	M	S	A	S	M	L	A
Everniastrum vexans (Zahlbr. *ex* W.L. Culb. & C.F. Culb.) Hale *ex* Sipman	C	F	M	AS	A,I	S	S	L	A
Fellhanera sp.	C	C	MC	S	A	SP	-	L	O
Fissurina sp.1	T	C	MC	S	L	SP	-	D	N
Fissurina sp.2	T	C	MC	S	L	SP	-	D	N
Fissurina triticea (Nyl.) Staiger	T	C	MC	S	L	SP	M	D	O
Flakea papillata O. E. Erikss	C	FN	MC	N	-	-	-	D	O
Flavopunctelia flaventior (Stirt.) Hale	C	FB	M	AS	A,S	S	M	D	A
Glyphis cicatricosa Ach.	T	C	MC	S	A	SP	M	L	N
Glyphis scyphulifera (Ach.) Staiger	T	C	MC	S	A	M	L	L	N
Graphis aff. bettinae Lücking, Umaña, Chaves & Sipman	T	C	MC	S	L	SP	L	L	N
Graphis aff. striatula (Ach.) Spreng.	T	C	MC	S	L	SP	M	L	N
Graphis anfractuosa (Eschw.) Eschw.	T	C	MC	S	L	SP	M	L	N
Graphis bettinae Lücking, Umaña, Chaves & Sipman	T	C	MC	S	L	SP	L	L	N
Graphis cinerea (Zahlbr.) M. Nakan.	T	C	MC	S	L	SP	L	L	N
Graphis conferta Zenker	T	C	MC	S	L	SP	M	L	N
Graphis elixiana A.W. Archer	T	C	MC	S	L	M	L	D	A
Graphis elongatoradians Fink.	T	C	MC	S	L	-	-	L	A
Graphis leptoclada Müll. Arg.	T	C	MC	S	L	SP	M	L	N
Graphis leptogramma Nyl.	T	C	MC	S	L	SP	M	L	N
Graphis myrtacea (Müll. Arg.) Lücking	T	C	MC	S	L	M	L	L	N
Graphis pinicola Zahlbr.	T	C	MC	S	L	SP	M	L	N
Graphis ruiziana (Fée) A. Massal.	T	C	MC	S	L	M	L	L	N
Graphis scaphella (Fée) A. Massal.	T	C	MC	S	L	M	L	L	N

Graphis sitiana Vain.	T	C	MC	S	L	SP	M	L	N
Graphis streblocarpa (Bél.) Nyl.	T	C	MC	S	L	M	L	L	A
Graphis subcontorta (Müll. Arg.) Lücking & Chaves	T	C	MC	S	L	M	L	L	N
Graphis subserpentina Nyl.	T	C	MC	S	L	M	L	L	N
Graphis sp.	T	C	MC	S	L	-	-	L	N
Gyalecta sp.	T	C	MC	S	A	SP	-	L	N
Haematomma africanum (J. Steiner) C.W. Dodge	C	C	MC	S	A	SP	M	L	A
Haematomma flexuosum Hillm.	C	C	MC	S	A	SP	M	L	A
Herpothallon aff. roseocinctum (Fr.) Aptroot, Lücking & G. Thor	T	CP	MC	A	I	-	-	D	O
Herpothallon confusum G. Thor	T	CP	MC	A	I	-	-	D	O
Herpothallon granulare (Sipman) Aptroot & Lücking	T	CP	MC	A	I	-	-	D	O
Herpothallon hypoprotocetraricum G. Thor	T	CP	MC	A	I	-	-	D	A
Herpothallon rubrocinctum (Ehrenb.) Aptroot & Lücking	T	CP	MC	A	I	-	-	D	O
Herpothallon sp.1	T	CP	MC	A	I	-	-	D	O
Herpothallon sp.2	T	CP	MC	A	I	-	-	D	O
Herpothallon sp.3	T	CP	MC	A	I	-	-	D	O
Heterodermia aff. galactophylla (Tuck.) W.L. Culb.	C	FN	M	A	S	-	-	L	A
Heterodermia comosa (Eschw.) Follmann & Redón	C	FN	M	S	A	SP	L	L	A
Heterodermia corallophora (Taylor) Skorepa	C	FN	M	AS	A,I	SP	L	L	A
Heterodermia diademata (Taylor) D.D. Awasthi	C	FN	M	S	A	SP	M	L	A
Heterodermia galactophylla (Tuck.) W.L. Culb.	C	FN	M	A	S	-	-	L	A
Heterodermia hypochraea (Vain.) Swinscow & Krog	C	FN	M	A	I	-	-	L	A
Heterodermia hypoleuca (Mühl.) Trevis.	C	FN	M	S	A	SP	M	L	A
Heterodermia isidiophora (Nyl.) D.D. Awasthi	C	FN	M	AS	A,I	SP	M	L	A

Heterodermia japonica (M. Satô) Swinscow & Krog	C	FN	M	AS	A,S	SP	L	L	A
Heterodermia leucomela (L.) Poelt	C	FN	M	AS	A,S	SP	L	L	A
Heterodermia microphylla (Kurok.) Swinscow & Krog	C	FN	M	A	S	-	-	L	A
Heterodermia palpebrata (Taylor) Trass	C	FN	M	S	A	SP	L	L	A
Heterodermia sitchensis Goward & W.J.Noble	C	FN	M	AS	A,S	SP	S	L	A
Heterodermia spathulifera Moberg & Purvis	C	FN	M	AS	A,S	SP	L	L	A
Heterodermia subcitrina Moberg	C	FN	M	AS	A,S	SP	M	L	A
Heterodermia sp.	C	FN	M	A	S	-	-	L	A
Hypoflavia velloziae (Kalb) Marbach	C	C	MC	S	A	SP	-	L	N
Hypotrachyna aff. degelii (Hale) Hale	C	FN	M	A	S	-	-	L	A
Hypotrachyna bogotensis (Vain.) Hale	C	FN	M	AS	A,I	S	S	L	A
Hypotrachyna costaricensis (Nyl.) Hale	C	FN	M	AS	A,I	S	S	L	A
Hypotrachyna densirhizinata (Kurok.) Hale	C	FN	M	AS	A,S	S	M	L	A
Hypotrachyna eitenii (Hale) Hale	C	FN	M	S	A	S	S	L	A
Hypotrachyna rachista (Hale) Hale	C	FN	M	A	I	-	-	L	A
Hypotrachyna reducens (Nyl.) Hale	C	FN	M	S	A	S	S	D	A
Hypotrachyna revoluta (Flörke) Hale	C	FN	M	AS	A,S	S	S	L	A
Hypotrachyna rockii (Zahlbr.) Hale	C	FN	M	AS	A,S	S	S	L	A
Hypotrachyna sp.	C	FN	M	A	S	-	-	L	A
Lecanora caesiorubella Ach.	C	C	MC	S	A	S	S	L	A
Lecanora chlarothera Nyl.	C	C	MC	S	A	S	S	L	A
Lecanora flavidomarginata B. de Lesd.	C	C	MC	S	A	S	S	L	A
Lecanora helva Stizenb.	C	C	MC	S	A	S	M	L	A
Lecanora neonashii Lumbsch	C	C	MC	S	A	S	S	L	A
Lecanora varia (Hoffm.) Ach.	C	C	MC	S	A	S	S	L	A
Lecanora sp.	C	C	MC	S	A	S	-	L	A

Leioderma glabrum D. J. Galloway & P. M. Jørg.	CY	FB	M	S	A	S	S	L	N
Leiorreuma exaltatum (Mont. & Bosch) Staiger	C	C	MC	S	A	SP	M	D	N
Lepraria sp.1	C	C	MC	A	S	-	-	L	A
Lepraria sp.2	C	C	MC	A	S	-	-	L	A
Leptogium austroamericanum (Malme) C.W. Dodge	CY	G	M	AS	A,I	SP	M	D	N
Leptogium azureum (Sw.) Mont.	CY	G	M	S	A	SP	M	D	N
Leptogium burgesii (L.) Mont.	CY	G	M	S	A	M	M	D	N
Leptogium burnetii Dodge	CY	G	M	A	I	-	-	D	N
Leptogium chloromelum (Ach.) Nyl.	CY	G	M	S	A	M	M	D	N
Leptogium cochleatum (Dicks.) P.M. Jørg. & P. James	CY	G	M	S	A	M	M	D	N
Leptogium coralloideum (Meyen & Flot.) Vain.	CY	G	M	AS	A,I	M	M	D	N
Leptogium corticola (Taylor) Tuck.	CY	G	M	S	A	M	M	D	N
Leptogium cyanescens (Pers.) Körb.	CY	G	M	AS	A,I	M	M	D	N
Leptogium diaphanum (Sw.) Mont.	CY	G	M	A	I		-	D	N
Leptogium laceroides B. de Lesd.	CY	G	M	AS	A,I	M	M	D	N
Leptogium marginellum (Sw.) Gray	CY	G	M	AS	A,I	M	M	D	N
Leptogium millegranum Sierk	CY	G	M	A	A,I	SP	M	D	N
Leptogium olivaceum (Hook.) Zahlbr.	CY	G	M	A	I		-	D	N
Leptogium phyllocarpum (Pers.) Mont.	CY	G	M	S	A	M	L	D	N
Lithothelium sp.1	T	C	MC	S	P	SP	-	D	N
Lithothelium sp.2	T	C	MC	S	P	SP	-	D	N
Lobaria erosa (Eschw.) Nyl.	CY	FB	M	S	A	SP	-	D	N
Lobaria tenuis Vain.	C	FB	M	AS	A,I	SP	M	D	A
Lobariella crenulata (Hook.) Yoshim.	CY	FB	M	S	A	SP	M	D	O

Lobariella exornata (Zahlbr.) Yoshim.	CY	FB	M	AS	A,I	SP	L	L	O
Lobariella pallida (Hook.) Yoshim.	CY	FB	M	S	A	SP	-	L	O
Lopezaria versicolor (Fée) Kalb & Hafellner	C	C	MC	S	A	SP	L	L	
Malcolmiella fuscella (Müll. Arg.) M. Cáceres & Lücking	C	C	MC	S	A	S	-	L	N
Malcolmiella gyalectoides (Vain.) Cáceres & Lücking	C	C	MC	S	A	S	-	L	N
Malcolmiella sp.	C	C	MC	S	A	S	-	L	N
Malmidea aff. rhodopis (Tuck.) Kalb, Rivas Plata & Lumbsch	C	C	MC	S	A	S	S	D	O
Maronea constans (Nyl.) Hepp	C	C	MC	S	A	S	S	L	O
Maronina multifera (Nyl.) Hafellner & R. W. Rogers	C	C	MC	S	A	SP	-	L	N
Megalaria sp.1	C	C	MC	S	A	SP	-	L	N
Megalaria sp.2	C	C	MC	S	A	SP	-	L	N
Megalospora admixta (Nyl.) Sipman	C	C	MC	S	A	M	L	L	O
Megalospora melanodermia (Müll. Arg.) Zahlbr.	C	C	MC	S	A	SP	L	L	A
Megalospora sulphurata var. nigricans (Müll. Arg.) Riddle	C	C	MC	S	A	SP	-	L	A
Megalospora sulphurata var. sulphurata Meyen	C	C	MC	S	A	SP	-	L	A
Megalospora tuberculosa (Fee) Sipman	C	C	MC	S	A	SP	L	L	A
Megalospora sp.	C	C	MC	S	A	SP	-	L	A
Micarea sp.1	C	C	MC	S	A	SP	-	L	N
Micarea sp.2	C	C	MC	S	A	SP	-	L	N
Micarea sp.3	C	C	MC	S	A	SP	-	L	N
Mycomicrothelia subfallens (Mull. Arg.) D. Hawksw.	T	C	MC	S	P	SP	S	L	N
Myeloconis sp.	T	C	MC	S	P	M	-	L	N
Normandina pulchella (Borrer) Nyl.	C	S	MC	AS	P,S	SP	M	L	N
Ocellularia sp.	T	C	MC	S	A	SP	-	L	O
Ochrolechia pseudopallescens Brodo	C	C	MC	S	A	S	L	L	O

Ochrolechia sp.	C	C	MC	S	A	S	-	L	O
Opegrapha sp.	C	C	MC	S	L	SP	-	L	N
Pannaria conoplea (Ach.) Bory	CY	FP	M	AS	A,I	S	M	D	O
Pannaria mosenii C.W. Dodge	CY	FP	M	AS	A,I	S	M	D	N
Pannaria prolificans Vain.	CY	FP	M	AS	A,I	S	-	D	N
Parmeliella andina P.M. Jørg. & Sipman	CY	FP	M	S	A	S	-	D	N
Parmeliella delicata P.M. Jørg. & Arv.	CY	FP	M	S	A	S	-	D	N
Parmeliella miradorensis Vain.	CY	FP	M	S	A	S	M	D	N
Parmeliella sp.	CY	FP	M	S	A	-	-	D	
Parmelinopsis miniarum (Vain.) Elix & Hale	C	FP	M	AS	A,I	S	M	L	A
Parmotrema aff. exquisitum (Kurok.) DePriest & B.W. Hale	C	FB	M	A	S	-	-	L	A
Parmotrema arnoldii (Du Rietz) Hale	C	FB	M	AS	A,S	S	M	L	A
Parmotrema austrosinense (Zahlbr.) Hale	C	FB	M	AS	A,S	S	M	L	A
Parmotrema cristiferum (Taylor) Hale	C	FB	M	A	A,S	S	M	L	A
Parmotrema exquisitum (Kurok.) DePriest & B.W. Hale	C	FB	M	A	S	-	-	L	A
Parmotrema internexum (Nyl.) Hale *ex* DePriest & B.W. Hale	C	FB	M	AS	A,I	S	S	L	A
Parmotrema mellisii (Dodge) Hale	C	FB	M	AS	A,I	S	M	L	A
Parmotrema peralbidum (Hale) Hale	C	FB	M	AS	A,I	S	S	L	A
Parmotrema rampoddense (Nyl.) Hale	C	FB	M	AS	A,S	S	S	L	A
Parmotrema zollingeri (Hepp) Hale	C	FB	M	S	A	S	M	L	A
Peltigera sp.	CY	FB	M	N	-	-	-	D	N
Pertusaria aff. papillata (Ach.) Tuck	C	C	MC	S	A	S	-	L	A
Pertusaria excludens Nyl.	C	C	MC	A	A,S	S	-	L	A
Pertusaria hypothamnolica Dibben	C	C	MC	S	A	S	-	L	A
Pertusaria multipunctoides	C	C	MC	S	A	S	-	L	A

Pertusaria ventosa Malme	C	C	MC	S	A	S	-	L	A
Pertusaria sp.1	C	C	MC	S	A	S	-	L	A
Pertusaria sp.2	C	C	MC	S	A	S	-	L	A
Pertusaria sp.3	C	C	MC	S	A	S	-	L	A
Pertusaria sp.4	C	C	MC	S	A	S	-	L	A
Phaeographis "scalpturatilla"	T	C	MC	S	L	SP	-	L	O
Phaeographis brasiliensis (A. Massal.) Kalb & Matthes-Leicht	T	C	MC	S	L	SP	M	L	A
Phaeographis brevinigra Sipman	T	C	MC	S	L	SP	-	L	O
Phaeographis dendritica (Ach.) Müll. Arg.	T	C	MC	S	L	SP	M	L	A
Phaeographis inconspicua (Fée) Müll. Arg.	T	C	MC	S	L	SP	S	L	A
Phaeographis scalpturata (Ach.) Staiger	T	C	MC	S	L	M	L	L	N
Phaeographis sp.	T	C	MC	S	L	SP	-	L	A
Phaeophyscia aff. limbata (Poelt) Kashiw.	C	FN	M	N	-	-	-	L	A
Phlyctella sp.1	C	C	MC	S	A	M	-	D	N
Phlyctella sp.2	C	C	MC	S	A	M	-	D	N
Phyllopsora chlorophaea (Müll. Arg.) Zahlbr.	C	S	MC	AS	A,I	S	S	D	N
Phyllopsora fendleri (Tuck. & Mont.) Müll. Arg.	C	S	MC	S	A	S	S	D	N
Phyllopsora furfuracea (Pers.) Zahlbr.	C	S	MC	AS	A,I	S	S	D	O
Phyllopsora glaucescens Timdal	C	S	MC	S	A	S	S	D	O
Phyllopsora hispaniolae Timdal	C	S	MC	AS	A,I	S	S	D	O
Phyllopsora isidiotyla (Vain.) Riddle	C	S	MC	AS	A,I	S	S	D	A
Phyllopsora parvifolia (Pers.) Mull. Arg.	C	S	MC	S	A	S	S	D	N
Phyllopsora parvifoliella (Nyl.) Mull. Arg.	C	S	MC	AS	A,I	S	S	D	A
Phyllopsora santensis (Tuck.) Swinscow & Krog	C	S	MC	AS	A,I	S	S	D	A
Phyllopsora sp.	C	S	MC	S	A	S	-	D	O
Porina aff. nucula	T	C	M	S	P	SP	L	D	N

Ach.			C						
Porina imitatrix Müll. Arg.	T	C	MC	S	P	SP	M	D	N
Porina internigrans (Nyl.) Müll. Arg.	T	C	MC	S	P	SP	M	D	N
Porina nucula Ach.	T	C	MC	S	P	SP	L	D	N
Porina sp.	T	C	MC	S	P	SP	-	D	N
Pseudocyphellaria aurata (Ach.) Vain.	C	FB	M	AS	A,S	SP	M	D	O
Pseudocyphellaria crocata (L.) Vain.	CY	FB	M	AS	A,S	SP	M	D	O
Punctelia crispa Marcelli, Jungbluth & Elix	C	FB	M	A	I	-	-	L	A
Punctelia reddenda (Stirt.) Krog	C	FB	M	A	I	-	-	L	A
Pyrenula aff. falsaria (Zahlbr.) R. C. Harris	T	C	MC	S	P	M	L	D	N
Pyrenula aff. mamillana (Ach.) Trevisan	T	C	MC	S	P	SP	M	D	N
Pyrenula andina Aptroot	T	C	MC	S	P	SP	M	D	O
Pyrenula cf. nitidula (Bresadola) R. C. Harris	T	C	MC	S	P	SP	M	D	N
Pyrenula macrocarpa A. Massal.	T	C	MC	S	P	SP	M	D	N
Pyrenula mastophoroides (Nyl.) Zahlbr.	T	C	MC	S	P	SP	L	D	N
Pyrenula microcarpa Mull. Arg.	T	C	MC	S	P	SP	M	D	N
Pyrenula microtheca R. C. Harris	T	C	MC	S	P	SP	M	D	N
Pyrenula tenuisepta R. C. Harris	T	C	MC	S	P	SP	M	D	N
Pyrenula sp.1	T	C	MC	S	P	SP	-	D	N
Pyrenula sp.2	T	C	MC	S	P	SP	-	D	N
Pyrenula sp.3	T	C	MC	S	P	SP	-	D	N
Pyrenula sp.4	T	C	MC	S	P	SP	-	D	N
Pyrgillus sp.	T	C	MC	S	P	SP	-	D	N
Ramalina celastri (Spreng.) Krog & Swinscow	C	F	M	S	A	SP	S	L	A
Ramalina cochlearis Zahlbr.	C	F	M	A	S	-	-	L	A
Ramalina peruviana Ach.	C	F	M	A	S	-	-	L	A
Ramalina sp.	C	F	M	S	A	-	-	L	A
Ramonia sp.	T	C	MC	S	A	S	-	L	N
Relicina abstrusa (Vain.) Hale	C	FN	M	AS	A,I	S	S	L	A

Rimelia subisidiosa (Müll. Arg.) Hale & A. Fletcher	C	FN	M	AS	A,I	S	M	L	A
Rimelia succinreticulata Eliasaro & Adler	C	FN	M	A	S	-	-	L	A
Rinodina sp.1	C	C	MC	S	A	SP	-	L	N
Rinodina sp.2	C	C	MC	S	A	SP	-	L	N
Sarcographa fenicis (Vain.) Zahlbr*.*	T	C	MC	S	L	SP	M	D	A
Squamacidia janeirensis (Müll. Arg.) Brako	C	S	MC	S	A	S	-	D	N
Squamacidia sp.	C	S	MC	S	A	S	-	D	N
Sticta andensis (Nyl.) Trevis.	CY	FB	M	S	A	SP	M	D	N
Sticta ferax Müll. Arg.	CY	FB	M	S	A	SP	-	D	N
Sticta fuliginosa (Dicks.) Ach.	CY	FB	M	AS	A,I	SP	M	D	N
Sticta humboldtii Hook.	CY	FB	M	S	A	SP	M	D	N
Sticta laciniata (Sw.) Ach.	CY	FB	M	S	A	SP	-	D	N
Sticta lobarioides Moncada & Coca	C	FB	M	S	A	SP	M	D	N
Sticta neolinita Gyeln*.*	C	FB	M	S	A	SP	M	D	N
Sticta neopulmonarioides Moncada & Coca	C	FB	M	S	A	SP	M	D	N
Sticta tomentosa (Sw.) Ach.	CY	FB	M	S	A	SP	M	D	N
Sticta weigelii (Ach.) Vain.	CY	FB	M	A	I	-	-	D	N
Sticta sp. 1	CY	FB	M	N	-	-	-	D	N
Sticta sp. 2	CY	FB	M	S	A	SP	-	D	N
Teloschistes flavicans (Sw.) Norman	C	F	M	AS	A,S	SP	S	D	A
Tephromela atra (Hudson) Hafellner	C	C	MC	S	A	S	S	L	A
Thelotrema aff. hawaiense (Hale) Hale	T	C	MC	S	A	M	-	L	A
Thelotrema hawaiense (Hale) Hale	T	C	MC	S	A	M	-	L	A
Thelotrema sp.1	T	C	MC	S	A	-	-	L	A
Thelotrema sp.2	T	C	MC	S	A	-	-	L	A
Thelotrema sp.3	T	C	MC	S	A	-	-	L	A
Trichothelium horridulum (Mull. Arg.) R. Sant.	T	C	MC	S	P	M	-	D	N
Trypethelium sp.	T	C	MC	S	P	SP	-	L	N
Usnea sp. 1	C	F	M	N	-	-	-	L	A

Usnea sp. 2	C	F	M	N	-	-	-	L	A
Usnea sp. 3	C	F	M	N	-	-	-	L	A
Usnea sp. 4	C	F	M	N	-	-	-	L	A
Yoshimuriella dissecta (Sw.)B. Moncada & Lücking	C	FB	M	AS	A,I	SP	-	D	N
Yoshimuriella subdissecta (Nyl.)B. Moncada & Lücking	C	FB	M	AS	A,I	SP	-	D	N

Photobiont type: C=Chlorococcoid; CY=Cyanobacteria; T=Trentepholia; Growth forms: C= Crustose; CP=Crustose with prothallus; FB= Foliose broad lobed; FN= Foliose narrow lobed; FP= Foliose placodiod; FL=Filamentose; F=Fruticose, G=Gelatinose; S=Squamulose; Size: M=Macrolichens; MC=Microlichens; Reproduction type: A=Asexual; S=Sexual; AS=Asexual and sexual; N=None; Reproductive structure: A=Apothecia; I=Isidia; L=Lirellae; P=Perithecia; S=Soredia; Ascospore septation: S=Simple; S=Septate; M=Muriform; Ascopore size: S=Small (<100 µm); M=Medium (>100 µm); L=Large (>500 µm); Thallus colour: D=Dark; L=Light; Chemistry: A=Acids; O = Other compounds; N= No compounds.

CAPÍTULO IV / CHAPTER IV

Lichen diversity in tropical dry forest is influenced by host preference more that disturbance

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Abstract

Tropical dry forests have been recognized as one of the most threatened ecosystems in the world resulting from deforestation. Epiphytes species might have high levels of endemism and play a major role in the functioning of these ecosystems. Lichens constitute an important fraction of the epiphytes. These poikilohydric organisms respond drastically to increasing disturbance that is strongly linked to humidity and light availability. We hypothesized that differences in richness and composition would be related to differences in forest structure (e.g. canopy openness), however epiphytic communities are limited by host preference, due to the fact that dry forests generally have poor microclimatic stratification and low diversity in tree species. In this study, we assessed the richness and composition of epiphytes (lichens and bryophytes) on the trunks of 513 trees in nondisturbed and disturbed forests of southern Ecuador. We found that total richness tended to decrease in disturbed forests. The impoverishment was particularly drastic due to changes in forest structure in disturbed forest and the removal of potential host trees (*Eriotheca ruizii* and *Cochlospermum vitifolium*). Although, epiphytic composition also differed significantly among the two types of forests, more variability was explicated by species of host trees. We concluded that epiphytic communities (lichens and bryophytes) in seasonally dry tropical forests of Ecuador are limited by host traits, particularly species of host trees and bark texture.

Keywords: Diversity, Dry forest, Ecuador, forest disturbance, host traits, bark texture, lichens.

Introduction

Tropical dry forests are one of the most threatened ecosystems in the world and harbor high levels of endemic species (Janzen 1988; Dinerstein et al., 1995; Fajardo et al., 2005; Miles et al., 2006). These forests have been intensively deforested over time, and a large proportion of the original woodlands has been transformed into isolated fragments, pastures and croplands, due to timber or fuelwood extraction and cattle grazing (Kalacska et al., 2005; Fajardo et al., 2005; Leal-Pinedo & Linares-Palomino 2005). In Ecuador, dry forests are located in the Tumbesian region (Dinerstein et al., 1995) which is recognized as a hotspot (Janzen 1988). Unfortunately, at present annual deforestation of these dry forests are near 1%, and only 5% of the 55,000 km^2 of remaining dry forests are currently protected (i.e, conservation areas) (Linares-Palomino et al., 2010; Sierra 2013).

However, dry forests have received little attention compared with rain forests, and studies analyzing the disturbance effects are still scarce (Gillespie et al., 2000; Avila-Cabadilla et al., 2009; Espinosa et al., 2011; Rosa-Manzano et al., 2014). Several studies show that dry forests have a lower vascular epiphyte diversity than tropical rain forests (Gentry & Dodson 1987; Yeaton & Gladstone 1982; Werner & Gradstein 2009; Higuera & Wolf 2010; Vergara-Torres et al., 2010; Rosa-Manzano et al., 2014). Nevertheless, dry forests epiphytes can have high levels of endemism and may play a major role in the functioning of these ecosystems (Werner 2008).

Understanding how disturbance of the original habitats affect epiphytes is critical for the conservation of biodiversity in the threatened dry forests. In general, most studies showed that forest disturbance greatly affect the diversity of epiphytic communities in tropical rain forests (Barthlott et al., 2001; Acebey et al., 2003; Krömer & Gradstein 2003; Wolf 2005; Gradstein 2008; Nöske et al., 2008; Gradstein & Sporn, 2010), including non-vascular epiphytes (bryophytes and lichens) (Werner & Gradstein 2009 Benitez et al., 2015). However very little is known about the effects of disturbance on epiphyte diversity of the dry forests.

Bryophytes and lichens constitute an important fraction of epiphytic organisms (Holz & Gradstein 2005; Mandl et al., 2010), and due to their physiology are strongly linked to humidity, solar irradiance and temperature conditions (Nash 1996; Green et al., 2008; Kranner et al., 2008; Aragón et al., 2010; Marini et al., 2011). Therefore, forest logging produces changes in the canopy layer that are associated with changes in microclimate (e.g. humidity and light availability), and which have negative consequences for shade-adapted species due to stress by desiccation (Werner et al., 2005; Gradstein 2008; Gradstein & Sporn 2010; Normann et al., 2010; Rosa-Manzano et al., 2014).

Epiphytes generally show little or no vertical stratification in seasonally dry forests, due to the fact that the gradients in humidity and exposures are not as great in comparison with wet forests (Benzing 1990; Graham & Andrade 2004). These forests are less complex in terms of tree diversity and forests structure (Murphy & Lugo 1986), and their canopies tend to be lower and more open, which results in poor microclimatic stratification (Graham & Andrade 2004). Thus, it is expected that epiphytes in dry forests could be more tolerant to the microclimatic consequences of canopy openness caused by disturbance.

Based on this premise, phorophyte specificity could be used indirectly to measure disturbance effects in the diversity of epiphytic, due to the fact that this process reduces the diversity of host trees (Cáceres et al., 2007). Epiphytic species directly exploit trees as substrate for their establishment, and it is well-known that forest logging has immediate negative effects on their persistence, due to the removal of host trees (Gradstein 2008). Thus, several studies have showed that epiphytes were influenced by the diversity of trees (McGee & Kimmerer 2002; Nascimbene et al., 2009, Király et al., 2013). This result emphasizes the importance of tree species related to host preference of epiphytes (Berg et al., 2002; García-Suárez et al., 2003; Szövényi et al. 2004; Löbel et al., 2006; Hirata et al., 2009; Vergara-Torres et al., 2010; Király et al., 2013). Host trees provide key traits limiting the epiphyte diversity and distribution, for example tree size, bark texture and chemistry; and the species of host tree (Cáceres et al., 2007; Hirata et al., 2009; Rosabal et al., 2013; Benitez et al., 2015). Tree size also plays an important role in colonization related to the available area for the epiphytes establishment (Fritz et al., 2008; Ranius et al., 2008; Aragón et al., 2010). As well, bark structure (roughness and texture) and pH determine distribution and establishment of epiphytes (Cáceres et al. 2007; Rosabal et al., 2013).

Host preference may be disadvantageous for epiphytes in tropical forests since it would reduce opportunities for establishment, due to high tree diversity and the complex structure of these forest (Cáceres et al., 2007; Rosabal et al., 2013). Most studies have found little or no evidence between host trees and epiphyte diversity in tropical forests (Sipman & Harris 1989; Cornelissen & ter Steege 1989; Montfoort & Ek 1990; Cáceres et al., 2007; Soto-Medina et al., 2012; Rosabal et al., 2013). However, the current knowledge cannot be extrapolated to those communities inhabiting dry forests, due to its peculiar characteristics: (1) strong seasonality of abiotic conditions related with water availability (Mooney et al., 1995), (2) forest structure with lower and more open canopies (Graham & Andrade 2004), and (3) low diversity of tree species (Murphy & Lugo 1986; Gentry 1995). In this context, host preferences may be an important factor influencing epiphyte communities in tropical dry forest. This idea is supported by several studies that found relation between host tree species and epiphyte diversity (Löbel et al., 2006; Hirata et al., 2009; Vergara-Torres et al., 2010). Host preference is driven by bark characteristics, such as texture, water-holding capacity, nutrient status, and chemical composition (Callaway et al., 2002; Cáceres et al., 2007; Rosabal et al., 2013).

The goal of this study was to compare richness and composition of epiphytic communities along a disturbance gradient in dry forests. We hypothesized that epiphytic diversity and composition would be affected by differences in forest structure (e.g., canopy openness) and microclimate caused by forest logging. A second objective was to determine the effects of the host traits (e.g., host species, tree size and bark texture) on the diversity of epiphytic communities.

Methods

Study area

The study was conducted in the Ecological Reserve Arenillas (REA), located in El Oro province (southwest Ecuador). The Reserve comprises approximately 17 ha (Figure 1), with a transitional vegetation of dry deciduous forests and dry scrubs of lowlands. The altitude ranged from 0–300 m a.s.l., with average temperature between 21-25 °C with a maximum variation of 3.4°C between the coldest and warmest months (Espinosa et al., 2015). The climate is characterized by two distinct seasons, the rainy and dry seasons with an average precipitation of 515 mm and 152 mm, respectively (weather station Huaquillas for a record period of 45 years, 1969-2014).

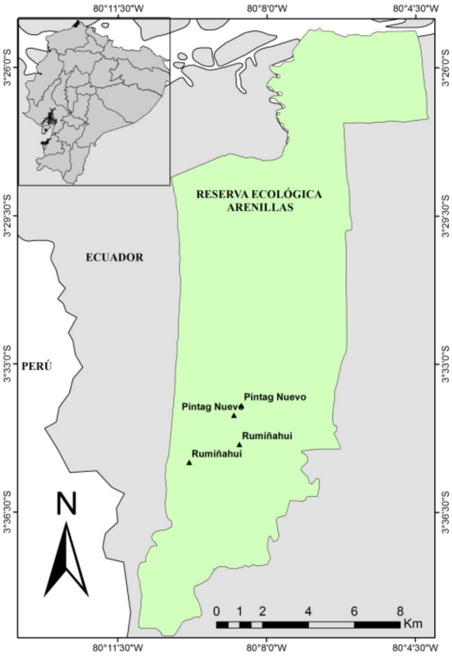

Figure 1. Study area in Ecological Reserve Arenillas (REA) of southern Ecuador showing the location of the four tropical dry forest sites.

Field work was carried out in four deciduous forests, at 40 - 50 m a.s.l. We selected two well-preserved forests within a protected area and two disturbed forests surrounding the protected area. The most conspicuous tree species occurring in well-preserved forests were *Bursera graveolens* (Kunth) Triana & Planch. (Burseraceae), *Eriotheca ruizii* (K. Schum.) A. Robyns (Malvaceae), *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae), *Cynophalla mollis* (Kunth) J. Presl (Capparaceae) and *Tabebuia chrysantha* G. Nicholson (Bignoniaceae), together with several shrubs as *Malpighia emarginata* L. (Malpighiaceae) and *Croton* species. Disturbed forests are characterized by having less shrub vegetation and tree density. These forests are characterized by scattered trees that had presumably established as isolated trees prior to abandonment of use (e.g. selective logging or pastures) and their architecture is resembled that of trees in undisturbed forest (Werner & Gradstein 2009).The dominant tree species were *T. chrysantha, C. mollis* and *Ziziphus thyrsiflora* Benth. (Rhamnaceae).

Sampling design and data collection

Four plots of 20 m × 20 m (400 m^2) were randomly selected within each forest. The distance between plots within a forest was over 100 m. Within each plot all trees and shrubs with mean tree diameter (DBH) above 5 cm were measured and identified.

For shrubs and trees, lichens and bryophytes were sampled using four 10×60 cm and 20×30 cm grids, respectively. Samples were taken on each tree at two different heights (0–100, and 101–200 cm) on the northern and southern exposed sides (a total of four samples per tree). We determined the presence and coverage of epiphytic lichens and bryophytes on 513 host trees. In addition, we measured the elevation (m asl), slope (°), aspect (cosine transformed), canopy openness (%) and mean tree diameter (cm) within each plot as a proxy to the stand forest structure. For species identification, we used general (Brodo et al. 2001, Nash et al. 2002, 2004, 2007) and specific keys (e.g. Egea & Torrente 1993; Tehler 1997; Rivas-Plata et al., 2006; Cáceres 2007; Aptroot et al., 2008; Lücking et al., 2008, 2009; Rivas-Plata et al., 2010; Aptroot 2012; Aptroot et al., 2014). The total species richness was defined as the total number of species found in the four grids per tree. For the lichen composition, we calculated the mean estimated cover of each species in the four sample grids.

Light conditions were recorded by measuring canopy openness (%) using sixteen digital hemispherical photographs by plot. The distance between photographs within a plot was 5 m. Digital photographs were always taken on overcast days and at breast height (1.3 meter height), using a horizontally leveled digital camera (Nikon Coolpix 4500) aimed at the zenith, using the fish-eye lens FCE8, Nikon. Photographs were analyzed using the free software Gap Light Analyzer (GLA) ver. 2.0 (Frazer et al., 2000).

Host tree traits

Measured host tree parameters included tree species, mean tree diameter (DBH), slope (°), aspect (cosine transformed), bark depth (mm) and bark texture Bark texture was assessed in four ordered categories: 1 = Completely smooth, 2 = Smooth without marked fissures, 3= Rough with fissures and 4 = Fissured with deep crevices (Mistry 1998, Mistry & Berardi, 2005; Cáceres et al., 2007; Vergara-Torres et al., 2010).

Data analyses

Alpha diversity was calculated using the Simpson diversity index and the Shannon diversity index (Magurran 2004). The Simpson index is considered as a measure of species dominances, and the Shannon index was based on the assumption that individuals were randomly selected and that all species were represented in the sample (Magurran, 2004). This diversity indices were calculated for each tree and plot with PRIMER v 6.1.11 software

The effect of environmental variables on the richness and diversity of epiphytes was modelled by fitting Generalized Mixed Linear Models (GLMMs) (McCullagh & Nelder 1989). Seven factors related to forest structure were used as predictors: canopy openness, elevation, slope, aspect, bark depth, mean tree diameter and tree richness. Predictors were included as explanatory variables (fixed factors), and forest and plot were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. We fitted the mixed models using a Poisson distribution. All GLMM computations were performed using SAS (GLIMMIX ver. 8 for SAS/STAT).

The effects of host traits on the richness of bryophyte and lichen species were also analyzed using generalized linear models (GLM; McCullagh & Nelder 1989), assuming Poisson errors for the response variables. Six host traits were used as predictors: tree species, trunk diameter (cm), slope (°), aspect (cosine transformed), bark depth (mm) and bark texture. In this model, only woody tree species were chosen as potential host trees (Table 1), since they are the most conspicuous and numerous tree species in the dry forest. In addition, the majority of epiphytes (112 species) preferred this small group of host species, leading us to adjust a dataset of 112 species × 336 trees.

To test whether the two levels of disturbance had different composition of epiphytic species and to detect the effects of forest, plot and host variability, we performed a three-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008). In this analysis, the experimental design included three factors: forest (4 levels, fixed factor), plot (4 levels, random factor nested within forest) and host tree (22 levels, random factor nested within plot and forest) and the trees constituted the replicate (N=513). The cover data (cover percentage of each lichen per tree) were log10 (x+1)-transformed to account for contributions by both rare and abundant taxa.

Non-metric multidimensional scaling (NMDS) was performed to detect the main factors influencing the epiphytic composition. We used the Bray–Curtis dissimilarity distance to compute the resemblance matrix between trees. The results were plotted in a NMDS ordination diagram. Values of the relative species cover and environmental variables were then fitted into the first two axes of the NMDS ordination. Squared correlation coefficients (r^2) and empirical *p*-values (*p*) were calculated for these linear fittings.

Ordination was performed with package ‘vegan’ (Oksanen et al., 2011) in the R environment (R Development Core Team, 2011).

Results

A total of 123 epiphytic species (122 lichens and one bryophyte) were recorded and collected in 513 trees (Appendix A). The highest epiphytic richness was found in non-disturbed forests (Fig. 2), which included 28 exclusive species (Appendix A). The more frequent lichen species were *Coniocarpon cinnabarinum*, *Syncesia leproloba*, *Pseudopyrenula subnudata* and *Leucodecton occultum*. Tree species like *Eriotheca ruizii* and *Cochlospermum vitifolium* showed a high epiphytic richness (Table 1). A similar pattern was observed for the richness estimator (Chao 2), confirming the highest species richness in these host trees (Table 1). In addition *Chapsa diploschistoides*, *Stirtonia dubia* and *Stirtonia ramosa*, are reported for the first time from Ecuador.

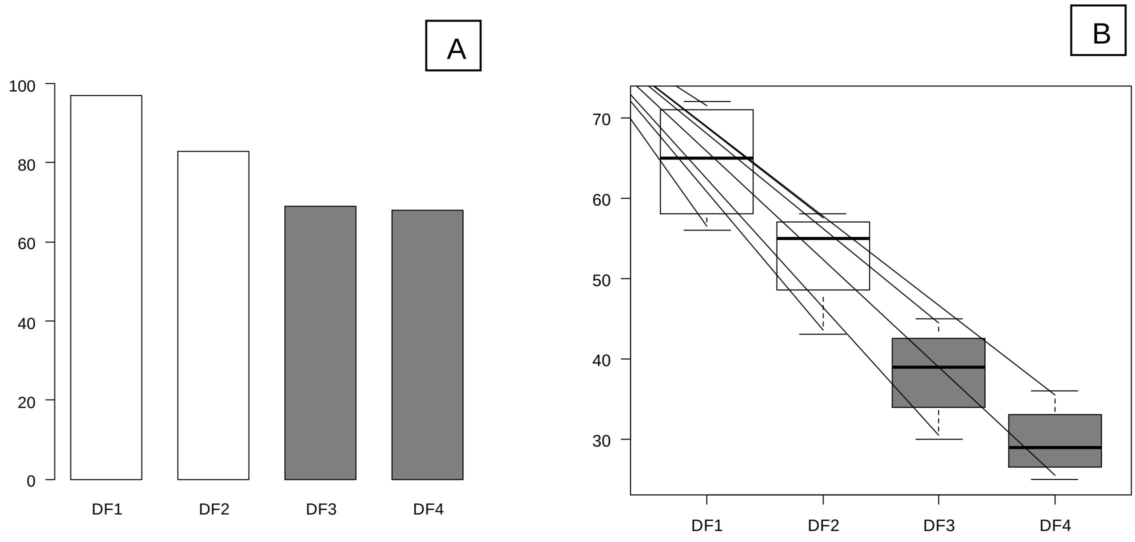

Figure 2. Species richness of epiphytic lichens and bryophytes in the two studied dry forest types (A) Forest level and (B) plot level. DF1 and DF2=undisturbed forest; DF3 and DF4=disturbed forest. Axis X, epiphytic species richness; Axis Y, forest type.

Table 1. Characteristics of woody tree species chosen as potential host trees. Species richness of bryophytes and lichens in the host trees is indicated as observed species (OS). Chao 2 estimates of total richness are shown in parenthesis. MTD: mean tree diameter; WD: Wood density; SE: Standard error.

Hots	Bark type	Sample	MTD (cm, ±SE)	OS (Chao 2; ±SE)	WD (gr cm–3)
Albizia multiflora (Kunth) Barneby & J.W. Grimes	Rough with fissures	20	8.33 (±4.0373)	28 (32; ±4.12)	0.544*
Bursera graveolens (Kunth) Triana & Planch.	Completely smooth	18	21.26(±6.5278)	33 (61; ±19.83)	0.32
Cochlospermum vitifolium (Willd.) Spreng.	Smooth without marked fissures	29	24.81(±11.9906)	53 (102; ±34.04)	0.22
Cynophalla mollis (Kunth) J. Presl	Rough with fissures	73	9.71(±4.2193)	38 (42; ±4.26)	0.88
Eriotheca ruizii (K. Schum.) A. Robyns	Completely smooth	58	18.84 (±11.0591)	58 (87; ±17.6)	0.39
Geoffroea spinosa Jacq.	Fissured with deep crevices	41	12.75 (±7.1152)	42 (75; ±21.43)	0.67
Tabebuia billbergii (Bureau & K. Schum.) Standl.	Fissured with deep crevices	63	19.53 (±9.9655)	45 (57; ±10.07)	0.92
Tabebuia chrysantha (Jacq.) G. Nicholson	Fissured with deep crevices	20	22.78 (±10.3925)	40 (52; ±8.6)	1
Ziziphus thyrsiflora Benth.	Rough with fissures	17	8.49 (±4.5695)	28 (36; ±6.87)	0.88

The analysis showed that host traits (e.g. bark depth) had a significant and positive effect on species richness and diversity at tree level. On the other hand, at plot level, species richness and diversity were higher in more closed canopy forests hosting a high diversity of tree species (Table 2). The random variable forest was not significant in any case.

Table 2. Results of the generalized linear mixed models of community traits at the tree and plot level. Coef. = coefficient, SE = Standard error.

Tree level	**Coef. (SE)**	***F*-value**	***P*-value**
Richness			
Tree diameter	-0.0474 (0.0229)	4.3	**0.0388**
Slope	0.0143 (0.0159)	0.82	0.3671
Bark depht	3.9617 (0.7270)	29.7	**<0.0001**
Canopy openess	-0.1143 (0.0596)	3.67	0.1238
Aspect	1.2229 (0.6346)	3.71	0.1397
Tree host richness	-0.3078 (0.2147)	2.06	0.2258
Shannon index			
Tree diameter	0.0006(0.0025)	0.06	0.8115
Slope	-0.0008 (0.0017)	0.26	0.6122
Bark depht	0.3989 (0.0769)	26.9	**<0.0001**
Canopy openess	-0.0220 (0.0065)	11.39	**0.0042**
Aspect	0.1507 (0.0683)	4.86	0.0485

Tree richness	-0.0451 (0.0228)	3.91	0.0708
Simpson inverse index			
Tree diameter	0.0021 (0.0027)	0.59	0.4438
Slope	-0.0013 (0.0019)	0.52	0.473
Bark depht	0.3896 (0.0850)	20.98	**<0.0001**
Canopy openess	-0.0290 (0.0074)	14.97	**0.0015**
Aspect	0.1642 (0.0771)	4.53	0.056
Tree richness	0.0665 (0.0259)	6.56	**0.0247**
Plot level			
Richness			
Canopy openess	-0.0153 (0.0049)	9.74	**0.0095**
Mean tree diameter	0.0006 (0.0098)	0	0.9508
Tree richness	0.0612 (0.0169)	13.01	**0.0039**
Shannon index			
Canopy openess	-0.0088 (0.0025)	12.16	**0.005**
Mean tree diameter	0.0094 (0.0052)	3.22	0.0998
Tree richness	0.0073 (0.0097)	0.57	0.4669
Simpson inverse index			
Canopy openess	-0.0398 (0.0104)	14.46	**0.0027**
Mean tree diameter	0.0590 (0.0228)	6.65	**0.0253**
Tree richness	0.0223 (0.0390)	0.33	0.5778

P-values < 0.05 are considered significant.

Analysis of host tree traits showed that tree species was the most relevant predictor of species richness (Table 3). However, mean tree diameter had a negative effect on epiphyte richness (Table 3). Models between epiphytic richness and host tree species showed that the tree species *Cochlospermum vitifolium* had the highest coefficient, followed by *Eriotheca ruizii* and *Bursera graveolens*, while the regression coefficients for *Tabebuia billbergii* and *Tabebuia chrysantha* had the lowest values (Table 3).

Table 3. Results of the generalized linear models between epiphyte richness and host traits. Coef. = coefficient, SE = Standard error, d.f. = degrees of freedom

Variable	**Coef.**	**SE**	***P*-value**
Species			
Bursera graveolens	0.6868	0.1442	**<0.0001**
Cochlospermum vitifolium	1.0284	0.1326	**<0.0001**
Cynophalla mollis	-0.0008	0.1214	0.9947
Eriotheca ruizii	0.7485	0.1235	**<0.0001**
Geoffroea spinosa	0.2475	0.1484	0.0954
Tabebuia billbergii	0.4574	0.1398	**0.00107**
Tabebuia chrysantha	0.4626	0.1630	**0.0045**
Ziziphus thyrsiflora	0.2846	0.1508	0.0591

Mean tree diameter	-0.0075	0.0024	**0.0020**
Slope	-0.0033	0.0018	0.0656
Bark depth	0.1791	0.1827	0.3269
Aspect	0.0217	0.0296	0.4623

P-values < 0.05 are considered significant.

Multivariate statistical analyses showed that epiphytic composition was structured according to the different spatial scales, and a large component of variation was associated with host tree species, followed by forest and plot (Table 4).

Table 4. Results of three-factor PERMANOVA analysis of species composition by forest, plot and host trees. df= degrees of freedom, MS= mean sum of squares, *Pseudo*-F= F value by permutation, CV=coefficient of variation.

Source	**df**	**MS**	**Pseudo-F**	**P**	**CV (%)**
Forest	3	33307	7.7048	0.001	17.048
Plot(Forest)	12	4247.6	2.8899	0.001	10.574
Host tree	21	32153	11.147	0.001	40.199
Error	299	1469.8			38.338

Host traits showed a significant relationship with the NMDS ordination axes (Table 5). Correlations were strong with tree species, bark characteristics and mean tree diameter (Table 5).

Table 5. Squared correlation coefficients (r^2) of values of environmental categorical factors and current environmental vectors fitted onto the first two axes of the NMDS ordination. Significant values ($p < 0.05$) with strong correlations are in bold.

Vectors				
	NMDS1	NMDS2	*r*^{2}	*P*-value
Mean tree diameter	**-0.9997**	**0.0204**	**0.3429**	**<0.0001**
Slope	0.9933	-0.1150	0.0159	0.0959
Bark depth	**-0.0455**	**0.9989**	**0.6105**	**<0.0001**
Aspect	-0.7373	-0.6755	0.0024	0.7042
Altitude	-0.991	0.133	0.0375	0.0039
Canopy openess	-0.9415	0.3369	0.0454	0.0019
Plot slope	0.8642	0.5030	0.0087	0.2467
Plot aspect	-0.6002	0.7998	0.0111	0.2037
Plot DBH	-0.7931	0.6090	0.0845	0.0009
Tree abundance per plot	0.7575	-0.6527	0.0875	0.0009
Tree richness per plot	0.7018	-0.7123	0.0851	0.0009

Tree shannon index per plot	0.6928	-0.7210	0.08	0.0009
Tree simpson index per plot	0.7025	-0.7115	0.0522	0.0009
Plot	0.2888	0.9573	0.0207	0.0479
Factors				
Disturbance			0.0404	0.0009
Disturbed	-0.2584	0.0843		
Undisturbed	0.0926	-0.0302		
Bark type			**0.7012**	**<0.0001**
Fissured with deep crevices	-0.2578	0.4669		
Rough with fissures	0.8108	-0.0745		
Smooth without fissures	-0.793	-0.19		
Completely smooth	-0.2345	-0.6159		
Host trees			**0.7684**	**<0.0001**
Albizia multiflora	0.2196	-0.2249		
Bursera graveolens	-0.1116	-0.4296		
Cochlospermum vitifolium	-0.793	-0.19		
Cynophalla mollis	0.8969	0.0507		
Eriotheca ruizii	-0.2663	-0.6641		
Geoffroea spinosa	-0.0644	0.4467		
Tabebuia billbergii	-0.367	0.4792		
Tabebuia chrysantha	-0.3197	0.4703		
Ziziphus thyrsiflora	0.3683	-0.7182		

Consistently, tree species was the most relevant predictor of epiphytic communities of tropical dry forests (Figure 3).

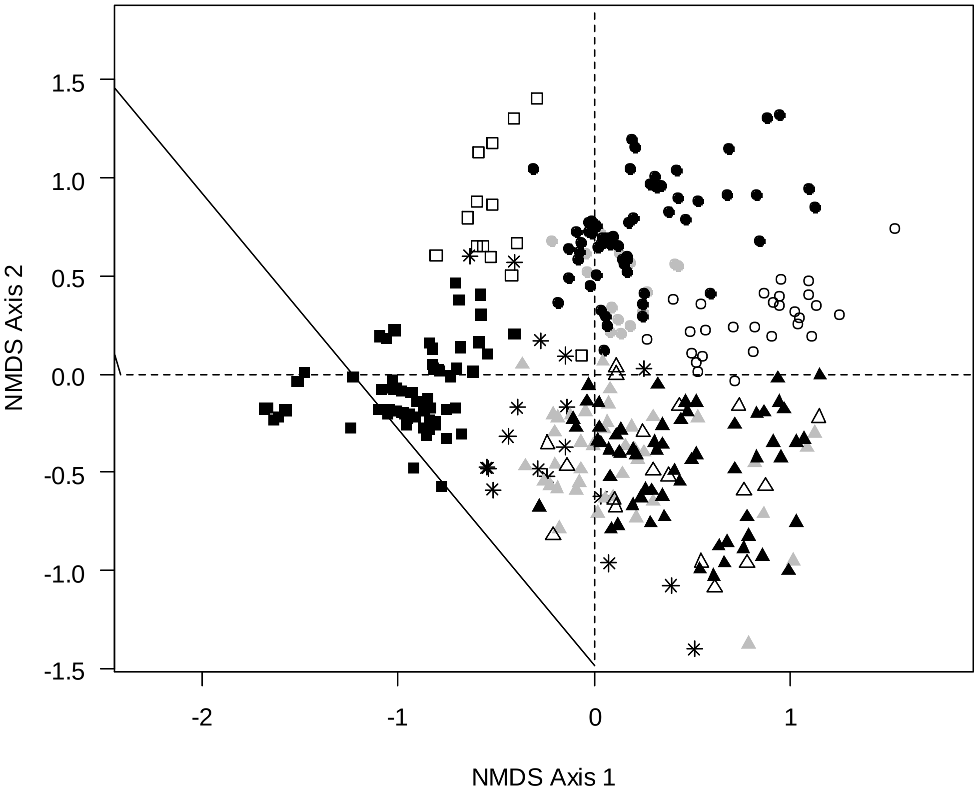

Figure 3. Non-metric multidimensional scaling analysis of species composition for the samples (host trees) in the studied dry forests (two remnants of each forest type). *Albizia multiflora* (✳); *Bursera graveolens* (●); *Cochlospermum vitifolium* (○); *Cynophalla mollis* (□); *Eriotheca ruizii* (○); *Geoffroea spinosa* (▲) *Tabebuia billbergii* (▲), *Tabebuia chrysantha* (△); *Ziziphus thyrsiflora* (□).

Discussion

Our results demonstrated that deforestation in tropical dry forests had a negative impact on epiphytic diversity, which was related to changes in forests structure (e.g. canopy openness), and particularly with the removal of potential host trees. Thus, host traits (i.e., tree species, bark texture and mean tree diameter), proved to be more sensitive for epiphytes than disturbance in tropical dry forests, due to the fact that the majority of epiphytes preferred a small group of host species with specific characteristics.

In this context, the negative correspondence between the canopy openness and epiphytes richness is a general phenomenon in the forests of the tropics (Gradstein 2008; Li et al., 2013; Benitez et al., 2012; 2015). Werner & Gradstein (2009) pointed out that disturbance in tropical dry forests in Ecuador is a cause in the loss of epiphytic richness that decreased together with canopy cover, although these results are restricted to monospecific forests of *Acacia macracantha* Willd. In our case, canopy disruption is related to the loss of tree species diversity that greatly improved epiphytic richness, due to the fact that disturbed forest is characterized by absence of shrub vegetation and low diversity and an abundance of potential host trees (e.g. *Eriotheca ruizii* and *Cochlospermum vitifolium*). These results suggest that the diversity in the forest community helps to maintain epiphyte richness in lowland dry forests.

Several studies in temperate and boreal forests have shown that the diversity of trees is a key factor for epiphyte richness that is related with host preference (Nascimbene et al., 2009; Király et al., 2013). In contrast, the correlation between phorophyte specificity and epiphytes that is rare in tropical rain forests, might be related to the high tree species diversity, complexity of forest structure, humus and moss cover on the bark surface or stochastic effects of species dispersion (Sipman & Harris, 1989; Cáceres *et al.*, 2007; Gradstein & Culmsee, 2010; Soto-Medina *et al.*, 2012). However, the seasonally dry tropical forests are characterized by low species tree diversity (Murphy

& Lugo 1986; Gentry 1995), caused by the occurrence of extensive arid periods with high light levels (Werner & Gradstein 2009). For example, during the rainy season (5 months), about 80% of precipitation is recorded and this can greatly exceed 100 mm per month. Conversely, during the dry months rainfall rarely exceeds 10 mm per month (Maass & Burgos 2011), creating a water deficit that causes the loss of leaves of most species (Gotsch et al., 2010). Consequently, humus layer and bryophyte diversity are generally low or absent in these forests, which are mostly inhabited by drought-tolerant epiphytes (Cornelissen & Ter Steege 1989, Gradstein et al., 2001).

In our study, much of the variability of the lichen species richness was explained by the host tree species. In fact, our data suggests that host preference of epiphytes is directly related with substrate quality (e.g. bark roughness). For example, host trees with smooth bark (*E. ruizii* and *C. vitifolium*) harboured higher total species richness than trees of fissured bark (e.g. *Cynophalla mollis*), that was much poorer in epiphyte species. In this regard, Löbel et al. (2006) and Rosabal et al. (2013) found a negative correlation between bark roughness and lichen species richness, due to the fact that host trees with fissured bark could limit the establishment and development of lichens, and particularly those inconspicuous pioneer crustose species.

Lichens with a crustose biotype were dominant in our study (over 90% of the total lichen species), therefore, the impoverishment of epiphytic species in the undisturbed forests was mainly due to the severe loss of potential host trees with smooth bark that decreased together with epiphytic richness. The crustose lichens are better associated with hosts of smooth bark, due to the fact that they have thin thalli and grow directly on the surface of the substrate attached through the medullary hyphae (Büdel & Scheidegger 2008). Thus, Fritz & Brunet (2010), have shown that several crustose lichens were associated with smooth bark of mature trees, and are therefore limited primarily by the availability of the bark substrate.

Epiphytic species composition also varies in relation to the host traits, mainly limited by host species, bark texture and trunk diameter. Therefore, epiphytes exhibit a strong degree of host preference, indicating the suitability of a host plant for epiphyte colonization. Similar results in the tropical dry forest of Mexico have shown a high concentration of epiphytes on a few host species, therefore suggesting host preference at a community-level (Vergara-Torres et al., 2010). In accordance to our expectations, bark characteristics (bark texture and depth) were correlated with host quality, which was an important factor for epiphytic communities of dry forests. Therefore, host trees of *E. ruizii* and *B. graveolens* with smooth bark hosted a different epiphyte community than *C. mollis and T. billbergii* trees with fissured bark. This is supported by several other studies, where it has been shown that bark characteristics such as bark stability, texture, water-holding and pH determine distribution and establishment of epiphytes (Löbel et al., 2006; Cáceres et al., 2007; Gradstein & Culmsee 2010; Soto-Medina et al., 2012; Rosabal et al., 2013).

Host traits related to tree diameter play an important role in epiphytic colonization in tropical dry forests. For example, larger trees of *E. ruizii* and *C. vitifolium* provided greater bark surface availability for epiphytes. Similarly, several studies have shown that trees with larger trunk diameters could maintain a greater number of suitable microsites on the bark for epiphytic colonization (Soto-Medina et al., 2012; Rosabal et al., 2013; Benitez et al., 2015). This is probably due to greater bark surface availability for colonization on large trees and the creation of additional microhabitats (Johansson et al., 2007; Fritz et al., 2008; Ranius et al., 2008; Lie et al., 2009; Belinchón et al., 2011). In addition, tree age has a positive correlation with tree size, therefore compositional changes in epiphytic lichens with increasing tree age has been reported in several studies (Nascimbene et al., 2009, Marmor et al., 2011). Thus, large trees will have greater surface area for epiphyte colonization than smaller trees (Flores-Palacios & García-Franco 2006; Benitez et al., 2015).

We therefore concluded that tropical forest disturbance reduces epiphyte diversity. Particularly, the removal of host trees proved to be more sensitive for epiphytes in tropical dry forests than in tropical rain forests. Species loss is most severe in disturbed forest due to loss of potential host trees such as *Eriotheca ruizii* and *Cochlospermum vitifolium* that maintain high species richness. Disruption of the canopy leads to microclimatic changes that affect species richness of epiphytic lichens related with tree diversity. Therefore host preference and change in the tree species composition play an important role in epiphytic communities of seasonal tropical dry forests. Consequently, only the protection of remnants of undisturbed dry forest characterized by potential host trees might help to preserve a rich and diverse community of epiphytic lichens.

Acknowledgments:

Financial support for this study was granted by the “Universidad Técnica Particular de Loja” (PROY_CCNN_941), the “Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación" of Ecuador and the "Ministerio de Ciencia e Innovación of Spain" (project EPICON, CGL2010-22049). We thank A. Arévalo, E. Gusmán, F. Gaona and G. Cango for his help with fieldwork and Ministerio del Ambiente del Ecuador by providing access to the study areas.

References

Acebey, A., Gradstein, S. R., & Krömer, T. (2003). Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of tropical ecology, 19(01), 9-18.

Anderson, M.J., Gorley, R.N. and K.R. Clarke. (2008). PERMANOVA + for PRIMER: Guide to Software and statistical Methods. PRIMER-E. Plymouth, UK.

Aptroot, A. (2012) A world key to the species of *Anthracothecium* and *Pyrenula*. *The Lichenologist* 44(1): 5 – 53.

Aptroot, A., Lücking, R., Sipman, H.J.M., Umaña, L. & Chaves, J.L. (2008) Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. *Bibliotheca Lichenologica* 94: 1–191.

Aptroot, A., Menezes, A. A., Xavier-Leite, A. B., dos Santos, V. M., Alves, M. M. E., & da Silva Caceres, M. E. (2014). Revision of the corticolous *Mazosia* species, with a key to *Mazosia* species with 3-septate ascospores. *The Lichenologist* 46 (4): 563 – 572.

Aragón, G., López, R., & Martínez, I. (2010). Effects of Mediterranean dehesa management on epiphytic lichens. Science of the total environment, 409(1), 116-122.

Avila-Cabadilla, L. D., Stoner, K. E., Henry, M., & Añorve, M. Y. A. (2009). Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. Forest Ecology and Management, 258(6), 986-996.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J., & Engwald, S. (2001). Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecology, 152(2), 145-156.

Belinchón, R., Martínez, I., Aragón, G., Escudero, A., & De la Cruz, M. (2011). Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean region. Fungal biology, 115(12), 1270-1278.

Benítez, Á., Prieto, M., & Aragón, G. (2015). Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. Forestry, 88(5), 521-527.

Benítez, Á., Prieto, M., González, Y., & Aragón, G. (2012). Effects of tropical montane forest disturbance on epiphytic macrolichens. *Science of the Total Environment*, *441*, 169-175.

Benzing, D. H. (1990) 'Vascular Epiphytes', Cambridge University Press, Cambridge, p. 354

Berg, Å., Gärdenfors, U., Hallingbäck, T., & Norén, M. (2002). Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden–analyses of data from a national survey. Biodiversity & Conservation, 11(8), 1479-1503.

Brodo, I. M., Sharnoff, S. D. & Sharnoff, S. (2001) *Lichens of north America.* Yale University Press, New Haven and London, 795 pp

Büdel, B. and Scheidegger, C. 2008. Thallus morphology and anatomy. In: Nash, T. H. III (ed.), Lichen Biology. Second Edition. pp. 40–68. Cambridge University Press, Cambridge.

Cáceres, M. E., Lücking, R., & Rambold, G. (2007). Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycological Progress, 6(3), 117-136.

Cáceres, M.E.S. (2007) Corticolous crustose and microfoliose lichens of northeastern Brazil. *Libri Botanici* 22: 1–168.

Callaway, R. M., Reinhart, K. O., Moore, G. W., Moore, D. J., & Pennings, S. C. (2002). Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia, 132(2), 221-230.

Cornelissen, J. T., & Ter Steege, H. (1989). Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. Journal of Tropical Ecology, 5(02), 131-150.

Dinerstein, E., D. M. Olson, D. J. Gram, A. L. Webster, S. A. Primn, M. P. O. Brookbinder, and G. Ledec. (1995). Una evaluación del estado de conservación de las eco-regiones de América Latina y Caribe. Banco Internacional de Reconstrucción y Fomento/Banco Mundial, Washington, DC.

Egea, J.M & Torrente, P. (1993) *Cresponea*, a new genus of lichenized fungi in the order Arthoniales (Ascomycotina). *Mycotaxon* 48: 301–31.

Espinosa, C. I., Cabrera, O., Luzuriaga, A. L., & Escudero, A. (2011). What Factors Affect Diversity and Species Composition of Endangered Tumbesian Dry Forests in Southern Ecuador?. Biotropica, 43(1), 15-22.

Espinosa, C. I., Cruz, M., Jara-Guerrero, A., Gusmán, E., & Escudero, A. (2015). The effects of individual tree species on species diversity in a tropical dry forest change throughout ontogeny. *Ecography*.

Fajardo, I., V. Gonzalez, J. Nassar, P. Lacabana, C. Portillo, F. Carrasquel, and J. Rodríguez.(2005). Tropical dry forests of Venezuela: Characterization and current conservation status. Biotropica 37: 531–546.

Flores-Palacios A, García-Franco JG (2006) The relationship between tree size and epiphyte species richness: testing four different hypotheses. J Biogeogr 33:323–330

Frazer, G. W., Canham, C. D., & Lertzman, K. P. (2000). Gap light analyzer, version 2.0.

Fritz, Ö., & Brunet, J. (2010). Epiphytic bryophytes and lichens in Swedish beech forests–effects of forest history and habitat quality. Ecological Bulletins,53, 95-107.

Fritz, Ö., Gustafsson, L., & Larsson, K. (2008). Does forest continuity matter in conservation?–A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biological conservation, 141(3), 655-668.

García-Suárez, M. D., Rico-Gray, V., & Serrano, H. (2003). Distribution and abundance of Tillandsia spp.(Bromeliaceae) in the Zapotitlán Valley, Puebla, México. Plant ecology, 166(2), 207-215.

Gentry, A. 1977. Endangered plant species and habitats of Ecuador and Amazonian Peru. In G. T. Prance and T. S. Elias (Eds.). Extinction is forever, pp. 136—149. The New York Botanical Garden, New York, New York.

Gentry, A. H. (1995) Diversity and floristic composition of neotropical dry forests. Seasonally dry tropical forests (ed. By S. H. Bullock, H. A. Mooney and E. Medina), pp. 146–194. Cambridge University Press, Cambridge.

Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, *74*(2), 205-233.

Gillespie, T. W., Grijalva, A., & Farris, C. N. (2000). Diversity, composition, and structure of tropical dry forests in Central America. Plant ecology, 147(1), 37-47.

Gradstein, R., & Culmsee, H. (2010). Bryophyte diversity on tree trunks in montane forests of Central Sulawesi, Indonesia. Tropical Bryology, 31, 95-105.

Gradstein, S. R., & Sporn, S. G. (2010). Land-use change and epiphytic bryophyte diversity in the tropics. Cambio en el uso de la tierra y diversidad de briófitas epífitas en los trópicos. Nova Hedwigia., 138, 311-323.

Gradstein, S.R. (2008). Epiphytes of tropical montane forests—impact of deforestation and climate change. In: *The tropical mountain forest. Patterns and Processes in a Biodiversity Hotspot*. Gradstein, S.R., Homeier, J. and Gansert, D. (eds). University Press, Göttingen, pp. 51–65.

Gradstein, S. R., Churchill, S. P., Salazar-Allen, N., & Reiner-Drehwald, M. E. (2001). *Guide to the bryophytes of tropical America* (p. 577). New York: New York Botanical Garden Press.

Graham, E. A., & Andrade, J. L. (2004). Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. American Journal of Botany, 91(5), 699-706.

Green, T. G. A., Nash III, T. H., & Lange, O. L. (2008). Physiological ecology of carbon dioxide exchange. Lichen biology. Cambridge University Press, Cambridge, 152-181.

Gotsch, S. G., Powers, J. S., & Lerdau, M. T. (2010). Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. *Plant Ecology*, *211*(1), 133-146.

Higuera, D., & Wolf, J. H. (2010). Vascular epiphytes in dry oak forests show resilience to anthropogenic disturbance, Cordillera Oriental, Colombia.*Caldasia*, *32*(1), 161-174.

Hirata, A., Kamijo, T., & Saito, S. (2009). Host trait preferences and distribution of vascular epiphytes in a warm-temperate forest. Plant Ecology, 201(1), 247-254.

Holz, I., & Gradstein, R. S. (2005). Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica–species richness, community composition and ecology. Plant Ecology, 178(1), 89-109.

Janzen, D. H. (1988). Management of habitat fragments in a tropical dry forest—growth. Ann. Missouri Bot. Gard. 75: 105–116.

Johansson, P., Rydin, H., & Thor, G. (2007). Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience, 14(1), 81-91.

Kalacska, M. E., Sánchez-Azofeifa, G. A., Calvo-Alvarado, J. C., Rivard, B., & Quesada, M. (2005). Effects of Season and Successional Stage on Leaf Area Index and Spectral Vegetation Indices in Three Mesoamerican Tropical Dry Forests1. Biotropica, 37(4), 486-496.

Király, I., Nascimbene, J., Tinya, F., & Ódor, P. (2013). Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. Biodiversity and Conservation, 22(1), 209-223.

Kranner, I., Beckett, R., Hochman, A., & Nash III, T. H. (2008). Desiccation-tolerance in lichens: a review. The Bryologist, 111(4), 576-593.

Krömer, T., & Gradstein, S. R. (2003). Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana*, 190-195.

Leal-Pinedo, J. M., & Linares-Palomino, R. (2005). The dry forests of the Biosphere Reserve of Northwestern (Peru): Tree diversity and conservation status. Caldasia, 27(2), 195-211.

Li, S., Liu, W. Y., & Li, D. W. (2013). Epiphytic lichens in subtropical forest ecosystems in southwest China: species diversity and implications for conservation. Biological Conservation, 159, 88-95.

Lie, M. H., Arup, U., Grytnes, J. A., & Ohlson, M. (2009). The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. Biodiversity and Conservation, 18(13), 3579-3596.

Linares-Palomino, R., Kvist, L.P., Aguirre-Mendoza, Z. and Gonzales-Inca, C. 2010. Diversity and endemism of woody plant species in the Equatorial Pacific seasonally dry forests. Biodiversity and Conservation 19: 169-185.

Löbel, S., Snäll, T., & Rydin, H. (2006). Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. Journal of Ecology, 94(4), 856-868.

Lücking, R., Archer, A.W. & Aptroot, A. (2009) A world-wide key to the genus *Graphis* (Ostropales: Graphidaceae). *The Lichenologist* 41: 363–452.

Lücking, R., Chaves, J.L., Sipman, H.J.M., Umaña, L. & Aptroot, A. (2008) A first assessment of the Ticolichen biodiversity inventory in Costa Rica: The genus *Graphis*, with notes on the genus *Hemithecium* (Ascomycota : Ostropales : Graphidaceae). *Fieldiana* 46: 1–130.

Maass, M., and A. Burgos. 2011. Water Dynamics at the Ecosystem Level in Seasonally Dry Tropical Forests. Page in R. Dirzo, H. S. Young, H. A. Mooney, and G. Ceballos, editors. Seasonally Dry Tropical Forests ecology and conservation. Island Press, Washington, DC 20009, USA.

Magurran, A. 2004 Measuring Biological Diversity. Backwell Publishing.

Mandl, N., Lehnert, M., Kessler, M., & Gradstein, S. R. (2010). A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. Biodiversity and Conservation, 19(8), 2359-2369.

Marini, L., Nascimbene, J., & Nimis, P. L. (2011). Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. Science of the Total Environment, 409(20), 4381-4386.

Marmor, L., Tõrra, T., Saag, L. & Randlane, T. 2011. Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. Ecological Indicators 11: 1270–1276.

McCullagh, P. & J.A. Nelder. (1989). Generalized linear models. 2nd ed. CRC Press, Chapman and Hall, Boca Raton, FL, US.

McGee, G. G., & Kimmerer, R. W. (2002). Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. Canadian Journal of Forest Research, 32(9), 1562-1576.

Miles, L., A. Newton, R. Defries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. Gordon. 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33: 491–505.

Mistry, J. (1998). Corticolous lichens as potential bioindicators of fire history: a study in the cerrado of the Distrito Federal, central Brazil. Journal of Biogeography, 25(3), 409-441.

Mistry, J., & Berardi, A. (2005). Effects of phorophyte determinants on lichen abundance in the cerrado of central Brazil. Plant Ecology, 178(1), 61-76.

Montfoort, D., & Ek, R. C. (1990). Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana. Institute of Systematic Botany.

Mooney, H.A., Bullock, S.H. & Medina, E. (1995) Introduction. Seasonally dry tropical forests (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 1–8. Cambridge University Press, Cambridge.

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. Annual review of ecology and systematics, 67-88.

Nascimbene, J., Marini, L., Motta, R. & Nimis, P.L. 2009. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. Biodiversity and Conservation 18: 1509–1522.

Nascimbene, J., Marini, L., Motta, R., & Nimis, P. L. (2009). Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. Biodiversity and Conservation, 18(6), 1509-1522.

Nash III, T. H., Gries, C. & Bungartz, F. (2007) *Lichen Flora of the Greater Sonoran Desert Region*, vol. 3. Lichens Unlimited, Tempe, Arizona, 567 pp.

Nash III, T. H., Ryan, B. D., Gries, C. & Bungartz, F. (2002) *Lichen Flora of the Greater Sonoran Desert Region,* vol. 1. Lichens Unlimited, Tempe, Arizona, 532 pp.

Nash III, T.H., Ryan, B.D., Diederich, P., Gries, C. & Bungartz, F. (2004) *Lichen Flora of the Greater Sonoran Desert Region,* vol. 2. Lichen Unlimited: Tempe, Arizona 742 pp.

Nash, T. H. (1996). Lichen biology. Cambridge University Press.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S. R., Sipman, H. J., Obregon, A., & Bendix, J. (2010). Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators, 10(6), 1111-1118.

Nöske, N. M., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J., & Gradstein, S. R. (2008). Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. Basic and Applied Ecology, 9(1), 4-12.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., & Oksanen, M. J. (2013). Package ‘vegan’. Community ecology package, version, 2(9).

Ranius, T., Johansson, P., Berg, N., & Niklasson, M. (2008). The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. Journal of vegetation science, 19(5), 653-662.

Rivas-Plata, E., Lücking, R., Aptroot, A., Sipman, H.J.M., Chaves, J.L., Umaña, L. & Lizano, D. (2006) A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (Ostropales: Coenogoniaceae), with a world-wide key and checklist and a phenotype-based cladistic analysis. *Fungal Diversity* 23: 255–321.

Rivas-Plata, E., Lücking, R., Sipman, H. J., Mangold, A., Kalb, K., & Lumbsch, H. T. (2010). A world-wide key to the thelotremoid Graphidaceae, excluding the *Ocellularia-Myriotrema-Stegobolus* clade. *The Lichenologist* 42: 139 – 185.

Rosabal, D., Burgaz, A. R., & Reyes, O. J. (2013). Substrate preferences and phorophyte specificity of corticolous lichens on five tree species of the montane rainforest of Gran Piedra, Santiago de Cuba. The Bryologist, 116(2), 113-121.

Rosa-Manzano, E., Andrade, J. L., Zotz, G., & Reyes-García, C. (2014). Epiphytic orchids in tropical dry forests of Yucatan, Mexico–Species occurrence, abundance and correlations with host tree characteristics and environmental conditions. Flora-Morphology, Distribution, Functional Ecology of Plants, 209(2), 100-109.

Sierra, R. 2013. Patrones y factores de deforestación en el Ecuador Continental, 1990-2010.Y un acercamiento a los próximos 10 años. Conservación Internacional Ecuador y Forest Trends. Quito, Ecuador.

Sipman, H.J.M. & Harris, R.C., 1989. Lichens. In: Lieth, H., Werger, M.J.A. (Eds.), Tropical Rain Forest Ecosystems. Ecosystems of the World 14A. Elsevier, Amsterdam, pp. 303–309

Soto-Medina, E., Lücking, R., & Rojas, A. B. (2012). Especificidad de forófito y preferencias microambientales de los líquenes cortícolas en cinco forófitos del bosque premontano de finca Zíngara, Cali, Colombia. Rev. Biol. Trop, 60(2), 843-856.

Szövényi, P., Hock, Z. S., & Tóth, Z. (2004). Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. Journal of Bryology, 26(2), 137-146.

Tehler, A. (1997) *Syncesia* (Arthoniales, Euascomycetidae). *Flora Neotropica* 74: 1-48.

Vergara-Torres, C. A., Pacheco-Álvarez, M. C., & Flores-Palacios, A. (2010). Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. Journal of Tropical Ecology, 26(06), 563-570.

Werner, F. A., & Gradstein, S. R. (2009). Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science, 20(1), 59-68.

Werner, F. A., Homeier, J., & Gradstein, S. R. (2005). Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. Ecotropica, 11, 21-40.

Werner, F.A. (2008). Effects of human disturbance on epiphyte assemblages in the Andes of Ecuador. Ph.D. diss., Univ. Göttingen, Germany.

Wolf, J. H. (2005). The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management, 212(1), 376-393.

Yeaton, R. I., & Gladstone, D. E. (1982). The pattern of colonization of epiphytes on Calabash Trees (Crescentia alata HBK.) in Guanacaste Province, Costa Rica. *Biotropica*, 137-140.

Appendix A. Number of trees on which each species appears in **the** four forests. Asterisks denotes exclusive species per forest.

Taxa	DF 1	DF 2	DF 3	DF 4
Arthonia pruinata (Pers.) Steud. ex A.L. Sm.	6	3	2	
Coniocarpon cinnabarinum DC.	139	97	26	26
Arthonia antillarum (Fée) Nyl.	22	15	14	5
Arthonia aff. *antillarum* (Fée) Nyl.	5*			
Arthonia aff. *conferta* (Fee) Nyl.		1*		
Arthonia elegans (Ach.) Almq.	4		1	
Arthonia sp	1	1		
Bacidia sp1	5	4		1
Bacidia sp2		1*		
Bacidia sp3	2	8		
Bactrospora denticulata (Vain.) Egea & Torrente				8*
Bactrospora myriadea (Fée) Egea & Torrente.			2*	
Bathelium degenerans (Vain.) R.C. Harris	14	3	3	7
Buellia sp	8	4	5	
Caloplaca sp	5	12	14	1
Caloplaca wrightii (Willey) Fink.	4	1	5	2
Coccocarpia pellita (Ach.) Müll. Arg.		1*		
Coenogonium pineti (Ach.) Lücking & Lumbsch	4	4		
Cololejeunea minutissima ssp. *myriocarpa* (Nees & Mont.) R.M. Schust.	29	30		7
Chapsa dilatata (Müll. Arg.) Kalb	2*			
Chapsa diploschistoides (Zahlbr.) Frisch	2	16		
Chapsa sp	1*			
Cresponea flava (Vainio) Egea & Torrente	6	17	7	4
Cryptothecia striata Thor		1	1	
Chrysothrix sp	1		2	4
Chrysothrix xanthina (Vain.) Kalb	1	9	20	5
Dirinaria aegialita (Afz.) B. Moore			4*	
Dirinaria papillulifera (Nyl.) D. D. Awasthi	8	13	6	7
Dirinaria picta (Sw.) Clem. & Shear	35	39	23	20
Dirinaria applanata (Fée) D.D.Awasthi	1	2		
Dirinaria aff. *aegialita* (Afzel. ex Ach.) B.J. Moore.	4	2		
Dirinaria confluens (Fr.) D.D.Awasthi.			1	1
Dirinaria aff. *confluens* (Fr.) D.D.Awasthi.			2	8
Dirinaria sp				1*
Diplolabia afzelii (Ach.) A.Massal.	2*			
Enterographa compunctula (Nyl.) Redinger	18	1		
Enterographa quassiaecola Fée	1	2		
Fibrillithecis halei (Tuck. & Mont.) Mangold	5	4	1	1
Fissurina incrustans Fée		1*		

Fissurina nitidescens (Nyl.) Nyl.	5	1		1
Fissurina egena (Nyl.) Nyl.		3	1	
Fissurina sp	1	4		
Glyphis scyphulifera (Ach.) Staiger	6	8	6	4
Glyphis cicatricosa Ach.	3	2		2
Graphis anfractuosa (Eschw.) Eschw.	23	4	2	3
Graphis argentata Lücking & Umaña.	4	10	1	4
Graphis dendrogramma Nyl.	31	13	4	6
Graphis aff. *dendrogramma* Nyl.	5*			
Graphis leptoclada Müll. Arg.	12*			
Graphis aff. *subcontorta* (Müll. Arg.) Lücking & Chavez	1		1	
Graphis subcontorta (Müll. Arg.) Lücking & Chavez	45	37	10	1
Graphis caesiella Vain.	2*			
Graphis sp	8	6	3	1
Gyalidea sp nov.	4	6		
Haematomma aff. *nicoyense* Nelsen, Lücking & Chaves			1*	
Helminthocarpon leprevostii Fee.	3*			
Herpothallon sp	31	12	19	2
Hyperphyscia adglutinata (Flörke)		1	2	
Lecanographa laingiana Diederich, Egea & Sipman	13	8	13	
Lecanographa illecebrosula (Müll. Arg.) Egea & Torrente.			1*	
Lecanographa lyncea (Sm.) Egea & Torrente	7	13	2	2
Lecanora chlarotera Nyl.	1	3		
Lecanora helva Stizenb.	50	39	15	12
Lecanora sp1	6	1	4	1
Lecanora sp2	4*			
Lecanora sp3			1*	
Leptogium cyanescens (Pers.) Körb.		1*		
Leucodecton occultum (Eschw.) A. Frisch.	52	53	13	6
Lithothelium illotum (Nyl.) Aptroot.	10	2	1	1
Mazosia carnea (Eckfeldt) Aptroot & M. Cáceres	8	1		
Megalospora sulphurata var. sulphurata Meyen		1*		
Melaspilea sp			1*	
Mycoporum eschweileri (Müll. Arg.) R. C. Harris	1		1	
Ocellularia sp	1	4		
Opegrapha trilocularis Müll. Arg.	55	53	34	12
Opegrapha difficilior Nyl.	40	22	6	3
Opegrapha aff. *vulgata* (Ach.) Ach.	6*			
Ophegrapha sp	6*			
Parmotrema exquisitum (Kurok.) DePriest & B. W. Hale	2	1		3
Pertusaria texana Mull. Arg.	3*			
Pertusaria sp1	1*			
Pertusaria sp2	14	4	11	1
Phaeographis punctiformis (Eschw.) Müll. Arg.				1*
Phaeographis decipiens Müll. Arg.	1*			

Phaeographis inusta (Ach.) Müll. Arg.	7	2		
Phaeographis subtigrina (Vainio) Zahlbr.	4	2		
Phaeographis intricans (Nyl.) Vain.	18	4	4	2
Phaeographis lobata (Eschw.) Müll. Arg.				1*
Phaeographis brasiliensis (A. Massal.) Kalb & Matthes-Leicht.	20	15	2	1
Phaeographis sp1		1*		
Phaeographis sp2	1*			
Porina nucula Ach.			1*	
Porina tetracerae (Afz. in Ach.) Müll. Arg	1	4	1	
Physcia crispa Nyl.		5	3	1
Physcia sorediosa (Vain.) Lynge.	15	21	14	7
Physcia endochrysea Kremp.	3	28	5	6
Phyllopsora sp	40	55	7	4
Polymeridium subcinereum (Nyl.) R.C. Harris	25	1		
Pyrenula immissa (Stirt.) Zahlbr.	9	25		
Pyrenula erumpens R. C. Harris	40	26	4	3
Pyrenula psoriformis Zahlbr.	2*			
Pyrenula subcongruens Müll.Arg.	34	18		
Pyrenula ochraceoflava (Nyl.) R.C. Harris	34	12	3	
Pseudopyrenula subnudata Müll.Arg.	68	49	24	16
Pseudopyrenula diluta (Fée) Müll. Arg.	12	5		1
Pyxine cocoës (Sw.) Nyl.	2	1	10	8
Ramalina darwiniana var. darwiniana Aptroot & Bungartz			1	3
Ramonia valenzueliana (Mont.) Stizenb.	1*			
Rinodina sp	2	6	3	1
Sarcographa tricosa (Ach.) Müll. Arg.	22	24	4	6
Schismatomma spierii Aptroot & Sparrius	5	10	7	3
Stigmatochroma gerontoides (Stirt.) Marbach		1*		
Stirtonia dubia A. L. Sm.	5*			
Stirtonia ramosa Makhija & Patw.	36	8	4	
Stirtonia sp	15		2	
Syncesia effusa (Fée) Tehler	2	7	1	
Syncesia glyphysoides (Fée) Tehler	2*			
Syncesia leprobola Nyl. ex Tehler	107	20	8	1
Syncesia farinacea (Fée) Tehler	3		1	1
Syncesia graphica (Fr.) Tehler.	5	4	3	2
Tephromela atra (Huds.) Hafellner	15	8	3	1
Thelotrema sp	1*			
Trypethelium eluteriae Spreng.	9	10	4	15

CAPÍTULO V / CHAPTER V

Additions to the bryophyte flora of Ecuador 2

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Benitez, A., Gradstein, R., Prieto, M., Aragón, G., Moscoso, A., & Burghardt, M. (2012). *Tropical Bryology 34: 99-106.*

Notothylas vitalii Udar & D.K. Singh

Abstract

Ecuador has a very diverse bryophyte flora with about 950 species of mosses and 700 of liverworts and hornworts. Nevertheless, the distribution of the species within the country remains incompletely explored and many species are only known from very few collections. This paper presents new additions to the liverwort and hornwort flora of Ecuador. The hornwort Notothylas vitalii and the liverworts Blepharostoma trichophyllum, Frullania setigera, Isopaches bicrenatus, Platycaulis renifolia and Symphyogyna apiculispina are new to the country, four species are new to southern Ecuador, eighteen are new to the province of Loja, ten are new to Napo, six are new to Pichincha and one species is new to the provinces of El Oro and Carchi respectively. The record of Notothylas vitalii is the first one outside Brazil and constitutes the first record of the genus Notothylas from mainland Ecuador. The rare monospecific genus Platycaulis was previously known only from the type locality in the Venezuelan Andes, and the holarctic Isotaches bicrenatus in the tropics only from two mountains in southeastern Brazil. Several new records were gathered in very humid and bryophyte-rich, wind-stricken, foggy superpáramo vegetation in the Páramo de la Virgen (Napo) at 4100-4300 m. For all species notes on their geographical distribution and habitats in Ecuador as well as their world range are provided.

Keywords: Anthocerophyta, *Isopaches bicrenatus*, Marchantiophyta, *Notothylas vitalii*, *Olgantha*, *Platycaulis renifolia*, new bryophyte records, superpáramo, *Triandrophyllum eophyllum.*

Introducción

La flora de briofitas en Ecuador es muy diversa con unas 950 especies de musgos (Churchill *et al.* 2000) y 700 de hepáticas y antocerotes (León-Yánez *et al.* 2006, Benitez & Gradstein 2011). Sin embargo, el conocimiento de su biodiversidad es todavía incompleto y poco estudiado. Las colecciones, en su mayoría, provienen de pocas áreas (León-Yánez *et al.* 2006, Schäfer-Verwimp *et al.* 2006, Benitez & Gradstein 2011). Recientemente, Benitez & Gradstein (2011) registraron ocho nuevas especies para Ecuador, entre ellas dos para el nuevo mundo, *Metzgeria saccata* Mitt., *Zoopsidella caledonica* (Steph.) R.M. Schust. Adicionalmente Gradstein & Schäfer-Verwimp (2012) registraron dos especies, y describen un nuevo taxón para la ciencia, *Archilejeunea nebeliana* Gradst. & Schäf.-Verw.

En esta publicación se presentan nuevas adiciones a la flora de hepáticas y antocerotes del Ecuador. Seis especies son nuevas para el país (*Blepharostoma trichophyllum* (L.) Dumort., *Frullania setigera* Steph., *Isopaches bicrenatus* (Schmidel) H. Buch*, Notothylas vitalii* Udar & D.K. Singh*, Platycaulis renifolia* R.M. Schust. y *Symphyogyna apiculispina* Steph.), cuatro son nuevas para el sur de Ecuador, 18 nuevas para la provincia de Loja, 10 nuevas para la provincia de Napo, seis nuevas para la provincia de Pichincha y una nueva para la provincia de El Oro y otra para la provincia del Carchi. Se confirma la existencia de *Anthelia* y *Lepidozia auriculata* Steph. para el país.

Hay nuevos registros del superpáramo, en el Páramo de la Virgen al este de Quito, en la provincia de Napo, cerca del borde con la provincia de Pichincha. Aquí, a los 4200-4300 m, justo bajo la estación de radio transmisión de la cumbre, se encuentra una vegetación de briofitas terrestres muy rica en especies. La zona corresponde a un superpáramo nublado, muy húmedo, expuesto y azotado por el viento, la vegetación de esta localidad se caracteriza por la presencia de arbustos enanos de *Loricaria ilinissae* (Benth.) Cuatrec. esparcidos en pendientes pronunciadas. Esta es la localidad tipo del género *Olgantha* (Schuster 1996; hoy = *Triandrophyllum*) y de *Harpalejeunea grandistipula* R.M. Schust. (Schuster 1999; ver también Schäfer-Verwimp *et al.* 2006), que fueron colectadas aquí por el Dr. Rudoph M. Schuster en 1993. Es la única localidad ecuatoriana para los géneros *Anthelia*, *Blepharostoma* e *Isopaches*. Durante una corta visita a esta localidad el 9 de diciembre de 2000 por SRGr, SLY y AM se registraron más de 60 especies, incluyendo cerca de 40 especies de hepáticas y más de 20 especies de musgos. Algunas de estas también fueron colectadas en junio de

2008 por uno de los coautores (MB). Las especies de musgos en la comunidad de briofitas terrestres incluyeron a *Andreaea rupestris* Hedw.*,* *Anomobryum julaceum* (P. Gaertn.*,* B. Mey. & Scherb.) Schimp., *Bartramia mathewsii* Mitt., *B. potosica* Mont., *Dicranum frigidum* Müll. Hal., *Entosthodon jamesonii* (Taylor) Mitt.*, Eobruchia ecuatoriana* Steere*, Pleurozium schreberi* (Brid.) Mitt.*, Rhacocarpus purpurascens* (Brid.) Paris*, Racomitrium crispipilum* (Taylor) A. Jaeger*, Syntrichia andicola* (Wilson) R.H. Zander, *Thuidium peruvianum* Mitt. y varios miembros no identificados de los géneros *Breutelia, Bryum, Campylopus, Pohlia, Zygodon* y Pottiaceae. Las briofitas encontradas en la rica vegetación incluyen a las hepáticas *Anastrophyllum auritum* (Lehm.) Steph. (una forma pequeña, depauperada*)*, *A. nigrescens* (Mitt.) Steph., *A. tubulosum* (Nees) Grolle, *Andrewsianthus jamesonii* (Mont.) Váňa, *Aneura pinguis* (L.) Dumort., *Anthelia juratzkana* (Limpr.) Trevis., *Blepharostoma trichophyllum, Cephalozia crossii* Spruce, *Cheilolejeunea oncophylla* (Ångstr.) Grolle & E. Reiner*, Chiloscyphus breutelii* (Gottsche) J.J. Engel & R.M. Schust., *Gongylanthus granatensis* (Gottsche) Steph., *G. liebmannianus* (Lindenb. & Gottsche) Steph., *G. limbatus* (Herzog) Grolle & Váňa*, Gymnomitrium laceratum* (Steph.) Horik.*, Herbertus acanthelius* Spruce*, Isopaches bicrenatus, Isotachis lopezii* (R.M. Schust.) Gradst.*, Jensenia spinosa* (Lindenb. & Gottsche) Grolle*, Leptoscyphus gibbosus* (Taylor) Mitt.*, Metzgeria fruticola* Spruce*, Plagiochila bifaria* (Sw.) Lindenb.*, P. cleefii* Inoue*, P. dependula* Taylor*, P. punctata* (Taylor) Taylor*, P. revolvens* Mitt.*, Riccardia* spp., *Solenostoma sphaerocarpum* (Hook.) Steph.*, Stephaniella paraphyllina* J.B. Jack*, Symphyogyna brasiliensis* Nees*, Syzygiella sonderi* (Lindenb. & Gottsche) K. Feldberg *et al.* (= *Cryptochila grandiflora* [Lindenb. & Gottsche] Grolle)*, Triandrophyllum eophyllum* (R.M. Schust.) Gradst. y *T. subtrifidum* (Hook f. & Taylor) Fulford & Hatcher*.* Además, observamos una rica comunidad de hepáticas epífitas en las ramas de *Loricaria* y *Baccharis* a 4100-4250 m, la cual incluye muchas especies características de los altos Andes como *Chiloscyphus fragmentissimus* (R.M. Schust.) J.J. Engel & R.M. Schust. (= *Campanocolea fragmentissima* R.M. Schust.)*, Diplasiolejeunea replicata* (Spruce) Steph.*, Drepanolejeunea andina* Herzog, *Frullania peruviana* Gottsche*, F. tetraptera* Nees & Mont.*, Harpalejeunea grandistipula* R.M. Schust*, Metzgeria agnewii* Kuwah.*, Microlejeunea colombiana* Bischler*, Lejeunea catinulifera* Spruce y *Radula tenera* Mitt*.*

En este artículo se detallan los registros nuevos más interesantes entre nuestras colecciones. Previamente, A. Schäfer-Verwimp y otros obtuvieron registros florísticos nuevos de los parches de bosque de *Polylepis pauta* Hieron. en el paso de Papallacta a 4000 m, en la provincia de Pichincha (Schäfer-Verwimp et al. 2006). Ellos registraron numerosas especies nuevas para Napo y Pichincha. Muchas de las especies encontradas por estos autores fueron nuevamente registradas durante nuestra visita en el 2009.

Los especímenes están depositados en los Herbarios de la Universidad Técnica Particular de Loja (HUTPL; colecciones de A. Benítez) y de la Pontificia Universidad Católica del Ecuador, Quito (QCA; colecciones de S.R. Gradstein *et al.* y de M. Burghardt *et al.*), algunos duplicados están en el herbario privado de A. Schäfer-Verwimp, Alemania. A continuación se presentan las especies de hepáticas y antoceros en orden alfabético con una breve descripción de su ecología y distribución geográfica. Los nuevos registros para el país llevan un asterisco. La nomenclatura de las especies de hepáticas y antoceros y su distribución geográfica sigue a Léon-Yánez *et al.* (2006) y al nuevo catálogo de las hepáticas de Colombia (Gradstein & Uribe en prep.).

ANTHOCEROTOPHYTA (HORNWORTS)

Anthoceros punctatus L.

Loja: ciudad de Loja, invernadero de orquídeas UTPL, 3°59’16”S, 79°11’52”W, 2120 m, en suelo formando manchas verde oscuras junto a *Lunularia cruciata* (L.) Dumort., muy abundante, 14/06/2011, *Benitez 6* (HUTPL).

Distribución geográfica: subcosmopolita, en Ecuador previamente conocida en las islas Galápagos y la provincia de Zamora Chinchipe a 650-2150 m. Nueva para la provincia de Loja.

Notothylas vitalii Udar & D.K. Singh

Loja: Zapotillo, bosque seco tropical, 4°16’20”S, 80°19’43”W, 400 m, en suelo formando grandes manchas verdes en lugares más o menos expuestos y junto a *Riccia* sp., muy rara, 15/3/2012, det. A. Schäfer-Verwimp**,** *Benitez 423* (HUTPL). **El Oro:** Reserva Ecológica Arenillas (REMA), bosque seco tropical, 3°34’7”S, 80°8’49”W, 10-50 m, en suelo formando grandes manchas verdes junto a *Riccia* sp., muy común, 5/5/2012, *Benitez 536* (HUTPL).

Notothylas vitalii se caracteriza por presentar talos pequeños de 0,5 a 2 cm de diámetro, esporas amarillas, eláteres unicelulares y cápsulas que se abren en dos valvas longitudinales (Gradstein & Costa 2003).

Distribución geográfica: previamente conocida de Brasil, con una distribución general sobre los 500 m (Gradstein & Costa 2003). Nueva para Ecuador y primer registro del género *Notothylas* en Ecuador continental. La presencia de *N. vitalii* en el sur de

Ecuador constituye una extensión notable de su distribución. El registro de la especie en el bosque seco tropical de la provincia de El Oro, a 50 m, es el más bajo en América tropical.

MARCHANTIOPHYTA (LIVERWORTS)

Andrewsianthus jamesonii (Mont.) Váňa

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12177* (QCA).

Distribución geográfica: México a Bolivia, E África; en Ecuador previamente conocida de las provincias de Pichincha y Tungurahua a 3000-4000 m. Nueva para la provincia de Napo.

Aneura pinguis (L.) Dumort.

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre, cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12178* (QCA).

Distribución geográfica: subcosmopolita; en Ecuador previamente conocida de las provincias de Tungurahua y Zamora Chinchipe a 1200-2150 m. Nueva para la provincia de Napo y el registro más alto en el país.

Se estima que *A. pinguis* incluye un complejo de especies (Wachowiak *et al.* 2007). Se desconoce cuál es la relación taxonómica de las plantas del Ecuador en este complejo de especies.

Anthelia juratzkana (Limpr.) Trevis.

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12208* (QCA).

Distribución geográfica: ampliamente distribuida en la región holártica, rara en el trópico, colectada algunas veces en localidades alto-alpinas por encima de 4000 m en México, Venezuela, Ecuador y Bolivia (Gradstein *et al.* 2001). En Ecuador, este especie era conocida solamente del Páramo de la Virgen donde fue colectada una vez por Dr. Schuster en 1993 (Schuster 1996); el material falta en los herbarios ecuatorianos. Con este registro se confirma la presencia de la especie en el país. La presencia de *Anthelia* en el país no está mencionada en el Catálogo de las Hepáticas del Ecuador (León-Yánez *et al.* 2006).

Austrofossombronia peruviana (Gottsche) Crand.-Stotl., Stotler & A.V.Freire
Loja: ciudad de Loja, fragmento de bosque montano secundario, 3°59'39"S, 79°15'56"W, 2620 m, forma grandes manchas verdes junto a *Marchantia* sp., sobre suelo fangoso en un arroyo, muy rara, 14/3/2010, *Benitez 233* (HUTPL). **Pichincha:** páramo muy húmedo con *Plantago rigida* ca. 1 km E de la cumbre del Guagua Pichincha, 4000 m, en suelo, 18/1/2008, *Burghardt et al. 6526* (QCA).
Distribución geográfica: Andes tropicales, de 3500 hasta 4750 m; en Ecuador previamente conocida de las provincias de Carchi, Chimborazo y Morona Santiago a 3600–4000 m. Nueva para las provincias de Loja y Pichincha. El registro de Loja es el más bajo para esta especie y extiende su área de distribución ecuatoriana al sur del país.

Blepharostoma trichophyllum (L.) Dumort.
Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12179* (QCA).
Distribución geográfica: ampliamente distribuida en la región holártica; especie rara en las montañas tropicales (Gradstein & Váňa 1987), en el Neotrópico conocida de Costa Rica, Venezuela, Colombia y Perú, a 2500-4000 m. Nueva para Ecuador.

Cephalozia crossii Spruce
Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12180* (QCA).
Distribución geográfica: ampliamente distribuida en América tropical; en Ecuador previamente conocida de las provincias de Tungurahua y Zamora Chinchipe a 1200-2150 m. Nueva para la provincia de Napo y el registro de mayor altura en el país.

Cheilolejeunea oncophylla (Ångstr.) Grolle & E. Reiner

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12206* (QCA).

Distribución geográfica: ampliamente distribuida en América tropical; en Ecuador previamente solo conocida de la Reserva Biológica San Francisco (prov. Zamora Chinchipe) a 2150-2650 m. Nueva para la provincia de Napo, segundo registro en el país y el registro de mayor altura de *C. oncophylla*.

Chiloscyphus vermicularis (Lehm.) Hässel de Menendez (*Clasmatocolea vermicularis* (Lehm.) Grolle)

Loja: Amaluza, bosque montano primario, 4°33'47"S, 79°23'32"W, 2600 m, en suelo fangoso junto a un arroyo, formando grandes matas verde pálidas o amarillas junto a *Marchantia* sp., muy rara, 19/5/2010, *Benitez 318* (HUTPL).

Distribución geográfica: América tropical, África, regiones templadas del Sur; en Ecuador previamente conocida de las provincias de Pichincha, Tungurahua y Zamora Chinchipe a 1800-4000 m. Nueva para la provincia de Loja.

****Frullania setigera*** Steph.

Loja: Parque Nacional Podocarpus, Cajanuma, bosque nublado alto-montano, 3°59'29"S, 79°8'46"W, 2800 m, en tronco, 11/11/2009, *Gradstein 11271* (QCA).

Distribución geográfica: América tropical (Guatemala, Costa Ria, Colombia, Trinidad, Brasil), especie poco conocida. Nueva para Ecuador.

Gongylanthus liebmannianus (Lindenb. & Gottsche) Steph.

Loja: ciudad de Loja, Punzara alto, páramo, 4°2'41"S, 79°13'59"W, 2770 m, en suelo húmedo y rocas cubiertas de suelo, forma grandes matas pardo claras, muy abundante, 24/5/2010, *Benitez 427* (HUTPL).

Distribución geográfica: México a Bolivia, en Ecuador previamente conocida de las provincias de Chimborazo, Napo y Zamora Chinchipe, 1800-4100 m. Nueva para la provincia de Loja.

****Isopaches bicrenatus*** (Schmidel) H. Buch

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12207*, det. J. Váňa (QCA).

Distribución geográfica: ampliamente distribuida en la región holártica; especie rarísima en el trópico, previamente solamente conocida de dos localidades en la Sierra de Mantiqueira en el sureste de Brasil a 2400 m (Gradstein & Costa 2003). Nueva para Ecuador y primer registropara los Andes.

Isotachis lacustris Herzog

Loja: Parque Nacional Colambo-Yacuri, Jimbura, páramo, 4°42’43”S, 79°25’46”W, 3400 m, en suelo fangoso de un arroyo formado grandes matas pardas o negras, muy abundante, 8/7/2010, *Benitez 267* (HUTPL). **Napo/Pichincha:** Páramo de la Virgen, N del paso de Papallacta, ca. 0,5 km S de la estación de radio, 4200 m, en el margen de una laguna y en pequeños ríos, 5/4/2008, *Burghardt et al. 6869, 6875* (QCA).

Distribución geográfica: Andes tropicales, en Ecuador previamente solamente conocida del páramo de El Ángel (Carchi), 3700-4000 m. Nueva para las provincias de Loja, Napo y Pichincha. El registro de Loja amplía su área de distribución ecuatoriana al sur del país.

Isotachis lopezii (R.M. Schust.) Gradst.

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293’S, 78°11.544’W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12190* (QCA).

Distribución geográfica: Andes tropicales (Venezuela a Bolivia), Costa Rica; en Ecuador previamente conocida de las provincias de Carchi y Zamora Chinchipe a 2800-3400 m. Nueva para la provincia de Napo y el registro de mayor altura de *I. lopezii.*

Isotachis serrulata (Sw.) Gottsche

Loja: Jimbilla, bosque húmedo de neblina montano, 3°49’18”S, 79°9’21”W, 2740 m, crece en el suelo fangoso y sobre rocas de un arroyo junto a *Marchantia* sp., muy abundante, 10/6/2011, *Benitez 256* (HUTPL).

Distribución geográfica: América tropical, en Ecuador previamente conocida de las provincias de Esmeraldas, Morona Santiago, Pichincha y Zamora Chinchipe a 750-1850 m. Nueva para la provincia de Loja.

Jensenia spinosa (Lindenb. & Gottsche) Grolle

Loja: Parque Nacional Podocarpus, Cajanuma, páramo, 4°7’6”S, 79°9’16”W,

3150 m, crece en el suelo fangoso de la vegetación, muy común, 2/4/2010, *Benitez 258* (HUTPL).
Distribución geográfica: América tropical, África; en Ecuador previamente conocida de las provincias de Carchi, Napo y Zamora Chinchipe, 1900-4000 m (León-Yánez *et al.* 2006; Benitez & Gradstein 2011). Nueva para la provincia de Loja.

Lejeunea reflexistipula (Lehm. & Lindenb.) Gottsche
Loja: Loma del Oro, páramo, 3°40'57"S, 79°14'23"W, 3300 m, crece en el suelo húmedo y en el mantillo de la vegetación y en la base de arbustos junto a *Metzgeria* sp., muy abundante, 10/5/2010, *Benitez 256*, det. A. Schäfer-Verwimp (HUTPL).
Distribución geográfica: América tropical, en Ecuador previamente conocida de las provincias de Carchi, Morona Santiago, Napo, Pastaza, Tungurahua y Zamora Chinchipe a 600-3750 m. Nueva para la provincia de Loja.

****Lepidozia auriculata*** Steph.
Pichincha: paso de Papallacta, 00°20.580'S, 78°12.682'W, 4000 m, en bosque muy húmedo de *Polypelis pauta*, sobre base de tronco, 7/12/2009, *Gradstein et al. 12248* (QCA).
Distribución geográfica: Colombia y Perú a 3300-4000 m; reportado de Ecuador (Chimborazo) como registro dudoso (Léon-Yánez et al. 2006). Primer registro confirmado para el Ecuador.

Lepidozia cupressina (Sw.) Lindenb.
Pichincha: paso de Papallacta, 00°20.580'S, 78°12.682'W, 4000 m, en bosque muy húmedo de *Polypelis pauta* Hieron. sobre base de tronco, 7/12/2009, *Gradstein et al. 12247* (QCA).
Distribución geográfica: América tropical, África, W Europa; en Ecuador previamente conocida de la provincia de Zamora Chinchipe a 1800-2150 m. Nueva para la provincia de Pichincha y segundo registro del país.

Lunularia cruciata (L.) Dumort.
Loja: ciudad de Loja, invernadero de orquídeas UTPL, 3°59'16"S, 79°11'52"W, 2120 m, en suelo, forma grandes manchas verdes junto a *Anthoceros punctatus* L. muy abundante, 14/8/2011, *Benitez 255* (HUTPL).
Distribución geográfica: subcosmopolita pero escasa en los trópicos; en Ecuador previamente conocida en la provincia de Pichincha a 2850 m. Nueva para la provincia de Loja. Este registro amplía su área de distribución ecuatoriana al sur del país.

Noteroclada confluens Hook. & Wils.

Loja: Parque Nacional Colambo-Yacuri, Jimbura, páramo, 4°42’43”S, 79°25’46”W, 3400 m, en suelo fangoso junto a un arroyo formando grandes matas verde pálidas, muy rara, 8/7/2010, *Benitez 272* (HUTPL).

Distribución geográfica: América tropical y austral (Crandall-Stotler *et al.* 2010), en Ecuador previamente conocida de las provincias de Carchi, Chimborazo, Morona Santiago, Pichincha y Zamora Chinchipe a 1800-4000 m. Nueva para la provincia de Loja.

Plagiochasma rupestre (J.R. Forst. & G. Forst.) Steph.

Loja: Catamayo-Palo Blanco, matorral seco, 4°5’39”S, 79°21’18”W, 1100-1300 m, crece en suelo y en rocas húmedas en lugares expuestos y soleados cerca de un arroyo, forma grandes manchas verdes, muy rara, 24/1/2012**,** *Benitez 420* (HUTPL).

Distribución geográfica: pantropical y regiones mediterráneas; en Ecuador previamente conocida de las provincias de Pastaza, Tungurahua y las Islas Galápagos a 50-2570 m. Nueva para la provincia de Loja. Este registro amplía su área de distribución ecuatoriana al sur del país.

Plagiochila cleefii Inoue

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293’S, 78°11.544’W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12198* (QCA).

Distribución geográfica: páramos de Colombia y Ecuador, en Ecuador previamente conocida de Cajanuma, Parque Nacional Podocarpus (prov. Loja) a 3150 m. Nueva para la provincia de Napo, segundo registro en el país y el registro de mayor altura de *P. cleefii.*

Plagiochila dependula Taylor

Loja: Parque Nacional Podocarpus, Cajanuma, páramo, 4°7’6”S, 79°9’16”W, 3150 m, sobre la base de arbustos (*Miconia* sp.) y entre la hojarasca de la vegetación junto a *Plagiochila ensiformis* Taylor, muy abundante, 2/4/2010, *Benitez 258* (HUTPL).

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca del estación de radio, 00°19.293’S, 78°11.544’W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12199* (QCA).

Distribución geográfica: Andes tropicales, en Ecuador previamente conocida de las provincias de Pichincha y Zamora Chinchipe, 3400-4200 m (León-Yánez *et al.* 2006; Benitez & Gradstein 2011). Nueva para las provincias de Loja y Napo.

Plagiochila fuscolutea Taylor
Loja: Parque Nacional Podocarpus, bosque nublado alto-montano, 3°59'29"S, 79°8'46"W, 2900 m, sobre la base de arbustos y entre la hojarasca de la vegetación junto a *Metzgeria* sp. *y Riccardia* sp., muy abundante, 2/4/2010, *Benitez 258* (HUTPL).
Distribución geográfica: Andes tropicales, en Ecuador previamente conocida de las provincias de Azuay, Carchi, Cotopaxi, Pichincha, Tungurahua y Zamora Chinchipe a 2200-4000 m. Nueva para la provincia de Loja.

***Plagiochila* ovata** Lindenb.
Pichincha: paso de Papallacta, 00°20.580'S, 78°12.682'W, 4000 m, en bosque muy húmedo de *Polypelis pauta*, en suelo con *Plagiochila dependula*, *P. ensiformis* y *Syzygiella rubricaulis*, 7/12/2009, *Gradstein et al. 12252* (QCA), ibid., en bosque de *Gynoxis*, 4000 m, en suelo con *Plagiochila dependula* y *P. ensiformis*, 20/6/2008, *Burghardt et al. 7444* (QCA).
Distribución geográfica: México a Bolivia por encima de 2600 m (Müller *et al.* 1999); en Ecuador previamente conocida las provincias de Morona Santiago y Napo a 3700-4200 m. Nueva para la provincia de Pichincha.

Plagiochila punctata (Taylor) Taylor
Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293'S, 78°11.544'W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12200* (QCA).
Distribución geográfica: América tropical, E África y W Europa (Heinrichs *et al.* 2005); en Ecuador previamente conocida de las provincias de Tungurahua y Zamora Chinchipe a 1800-3150 m. Nueva para la provincia de Napo y el registro de mayor altura de *P. punctata.*

Platycaulis renifolia R.M. Schust.
Carchi: Volcán Chiles, N de Tufiño-Maldonado road, 3600 m, en humedal de páramo creciendo entre almohadillas densas de *Oreobolus obtusangulus* Gaudich., 25/8/1997, *P.M. Ramsay et al. 2078* (QCA).

Distribución geográfica: única especie en el género *Platycaulis* y endémica de los Andes del Norte, previamente conocida solo del ejemplar tipo de los Andes de Venezuela (Páramo de Tamá), donde fue colectado por Dr. Schuster en 1978 (Schuster 1995). Segundo registro en el mundo y primer registro para el Ecuador.

Platycaulis renifolia (familia Lophocoleaceae) es una especie rara de las turberas parameñas, reconocida por su color pardo oscuro, hábito lateralmente comprimido, hojas reniformes, anfigastros bífidos con lobos ciliados y rizoides fasciculados en las bases de los anfigastros. La especie es algo similar a *Plagiochila dependula* pero se reconoce por su estatura más pequeña, la presencia de anfigastros y sus rizoides fasciculados (anfigastros ausentes y rizoides dispersos en *P. dependula*). La ortografía "*Platycaulis renifolius*" en la publicación original (Schuster 1995) es un error.

Porella brachiata (Taylor) Spruce

Loja: ciudad de Loja, fragmento de bosque montano secundario, 3°59’39”S, 79°15’56”W, 2600 m, epífita sobre la corteza y base de árboles (*Myrcianthes fragans* (Sw) McVaught) y en el suelo sobre rocas, forman grandes manchas verdes oscuras, muy rara, 6/7/2010, *Benitez 253*, det. A. Schäfer-Verwimp (HUTPL).

Distribución geográfica: especie endémica de los Andes del Norte, en Ecuador previamente conocida de la provincia de Pichincha. Nueva para la provincia de Loja. Este registro amplía su área de distribución ecuatoriana al sur del país.

Pseudocephalozia quadriloba (Steph.) R.M. Schust.

Pichincha: Páramo de Pichincha, 1 km E de la cumbre del Guagua Pichincha, páramo muy húmedo, 4000 m, entre *Campylopus* sp., 7/2/2008, *Burghardt et al. 6628* (QCA).

Distribución geográfica: Costa Rica, Andes tropicales, regiones templadas del S; en Ecuador previamente conocida de la provincia de Carchi y Zamora Chinchipe, 3200-4100 m. Nueva para la provincia de Pichincha.

Riccardia andina (Spruce) Herzog

Pichincha: paso de Papallacta, 00°20.580’S, 78°12.682’W, 4000 m, en bosque muy húmedo de *Polypelis pauta*, en corteza con *Herbertus grossispinus* (= *H. sendtneri* auct.), *Leptoscyphus gibbosus, Plagiochila dependula* y varios musgos, 7/12/2009, *Gradstein et al. 12253* (QCA).

Distribución geográfica: Andes tropicales; en Ecuador previamente conocida de las provincias de Los Ríos, Napo, Pastaza y Zamora Chinchipe, 300-2150 m. Nueva para la provincia de Pichincha y el registro de mayor altitud de *R. andina.*

Solenostoma callithrix (Lindenb. & Gottsche) Steph. **(***Jungermannia callithrix* Lindenb. & Gottsche)

Loja: Zamora Huayco Alto, Reserva Privada “El Madrigal” 5 km de la ciudad de
Loja, zona de amortiguamiento del Parque Nacional Podocarpus, bosque siempre verde montano alto, 4°2’50”S, 79°10’31”W, 2400 m, crece en taludes sobre suelo húmedo en el sendero de llegada a la reserva, muy rara, 8/11/2010, *Benitez 348*, verif. A. Schäfer-Verwimp y J. Váňa (HUTPL).

Distribución geográfica: América tropical, en Ecuador previamente conocida de las provincias de Carchi, Pichincha, Tungurahua y Zamora Chinchipe, 1800-3300 m. Nueva para la provincia de Loja.

Solenostoma hyalinum (Hook.) Mitt. **(***Jungermannia hyalina* Hook.)

Loja: Zamora Huayco Alto, Reserva Privada “El Madrigal” 5 km de la ciudad de
Loja, zona de amortiguamiento del Parque Nacional Podocarpus, bosque siempre verde
montano alto, 4°2’50”S, 79°10’31”W, 2400 m, crece en taludes sobre suelo húmedo y en lugares sombríos, muy común, 11/6/2011, *Benitez 257*, verif. A. Schäfer-Verwimp y J. Váňa (HUTPL).

Distribución geográfica: pantropical y región holártica; en Ecuador previamente conocida de las provincias de Pichincha y Zamora Chinchipe, 1800-1900 m. Nueva para la provincia de Loja y el registro de mayor altitud en Ecuador.

Solenostoma sphaerocarpum (Hook.) Steph. **(***Jungermannia sphaerocarpa* Hook.)

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293’S, 78°11.544’W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 7/12/2009, *Gradstein et al. 12192* (QCA).

Distribución geográfica: ampliamente distribuida en la región holártica y en las montañas tropicales (Gradstein & Váňa 1987); en Ecuador previamente conocida de las provincias de Carchi y Zamora Chinchipe a 1800-4100 m. Nueva para la provincia de Napo.

Symphyogyna apiculispina Steph.

Loja: Zamora Huayco Alto, Reserva Privada “El Madrigal” 5 km de la ciudad de
Loja, zona de amortiguamiento del Parque Nacional Podocarpus, bosque siempre verde montano alto, 4°2’50”S, 79°10’31”W, 2400 m, crece sobre troncos en descomposición y entre la hojarasca de la vegetación, en lugares sombríos y húmedos

cerca de arroyos, muy rara, 26/3/2010, *Benitez 202*, verif. A. Schäfer-Verwimp (HUTPL).

Symphyogyna apiculispina es muy similar a *S. brogniartii* Mont., pero difieren en que la primera presenta papilas mucilaginosas solo en el margen del talo con dos células de longitud y las lobulaciones del talo no llegan hasta el nervio central, a diferencia en *S. brogniartii* donde las lobulaciones del talo llegan al nervio central y las papilas se localizan en el margen y la superficie dorsal del talo (Uribe & Aguirre 1995).

Distribución geográfica: previamente conocida solo de Bolivia y Colombia, 500-3600 m. Nuevo registro para Ecuador. A pesar de ser una especie cortícicola, también crece sobre troncos en descomposición, hojarasca, base de troncos y en el suelo en zonas muy húmedas y sombrías (Uribe & Aguirre 1995), lo que concuerda con nuestras observaciones.

Triandrophyllum eophyllum (R.M. Schust.) Gradst. (*Olgantha eophylla* R.M. Schust.)

Napo: Páramo de la Virgen, N del paso de Papallacta, en ladera rocosa NW de la cumbre cerca de la estación de radio, 00°19.293’S, 78°11.544’W, 4200-4300 m, hepática terrestre en superpáramo muy húmedo, 20/6/2008, *M. Burghardt et al. 7407, 7434b* (QCA), ibid., 7/12/2009, *Gradstein et al. 12204* (QCA).

Distribución geográfica: especie endémica para Ecuador y solamente conocida de la localidad tipo en el Páramo de la Virgen donde fue colectada por Dr. Schuster en 1993 (Schuster 1996). La especie fue descrita como un género nuevo monospecífico, *Olgantha* R.M. Schust., qué es actualmente considerado como sinónimo de *Triandrophyllum* (Gradstein et al. 2001).

Las colecciones reportadas de *T. eophyllum* son las primeras desde 1993; estas confirman la ocurrencia de la especie en su única localidad conocida. La especie crece junto con *T. subtrifidum* (Hook.f. & Taylor) Fulford & Hatcher (especímenes *Burghardt 7434a* y *Gradstein 12205,* herbario QCA), segunda especie neotropical en el género *Triandrophyllum* y ampliamente distribuida en los Andes. A veces las dos especies crecen mezcladas y pueden ser dificiles de distinguir. Se reconoce a *T. eophyllum* por sus hojas más cóncavas y tan anchas como largas (más largas que anchas en *T. subtrifidum*) y el ápice de las hojas minutamente bífido (a veces trífido) hasta 1/10 de la hoja (más profundamente bífido o trífido, hasta 1/8-1/4(-1/2) de la hoja en *T. subtrifidum*).

Agradecimientos

Agradecemos a A. Schäfer-Verwimp y J. Váňa por ayudar en la identificación de algunas especies y a dos revisores anónimos por sus correcciones del manuscrito. El trabajo de campo en el sur del país fue financiado por la Universidad Técnica Particular de Loja y la Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación del Ecuador (SENESCYT). También agradecemos a Cesar Aguirre, Ministerio del Ambiente de El Oro-Reserva Ecológica Arenillas (REMA) y Naturaleza y Cultura Internacional por proporcionar el acceso a las áreas de estudio.

Bibliografía

Benitez, A. & S. R. Gradstein 2011. Adiciones a la flora de briófitas del Ecuador. Cryptogamie Bryologie 32: 65-74.

Churchill, S. P., D. Griffin & J. Muñoz 2000. A Checklist of the mosses of the tropical Andean countries. Ruizia 17: 1-203.

Crandall-Stotler, B., R. E. Stotler, L. Zhang & L. L. Forrest 2010. On the morphology, systematics and phylogeny of *Noteroclada* (Noterocladaceae, Marchantiophyta). Nova Hedwigia 91: 421-450.

Gradstein, S. R. & D. P. Costa 2003. The Hepaticae and Anthocerotae of Brazil. Memoirs of the New York Botanical Garden 87: 1-317.

Gradstein, S. R. & A. Schäfer-Verwimp 2012. A new species of *Archilejeunea* (Spruce) Schiffn. (Lejeuneaceae) from Ecuador. Cryptogamie Bryologie 33: 107-112.

Gradstein, S. R. & J. Vána 1987. On the occurrence of Laurasian liverworts in the Tropics. Memoirs of the New York Botanical Garden 45: 388-425.

Heinrichs, J., M. Lindner, H. Groth & C. Renker 2005. Distribution and synonymy of *Plagiochila punctata* (Taylor) Taylor, with hypotheses on the evolutionary history of *Plagiochila* sect. *Arrectae*. Plant Systematics and Evolution 250: 105-117.

León-Yánez, S., S. R. Gradstein & C. Wegner 2006. Hepáticas (Marchantiophyta) y Antoceros (Anthocerotophyta) del Ecuador, catálogo. Publicaciones del Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito.

Müller., J., J. Heinrichs & S. R. Gradstein 1999. A revision of *Plagiochila* sect. *Plagiochila* in the Neotropics. The Bryologist 102: 729-746.

Schäfer-Verwimp, A., R. Wilson, S. Yandún, K. Feldberg, M. Burghardt & J. Heinrichs 2006. Additions to the bryophyte flora of Ecuador. Cryptogamie Bryologie 27: 313-332.

Schuster, R. M. 1995. Venezuelan Hepaticae VI. On *Platycaulis* Schust. (Jungermanniales). Nova Hedwigia 61: 391-396.

Schuster, R. M. 1996. On *Olgantha* Schust., gen. n. Isophylly an evolution of Jungermanniales. Nova Hedwigia 63: 529-543.

Schuster, R. M. 1999. *Harpalejeunea* (Spr.) Schiffn. I. Studies on a new Andean species of *Harpalejeunea*. Journal of the Hattori Botanical Laboratory 87: 287-294.

Uribe, J. & J. Aguirre 1995. Las especies Colombianas del género *Symphyogyna* (Hepaticae: Pallaviciniaceae). Caldasia 17: 429-458.

Wachowiak, W., A. Bączkiewicz, E. Chudzińska & K. Buczkowska 2007. Cryptic speciation in liverworts – a case study in the *Aneura pinguis* complex. Botanical Journal of the Linnean Society 155: 273–282.

CAPÍTULO VI / CHAPTER VI

More than one hundred new records of lichens from Ecuador

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Artículo subido en Acta Botanica Brasilica

Chapsa diploschistoides (Zahlbr.) Frisch

Abstract

Ecuador is considered one of the richest and most diverse country on Earth, and it is expected to hold a high richness of lichenized fungi. However, studies centered on these organisms are still scarce and focused on very specific areas, so that the actual knowledge of the species number is still incomplete. In this study we report twelve species new to South America and 50 species new to Ecuador, for which we provide data on ecology and distribution. In addition, we found 41 species that were previously recorded from Galapagos Islands and were found for the first time in mainland Ecuador. Finally, 31 species have been found for the first time in El Oro or Loja provinces. In total 134 species are new for South America, Ecuador or different provinces, thus widening considerably the known distribution of the species and the lichen Flora of the country. The results of this research support the need to conduct additional taxonomic and floristic studies in the near future.

Key words: diversity, epiphytic lichens, South America, tropical montane forests, dry forests.

Introduction

Lichens are a very diverse group with ca. 28000 estimated species around the world (Lücking *et al.* 2009a), and ca. 7000 species estimated for the Neotropics. Tropical Andes is considered the most diverse area for lichens (Lücking *et al.* 2009a; Sipman 2011). However, the present knowledge is still far from the estimates, and in countries like Bolivia, Chile, Peru and Venezuela only a quarter of the estimated number of species have been reported (Marcano *et al.* 1996; Galloway & Quilhot 1998; Ramos 2014; Rodriguez-Flakus *et al.* 2014).

In Ecuador, ca. 900 lichen species have been recorded for mainland (Cevallos 2012; Prieto et al. in prep.) and 797 for Galapagos Islands, a relatively low species number compared with the estimates. Collecting efforts have focused on sites and habitats located in Napo, Pichincha and Zamora Chinchipe provinces, while in provinces such as Esmeraldas, Los Ríos and Manabí there are scarce contributions (Lücking 1999a; Nöske *et al.* 2007; Cevallos 2012). Moreover, most studies have focused on the most conspicuous species rather than on crustose microlichens, therefore not allowing reliable estimates of total species richness (Arvidsson 1991; Lücking 1999; Nöske *et al.* 2007; Lücking *et al.* 2009a; Cevallos 2012).

Recently, Benitez *et al.* (2012) documented about 119 macrolichen species in six forests in Loja province, which demonstrates the great diversity that the southern region of Ecuador houses. Thus, the main objective of this study is to contribute to the knowledge of the lichen diversity in Ecuador, by providing information on the ecology and distribution of the less known species.

Materials and methods

The study was conducted in the southern region of Ecuador in different tropical forest fragments (montane and dry forests) located in El Oro and Loja provinces, in the private Madrigal reserve, the Colambo-Yacuri National Park and the ecological reserve Arenillas (REMA) (Fig. 1).

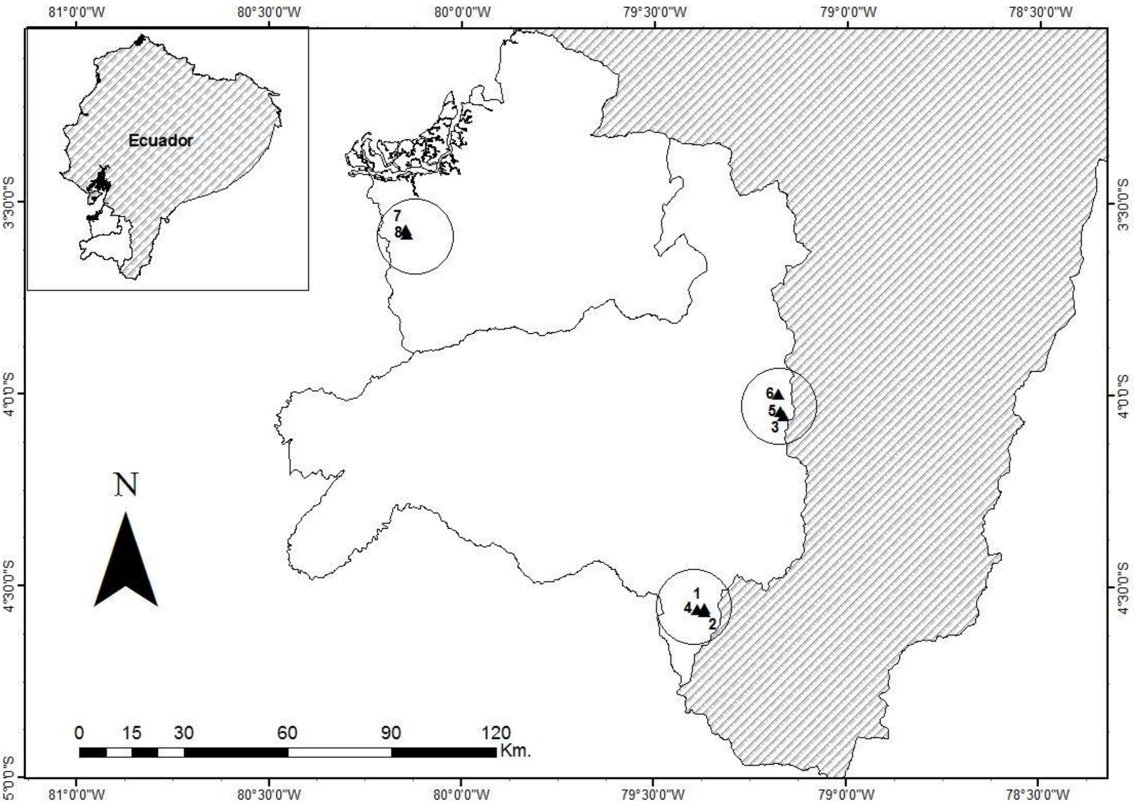

Figure 1: Ecuadorian map showing collection sites of lichens.

Specimens were collected as part of parallel ecological studies carried out by the authors. The specimens were identified using numerous published keys which are incorporated in the text for species reported for the first time from Ecuador. General keys (Brodo *et al.* 2001; Nash *et al.* 2002, 2004, 2007) were also used for identification. Standard microscopy techniques and spot tests based on thallus fluorescence under ultraviolet light (UV), reactions with K (10% water solution of potassium hydroxide), C (commercial bleach) and Lugol´s solution (I) were checked in some species. For the nomenclature of the species we followed MycoBank (www.mycobank.org/) and LIAS 1995-2016 (A Global Information System for Lichenized and Non-Lichenized Ascomycetes: www.lias.net). Specimens were deposited in the Herbarium of Universidad Técnica Particular de Loja (HUTPL), at the Bryophytes and Lichens Collection. New records from Ecuador are marked with an asterisk (*) and those new for South America with two asterisks (**).

For each new record the following information has been included 1) locality and collection number, 2) references where morphological or anatomical characteristics are described, 3) iconography, where an image or drawing of habit or some morphological or anatomical character appears, 4) ecology, in the study area, 5) general distribution (mainly in the Neotropics and Paleotropics) and 6) ecology and altitudinal range where the species has been cited previously. New records for mainland Ecuador and the new provincial records are listed in Table 1.

List of localities

Locality 1

Ecuador, Loja, Espíndola, upper part of buffer zone of Colambo-Yacuri National Park. Very dense primary montane forest, evergreen, unmanaged and characterized by a dense canopy layer (wood density above 75%). Common trees are *Podocarpus oleifolius* D. Don, *Cinchona macrocalyx* Pav. ex DC. and *Myrica pubescens* Humb. & Bonpl. ex Willd. 2700–2882 m altitude. 4°33’27”S; 79°22’9”W. 10 may 2011.

Locality 2

Ecuador, Loja, Espíndola, lower part of buffer zone of Colambo-Yacuri National Park. Dense primary montane forest, evergreen, unmanaged and characterized by a dense canopy layer with wood density above 75%. Mature trees of 30-40 m (*P. oleifolius* and *C. macrocalyx*) forming various layers. 2518–2630 m altitude. 4°33’54”S; 79°22’13”W. 10 may 2011.

Locality 3

Ecuador, Loja, Madrigal Private Reserve. Secondary forest, re-grown after selective or total logging events on primary montane forest, currently without anthropic use. Trees of 25 m high, mainly composed of Melastomataceae and Lauraceae species, and canopy cover around 60-70%. 2665–2712 m altitude. 4°3’9”S; 79°9’55”W. 10 may 2011.

Locality 4

Ecuador, Loja, Espíndola, buffer zone of Colambo-Yacuri National Park. Secondary managed forest, re-grown after selective or total logging events on primary montane forest. It is dominated by Lauraceae and Melastomataceae species, with canopy cover around 70%. 2211–2537 m altitude. 4°33’35”S; 79°23’21”W. 10 may 2011.

Locality 5

Ecuador, Loja, lower part of Madrigal Private Reserve. Monospecific forests of *Alnus acuminata* Kunth, originated by natural regeneration of forests, re-grown after logging or burning the primary vegetation. Characterized by a single strate of trees. 2280–2420 m altitude. 4°2’36”S; 79°10’20”W. 10 may 2011.

Locality 6

Ecuador, Loja, Zamora Huayco alto. Monospecific forest of *A. acuminata,* originated by natural regeneration of forest, re-grown after logging or burning the primary vegetation.

Characterized by a uniform structure and the absence of understory. 2167–2245 m altitude. 3°59’53”S; 79°10’46”W. 10 may 2011.

Locality 7

Ecuador, El Oro, Arenillas, Ecological Reserve Arenillas (REMA). Tropical dry deciduous forest with different tree layers dominated by species of *Bursera graveolens* (Kunth) Triana & Planch., *Cochlospermum vitifolium* (Willd.) Spreng, *Eriotheca ruizii* (K. Schum.) A. Robyns, *Tabebuia billbergii* (Bureau & K. Schum.) Standl., *Tabebuia chrysantha* G. Nicholson and *Ziziphus thyrsiflora* Benth. 32–47 m altitude. 3°34’12”S; 80°8’46”W. 15 January 2013.

Locality 8

Ecuador, El Oro, Arenillas, Ecological Reserve Arenillas (REMA). Tropical dry deciduous forest with different tree layers dominated by species of *C. vitifolium*, *E. ruizii,* and *T. chrysantha.* 51–68 m altitude. 3°34’54”S; 80°8’38”W. 15 January 2013.

Results and Discussion

We recorded 50 lichen species for the first time in Ecuador, and twelve new records from South America. We also found 72 new species, of which 41 are new records to mainland Ecuador, 26 are reported for the first time for Loja province and five for El Oro province (Table 1).

Table 1: List of new records for mainland Ecuador and provincial records in El Oro and Loja provinces.

Species	Locality	Mainland Ecuador	Loja	El Oro
Arthonia antillarum (Fée) Nyl.	7, 8	X		
Coniocarpon cinnabarinum DC.	1, 2, 3, 4, 5, 6, 7, 8		X	X
Bactrospora myriadea (Fée) Egea & Torrente	7	X		
Bathelium degenerans (Vain.) R.C. Harris	7	X		
Brigantiaea leucoxantha (Spreng.) R. Sant. & Hafellner	1, 2, 3, 4		X	
Buellia rhombispora Marbach	5, 6		X	
Coenogonium leprieurii (Mont.) Nyl.	1, 2, 3,4		X	
Coenogonium linkii Ehrenb.	2		X	

Coenogonium pineti (Ach.) Lücking & Lumbsch	1	X		
Cresponea flava (Vain.) Egea & Torrente	7, 8	X		
Cresponea leprieurii (Mont.) Egea & Torrente	1, 2, 3, 4		X	
Cryptothecia effusa (Müll. Arg.) R. Sant.	2		X	
Cryptothecia exilis G. Thor	2	X		
Cryptothecia punctisorediata Sparrius & Saipunkaew	1, 2	X		
Cryptothecia striata Thor (Loc. 2)	2	X		
Dichosporidium boschianum (Mont.) G. Thor	1, 3, 4, 5, 6		X	
Dirinaria aegialita (Afzel. ex Ach.) B.J. Moore	7, 8	X		
Dirinaria applanata (Fée) D.D. Awasthi	7, 8	X		
Dirinaria confluens (Fr.) D. D. Awasthi	7, 8	X		
Dirinaria confusa D. Awasthi	7, 8	X		
Dirinaria papillulifera (Nyl.) D.D. Awasthi	7, 8	X		
Dirinaria picta (Sw.) Schaer. ex Clem.	7, 8			X
Dyplolabia afzelii (Ach.) A. Massal.	8	X		
Glyphis cicatricosa Ach.	5, 6, 7, 8		X	X
Glyphis scyphulifera (Ach.) Staiger	1, 2, 3, 4, 7, 8	X		
Graphis anfractuosa (Eschw.) Eschw.	6, 7, 8	X		
Graphis conferta Zenker	1, 2, 3, 4	X		
Graphis dichotoma (Müll. Arg.) Lücking	5, 6	X		
Helminthocarpon leprevostii Fée	8	X		
Herpothallon granulare (Sipman) Aptroot & Lücking	1, 2, 3, 4	X		
Herpothallon rubrocinctum (Ehrenb.) Aptroot & Lücking	2	X		
Lecanographa laingiana Diederich, Egea & Sipman	7, 8	X		
Lecanographa lyncea (Sm.) Egea & Torrente	7, 8	X		
Lecanora caesiorubella Ach.	3, 4, 5	X		
Lecanora chlarothera Nyl.	4		X	X

Lecanora flavidomarginata B. de Lesd	4, 5, 6		X	
Lecanora varia (Hoffm.) Ach.	3, 5, 6	X		
Leucodecton occultum (Eschw.) Frisch	7, 8	X		
Lopezaria versicolor (Fée) Kalb & Hafellner	4		X	
Maronea constans (Nyl.) Hepp	2, 5		X	
Megalospora admixta (Nyl.) Sipman	4		X	
Megalospora sulphurata var. *nigricans* (Müll. Arg.) Riddle	3, 4		X	
Megalospora tuberculosa (Fee) Sipman	1, 2 , 3, 4		X	
Mycomicrothelia subfallens (Mull. Arg.) D. Hawksw.	1, 2	X		
Normandina pulchella (Borrer) Nyl.	4		X	
Opegrapha difficilior Nyl.	7, 8	X		
Opegrapha trilocularis Müll. Arg.	7, 8	X		
Phaeographis brasiliensis (A. Massal.) Kalb & Matthes-Leicht	5, 7, 8		X	
Phaeographis dendritica (Ach.) Müll. Arg.	5		X	
Phaeographis inconspicua (Fée) Müll. Arg.	4, 5	X		
Phaeographis lobata (Eschw.) Müll. Arg.	7	X		
Phaeographis intricans (Nyl.) Staiger	7, 8	X		
Phaeographis scalpturata (Ach.) Staiger	5, 6		X	
Phyllopsora furfuracea (Pers.) Zahlbr.	1, 2, 3, 4		X	
Phyllopsora parvifolia (Pers.) Mull. Arg.	1, 2 , 3, 4		X	
Phyllopsora parvifoliella (Nyl.) Mull. Arg.	1, 2, 3		X	
Porina imitatrix Müll. Arg.	1, 2, 4, 5, 6		X	
Porina nucula Ach.	1, 2, 3, 4		X	
Pseudopyrenula diluta (Fée) Müll. Arg.	7, 8	X		
Pseudopyrenula subnudata Müll. Arg.	7, 8	X		
Pyrenula erumpens R.C. Harris	7, 8	X		
Pyrenula microtheca R. C. Harris	5	X		
Pyrenula ochraceoflava (Nyl.) R.C. Harris	7, 8	X		
Ramonia valenzueliana (Mont.) Stizenb.	7	X		
Sarcographa tricosa (Ach.) Müll. Arg.	7, 8	X		
Schismatomma spierii Aptroot & Sparrius	7, 8	X		
Tephromela atra (Hudson) Hafellner	5, 6, 7, 8		X	X
Trypethelium eluteriae Spreng.	7, 8	X		

**Amandinea submontana* Marbach

Description: Sipman (112: 2003); *Image*: Aptroot (www.tropicallichens.net)

Loja: Loc. 3 and 4, this species was found in two unmanaged secondary montane forests at altitudes between 2200-2700 m, A. Benitez 04 and 05.

It has been previously reported from few localities in Colombia and Guatemala, between 150-2600 m altitude (González-Román *et al.* 2014; Marbach 2000) and in North America (Hodkinson *et al.* 2009).

***Anthracothecium macrosporum* (Hepp) Müll. Arg.

Description: Aptroot *et al.* (35: 2008); *Image:* Aptroot *et al.* (36: 2008)

Loja: Loc. 2, it has been found only in one well-preserved and dense primary forest stand together with *Coccocarpia erythroxyli* (Spreng.) Swinscow & Krog, *Cresponea leprieurii* (Mont.) Egea & Torrente and *Sticta tomentosa* (Sw.) Ach, A. Benitez 06.

It was previously known from primary and secondary forests from Costa Rica and Cuba, growing between 400 and 690 m (Aptroot *et al.* 2008; Rosabal *et al.* 2012a).

**Baculifera remensa* (Stirt.) Marbach

Description: Marbach (144: 2000), Sipman (85: 2003); *Image:* Sipman (www.tropicallichens.net)

Loja. Loc. 5, this lichen has been found only in open and managed forests of *Alnus acuminata* growing together with *Bulbothrix isidiza* (Nyl.) Hale*, Heterodermia japonica* (M. Satô) Swinscow & Krog and *Parmotrema cristiferum* (Taylor) Hale, A. Benitez 20.

It is rather frequent in Central and South America (Marbach 2000).

**Chiodecton sphaerale* Ach.

Description: Thor (30: 1990); *Image:* Nelsen *et al.* (139: 2009)

Loja: Loc. 1, this is a very rare epiphytic species found on a well-preserved primary montane forest together with *Leptogium azureum* (Sw.) Mont*., P. hispaniolae* and *S. lobarioides*, A. Benitez 32.

Its distributional area is restricted to montane forests of Brazil, Colombia and Venezuela, at altitudes between 2000 and 2700 m (Marcano *et al.* 1996; Aptoot 2002).

**Coenogonium bacilliferum* (Malme) Lücking, Aptroot & Sipman

Description: Rivas-Plata *et al.* (303: 2006)

Loja: Loc. 2, it was found only in one well-preserved and dense evergreen forest stand, together with *C. erythroxyli*, *Leptogium cyanescens* (Pers.) Körb. and *Punctelia crispa* Marcelli, Jungbluth & Elix., A. Benitez 48.

Outside of the ecuadorian territory, it is only known from few localities in Brazil and Costa Rica (Rivas-Plata *et al.* 2006).

**Coenogonium eximium* (Nyl.) Kalb & Lücking

Descripción: Rivas-Plata *et al.* (308: 2006).

Loja: Loc. 1, this rare species has been found in an unmanaged montane evergreen forest, with a dense canopy. Other lichens of the same community were *Graphis conferta* Zenker & Hampe and *Leptogium phyllocarpum* (Pers.) Mont., A. Benitez 50.

It is previously known from Colombia and Costa Rica (Rivas-Plata *et al.* 2006).

**Coenogonium isidiosum* (Breuss) Rivas Plata, Lücking, Umaña & Chavez

Description: Rivas-Plata *et al.* (302: 2006); *Image:* Cáceres (57: 2007)

Loja: Loc. 1, we have found a small population of this species in a well-preserved primary forest. Other lichens of the same community were *Porina imitatrix* Müll. Arg. and *Pseudocyphellaria aurata* (Ach.) Vain., A. Benitez 51.

It has a sparse distribution in South America, only known from Brazil, Costa Rica and Nicaragua (Rivas-Plata *et al.* 2006; Cáceres 2007).

***Coenogonium kalbii* Aptroot, Lücking & Umaña

Description: Rivas-Plata *et al.* (281: 2006); *Image:* Rivas-Plata *et al.* (278: 2006)

Loja: Loc. 1, 2 and 4, this species is relatively common in primary and secondary montane forests, at altitudes between 2300 and 2800 m, A. Benitez 52, 53 and 54.

It was previously known from Costa Rica, growing in open sites in low montane rain forests between 350 and 1300 m (Rivas-Plata *et al.* 2006).

***Coenogonium lutescens* (Vezda & Malcolm) Malcolm

Description: Rivas-Plata *et al.* (306: 2006); *Image:* Seavey & Seavey (www.seaveyfieldguides.com)

Loja: Loc. 1, it is a very rare species found on bark in a dense evergreen primary forest stand, together with *S. tomentosa* and *Yoshimuriella subdissecta* (Nyl.) Moncada & Lücking., A. Benitez 58.

It was previously known from North America (Seavey *et al.* 2014).

**Coenogonium magdalenae* Rivas Plata, Lücking & Lizano

Description: Rivas-Plata *et al.* (286: 2006); *Image:* Rivas-Plata *et al.* (278: 2006).

Loja: Loc. 1, 2, 3 and 4, this is a very common species growing on trees of primary and secondary montane forests, at altitudes between 2300 and 2700 m, A. Benitez 59, 60, 61, and 62.

It was previously known from Colombia and Costa Rica from moist lower montane forests, at altitudes between 1200 and 1546 m (Rivas-Plata *et al.* 2006; Rincón-Espitia *et al.* 2011).

**Coenogonium moniliforme* Tuck.

Description: Rivas-Plata *et al.* (286: 2006), Mateus *et al.* (429: 2011); *Image:* Mateus *et al.* (428: 2011).

Loja: Loc. 1, this is a very rare species found only in one well-preserved evergreen montane forest with an irregular and dense canopy. Other lichens of the same community were *Coenogonium epiphyllum* Vain., *C. leprieurii* and *Heterodermia isidiophora* (Nyl.) D.D. Awasthi, A. Benitez 63.

It was previously known from tropical and subtropical zones in Colombia and Cuba, above 100 m altitude (Rivas-Plata *et al.* 2006; Mateus *et al.* 2011).

**Coenogonium nepalense* (G. Thor & Vezda) Lücking, Aptroot & Sipman

Description: Rivas-Plata *et al.* (307: 2006); *Image:* Seavey & Seavey (www.seaveyfieldguides.com)

Loja: Loc. 1, 4, 5 and 6. It has been found growing on several trees in montane forests and managed forests, at altitudes between 2200 and 2800 m, A. Benitez 64, 65, 66 and 67.

It was previously known from montane forests of Argentina, Bolivia, Brazil and Costa Rica (Rivas-Plata *et al.* 2006; Cáceres 2007; Ferraro & Michlig 2013; Flakus *et al.* 2013).

***Coenogonium roumeguerianum* (Müll. Arg.) Kalb

Description: Rivas-Plata *et al.* (304: 2006).

Loja: Loc. 2, this rare species was found in one well-preserved primary forest stand, at 2600 m altitude, other lichens of the same community were *Coenogonium leprieurii* (Mont.) Nyl., *Parmeliella andina* P.M. Jørg. & Sipman and *Sticta weigelii* (Ach.) Vain, A. Benitez 70.

It was previously known from the Neotropics, easter Paleotropics (Rivas-Plata *et al.* 2006) and North America (Seavey *et al.* 2014).

**Cresponea melanocheloides* (Vain.) Egea & Torrente

Description: Egea & Torrente (321: 1993); *Image:* Rincón-Espitia *et al.* (338: 2011), Cáceres (64: 2007).

Loja: Loc. 1 and 2, this species has been collected in two well-preserved primary evergreen forests, in unmanaged stands, with a dense canopy layer. Associated lichens are *Cladonia subradiata* (Vainio) Sandst., *Coccocarpia pellita* (Ach.) Müll. Arg., and *S. tomentosa*, A. Benitez 73 and 74.

It has been reported in the Neotropics (Brazil, Caribbean, Colombia, French Guiana) growing in lowland forests between 100 and 650 m altitude (Egea & Torrente 1993; Cáceres 2007; Rincón-Espitia *et al.* 2011).

**Fibrillithecis halei* (Tuck. & Mont.) Mangold

Description: Mangold (90:2008); *Image:* Rivas-Plata *et al.* (145: 2010).

El Oro: Loc. 7, this is a rare corticolous species found on smooth bark of *Eriotheca ruizii* and *Cochlospermum vitifolium* deciduous trees, at 40-70 m altitude. Other lichens of the same community were *Lecanora helva* Stizenb., *Leucodecton occultum* (Eschw.) A. Frisch. and *Syncesia leprobola* Nyl. ex Tehler., A. Benitez 488.

Fibrillithecis halei grows on tree bark in tropical forests in altitudes ranging from sea level to 1350 m. This pantropical species has been reported from Hawaii, United States, Venezuela, Australia and Asia tropical (Mangold 2008).

**Fissurina triticea* (Nyl.) Staiger

Description: Makhija & Adawadkar (182: 2007)

Loja: Loc. 3, this species was found in a secondary forest regrown after selective logging events on primary montane forest, A. Benitez 87.

The species was previously known from the Neotropics, occurring in upper montane and cloud forests (Wirth & Hale 1978; Hafellner 1995; Staiger 2002; Sipman 2006; Sipman *et al.* 2008; Gatica *et al.* 2011; Schiefelbein *et al.* 2014).

***Graphis bettinae* Lücking, Umaña, Chaves & Sipman

Description: Lücking *et al.* (60: 2008; 417: 2009b). *Image:* Lücking *et al.* (45: 2008).

Loja: Loc. 5 and 6, it is a very common species, growing on trees of open and managed forests of *A. acuminata*, A. Benitez 95 and 96.

It usually appears together with *G. pinicola*, *Hypotrachyna revoluta* (Flörke) Hale and *Lecanora caesiorubella* Ach. It was previously reported from Costa Rica, in upper montane forests, above 2700 m altitude (Lücking *et al.* 2008).

**Graphis cinerea* (Zahlbr.) M. Nakan.

Description: Lücking *et al.* (66: 2008; 432: 2009b); *Image:* Lücking *et al.* (45: 2008)

Loja: Loc. 6, this species has been found only in an open and managed forest of *A. acuminata*, together with *Bulbothrix coronata* (Fée) Hale, *H. revoluta* and *Parmotrema rampoddense* (Nyl.) Hale, A. Benitez 97.

It was previously known from Costa Rica, at altitudes between 700 and 1800 m (Lücking *et al.* 2008), and in the Andean mountains of Colombia (Aguirre & Rangel 2007).

***Graphis elongatoradians* Fink

Description: Lücking *et al.* (426: 2009b).

Loja: Loc. 6, it is a very rare species growing on bark of *A. acuminata*, in an open and managed forest stand. Other lichens of the same community were *Heterodermia galactophylla* (Tuck.) W.L. Culb., *Hypotrachyna rockii* (Zahlbr.) Hale and *S. weigelii*, A. Benitez 100.

It was only previously known from the type locality in Puerto Rico (Wirth & Hale 1978; Lücking *et al.* 2009b).

***Graphis leptogramma* Nyl.

Description: Lücking *et al.* (392: 2009b); *Image:* Aptroot (website: www.tropicallichens.net)

Loja: Loc. 5, we have only found a small population in one managed forest, growing on bark of *A. acuminata,* together with *H. japonica*, *Hypotrachyna costaricensis* (Nyl.) Hale and *L. helva,* A. Benitez 102.

It was previously known from the Paleotropics (Lücking *et al.* 2009b), and thus, it is recorded for the first time from the Neotropics (South America).

**Graphis myrtacea* (Müll. Arg.) Lücking

Description: Lücking *et al.* (93: 2008); *Image:* Lücking *et al.* (52: 2008; 368: 2009b).

Loja: Loc. 5 and 6, it is a rare species growing on *A. acuminata*, in two open and managed forests, at altitudes between 2200 and 2300 m, A. Benitez 103 and 104.

It was previously reported from Brazil and Costa Rica, in secondary montane lowland forests and pasturelands, at 700-3000 m altitude (Lücking *et al.* 2008; Lücking *et al.* 2009b).

**Graphis pinicola* Zahlbr.

Description: Kukwa *et al.* (241:2013).

Loja: Loc. 5 and 6, it is a common species growing on *A. acuminata* in open and managed forests. A. Benitez 105 and 106.

The species has a typical Pantropical distribution (Lücking *et al.* 2009b; Lendemer 2010; Perlmutter *et al.* 2012). In the Neotropics it has been reported from Bolivia, growing in montane forests and open sites above 1500 m (Kukwa *et al.* 2013).

**Graphis ruiziana* (Fée) A. Massal.

Description: Lücking *et al.* (105: 2008); *Image:* Lücking *et al.* (51: 2008; 367: 2009b).

Loja: Loc. 3, 4, 5 and 6, it is a very common species growing on different trees in secondary forests, at altitudes between 200 and 2700 m, A. Benitez 107, 108, 109 and 110.

It was previously known from Bolivia, Brazil and Costa Rica, growing in cloud and low montane forests and pasturelands, at altitudes between 700 and 3100 m (Staiger 2002; Lücking *et al.* 2008; 2009b; Kukwa *et al.* 2013).

**Graphis scaphella* (Fée) A. Massal.

Description: Lücking *et al.* (415: 2009b); *Image:* Aptroot (website: www.tropicallichens.net).

Loja: Loc. 1, this extremely rare lichen has a unique collection in a well-preserved primary montane forest, A. Benitez 111.

It was found growing on bark of an old tree in a dense and montane evergreen primary forest together with *Coccocarpia palmicola* (Spreng.) Arv. & D.J. Galloway and *P. arnoldii* (Du Rietz) Hale. This species has a Neotropical distribution (Lücking *et al.* 2009b).

**Graphis sitiana* Vain.

Description: Lücking *et al.* (109: 2008); *Image:* Lücking *et al.* (41: 2008).

Loja: Loc. 5, it has been found only in one locality of open and managed forests of *A. acuminata* together with *Glyphis cicatricosa* Ach., *L. caesiorubella* and *Phaeographis dendritica* (Ach.) Müll. Arg., A. Benitez 112.

It was previously known from Bolivia, Brazil, Costa Rica, Panamá and Perú, in montane rainforests, disturbed forests and pasturelands, at altitudes between 500 and 1000 m (Lücking *et al.* 2008, 2009b; van den Boom & Sipman 2013; Rivas Plata & Lücking 2013; Schiefelbein *et al*. 2014).

**Graphis subcontorta* (Müll. Arg.) Lücking & Chaves

Description: Lücking *et al.* (110: 2008); *Image:* Lücking *et al.* (48: 2008).

Loja: Loc. 4, it is a very rare species growing on trees in open and managed secondary forests. Other lichens of the same community were *Brigantiaea leucoxantha* (Spreng.) R. Sant. & Hafellner, *G. ruiziana*, *Normandina pulchella* (Borrer) Nyl. and *Porina nucula* Ach., A. Benitez 114.

It was previously known from Costa Rica and Paraguay, found in low montane and disturbed forests, at altitudes between 850 and 1000 m (Lücking *et al.* 2008; 2009b).

**Haematomma africanum* (J. Steiner) C.W. Dodge

Description: Brodo *et al.* (383: 2008); *Image:* Messuti & Rosa (299:2009)

Loja: Loc. 6, this species was found in open and managed forests of *A. acuminata* together with *B. coronata*, *Chrysothrix chrysophtalma* (P. James) P. James & J. R. Laundon and *L. helva*, A. Benitez 118.

It was known from Colombia, Costa Rica, Cuba, Guatemala, Guayana, Hawai, Jamaica, Puerto Rico and Venezuela, between 500 and 2200 m altitude (Staiger & Kalb 1995; Marcano *et al.* 1996; Aguirre & Rangel 2007; Brodo *et al.* 2008).

**Haematomma flexuosum* Hillm.

Description: Brodo *et al.* (396: 2008), Messuti & Rosa (299: 2009); *Image:* Messuti & Rosa (302: 2009).

Loja: Loc. 3, this species was found in one unmanaged secondary forest stand, A. Benitez 119.

It was previously known from Argentina, Brazil, Colombia, Costa Rica, Cuba, Jamaica, México, Panamá, Paraguay, Uruguay and Venezuela, growing in xerophytic forests, on deciduous trees of *Fraxinus*, *Myrica*, *Prunus* and *Quercus* (Staiger & Kalb 1995; Aguirre & Rangel 2007; Brodo *et al.* 2008; Messuti & de la Rosa 2009).

**Herpothallon confusum* G. Thor

Description: Aptroot *et al.* (36: 2009); *Image:* Aptroot *et al.* (47: 2009)

Loja: Loc. 2, this rare epiphytic species was found in one well-preserved primary forest stand, with an irregular and dense canopy layer, growing together with *C. leprieurii* and *P. santensis*, A. Benitez 121.

It was previously known from Venezuela, growing in moist lowland forests at 110 m altitude (Aptroot *et al.* 2009).

**Hypoflavia velloziae* (Kalb) Marbach

Description: Sipman (91:2003)

Loja: Loc. 5 and 6, it was found in two open and managed forests of *A. acuminata*, together with *Coniocarpon cinnabarinum* DC., *C. stellata* Tuck. and *G. pinicola*, A. Benitez 144 and 145.

In South America it was previously reported from few localities in Brazil (Sipman 2003).

**Lecanora helva* Stizenb.

Description: Nash *et al.* (226: 2004), Cáceres (97: 2007); *Image:* Nash *et al.* (227: 2004), Cáceres (98: 2007).

Loja: Loc. 4, 5 and 6, this species has been found in managed secondary forests and in managed and monospecific forests of *A. acuminata*, A. Benitez 159, 160 and 161.

It was previously known from North America to Brazil (Nash *et al.* 2004; Cáceres 2007), in the latter growing in secondary forests, at altitudes between 800 and 900 m (Cáceres 2007).

**Lecanora neonashii* Lumbsch

Description: Nash *et al.* (245: 2004); *Image:* Nash *et al.* (246: 2004)

Loja: Loc. 6, this species was found growing in open and managed forests of *A. acuminata*, A. Benitez 162.

It was previously known from several localities in North America, Argentina, Brazil and Cuba (Calvelo & Liberatore 2002; Nash *et al.* 2004; Aragón & Rosabal 2010).

**Leiorreuma exaltatum* (Mont. & Bosch) Staiger

Description: Joshi *et al.* (56: 2013), Dal-Forno (103: 2009); *Image:* Joshi *et al*. (57: 2013), Dal-Forno (155: 2009).

Loja: Loc. 1, we have found a small population in one well-preserved and dense evergreen forest stand, at 2750 m altitude. It was growing together with *Glyphis scyphulifera* (Ach.) Staiger, *P. hispaniolae* and *Parmeliella miradorensis* Vain, A. Benitez 166.

It was previously reported from few locatities in Brazil, Costa Rica, Dominican Republic and Mexico (Wirth & Hale 1978; Breuss & Neuwirth 2007; Dal-Forno 2009).

**Malcolmiella fuscella* (Müll. Arg.) M. Cáceres & Lücking

Description: Cáceres (105: 2007); *Image:* Cáceres (108: 2007)

Loja: Loc. 1, 2 and 3, this species has been found in dense evergreen primary forests and secondary unmanaged forests, at altitudes between 2600 and 2800 m, A. Benitez 192, 193 and 194.

In South America it was previously known from few localities in Brazil, occurring in tropical rain forests, between 500 and 900 m altitude (Cáceres 2007).

**Malcolmiella gyalectoides* (Vain.) Cáceres & Lücking

Description: Cáceres (105: 2007); *Image:* Cáceres (108: 2007).

Loja: Loc. 6, this species has been found in one open and managed forest stand of *A. acuminata* growing together with *C. stellata*, *Graphis leptoclada* Müll. Arg. and *S. weigelii*, A. Benitez 195. It was known from Brazil, where it grows in closed rain forests and managed and open fragmented forests, at altitudes between 500 and 900 m (Cáceres 2007).

**Maronina multifera* (Nyl.) Hafellner & R. W. Rogers

Description: Cáceres (109: 2007); *Image:* Cáceres (112: 2007).

Loja: Loc. 3, 5 and 6, this species has been found in three secondary forest stands at altitudes between 2300 and 2750 m, A. Benitez 199, 200 and 201.

It was previously known from Brazil, Colombia and México, growing in open deciduous rain forests (Sipman & Wolf 1998; Cáceres 2007; Aguirre & Rangel 2007).

**Mazosia carnea* (Eckfeldt) Aptroot & M. Cáceres

Description: Aptroot *et al.* (564: 2014); *Image:* Aptroot *et al.* (565: 2014).

El Oro: Loc. 7, this is a very rare epiphytic species found on smooth bark of trees in deciduous forests, at 40-70 m altitude, together with *Coniocarpon cinnabarinum* DC. and *Pseudopyrenula subnudata* Müll.Arg., A. Benitez 371.

It is previously known from Brazil, Costa Rica, Guayana, Puerto Rico and USA at altitudes between 0 and 800 m (Aptroot *et al.* 2014)

***Ochrolechia pseudopallescens* Brodo

Description: Nash *et al.* (385: 2004); *Image:* Brodo (756:1991)

Loja: Loc. 3, 4, 5 and 6. This is a common species, found in secondary forests and managed forest stand of *A. acuminata*, A. Benitez 217, 218, 219 and 220.

It was previously known from Canada, Dominican Republic, Haiti and Mexico (Nash *et al.* 2004).

***Pertusaria hypothamnolica* Dibben

Description: Hodkinson *et al.* (77: 2009).

Loja: Loc. 1, 2, 3 and 4, this species was found in primary forests with a dense canopy layer and in secondary forests, at 2300-2800 m altitude, A. Benitez 244, 245, 246 and 247.

It was previously known from eastern North America (Hodkinson *et al.* 2009).

**Pertusaria multipunctoides* Dibben

Description: Hodkinson *et al.* (78: 2009)

Loja: Loc. 1 and 3, this species is frequent, growing in primary dense evergreen forests and secondary forests, A. Benitez 248 and 249.

It was previously known from eastern Noth America (Hodkinson *et al.* 2009).

Pertusaria ventosa Malme

Description: Cáceres (121: 2007); *Image:* Cáceres (122: 2007).

Loja: Loc.1, 2, 3, 4, 5 and 6, this is a common species growing from dense primary forests to open secondary vegetation, A. Benitez 250, 251, 252, 253, 254 and 255.

It was previously known from Brazil, growing in managed forests at altitudes between 500 and 600 m (Cáceres 2007).

Phaeographis brevinigra Sipman

Description: Neuwirth (149: 2008); *Image:* Neuwirth (21: 2008)

Loja: Loc. 5 and 6, it was found in two managed forests of *A. acuminata,* at 2200-2400 m altitude, together with *P. ventosa*, *T. flavicans* and *Tephromela atra* (Hudson) Hafellner, A. Benitez 262 and 263.

It was previously known from Venezuela, found in lowland primary forests at 100-150 m altitude (Neuwirth 2008).

**Phyllopsora chlorophaea* (Müll. Arg.) Zahlbr.

Description: Brako (34: 1991), Timdal (345: 2008; 329: 2011a; website: 2011b), Mishra *et al.* (34, 35: 2011); *Image:* Brako (6: 1991), Timdal (website: 2011b).

Loja: Loc. 1 and 2, it has been found in two well-preserved primary forest stands with an irregular and dense canopy, A. Benitez 271 and 272.

It is a common species known in Central and South America in Brazil, Costa Rica, Cuba, Dominican Republic, Haiti, Jamaica, Perú and Venezuela, growing in montane and moist lowland montane forests between 140 and 2300 m (Brako 1991; Marcano *et al.* 1996; Timdal & Krog 2001; Timdal 2008).

**Phyllopsora fendleri* (Tuck. & Mont.) Müll. Arg.

Description: Brako (44: 1991); *Image:* Brako (45: 1991), Timdal (website: 2011b).

Loja: Loc. 1, this is a very rare species collected only in one dense primary evergreen forest stand, at 2780 m altitude, together with *Dichosporidium boschianum* (Mont.) G. Thor, *P. glaucescens* and *P. tenuisepta*, A. Benitez 273.

It was previously known from Brazil, Costa Rica and Venezuela, in lowland and montane forests and páramos, at altitudes between 1200 and 3500 m (Brako 1991; Marcano *et al.* 1996).

**Phyllopsora glaucescens* Timdal

Description: Timdal (349: 2008); *Image:* Timdal (342: 2008; website: 2011b).

Loja: Loc. 1, this rare species was only found in a dense evergreen primary forest stand, with and irregular and dense canopy layer. Other lichens of the same community were *C. pellita*, *Leptogium marginellum* (Sw.) Gray and *Pannaria conoplea* (Ach.) Bory, A. Benitez 275.

It was previously known from Peru, growing in lowland primary rainforest and tree ferns, at 120-150 m altitude (Timdal 2008).

***Phyllopsora hispaniolae* Timdal

Description: Timdal (333: 2011a); *Image:* Timdal (website: 2011b)

Loja: Loc. 1, this species was found exclusively on trees of well-preserved primary evergreen montane forests together with *L. cyanescens*, *Phyllopsora parvifoliella* (Nyl.) Mull. Arg. and *S. tomentosa*, A. Benitez 276.

It was previously known from few localities in the Dominican Republic occurring in rain forests, at 1740-1990 m altitude (Timdal 2011a).

**Phyllopsora isidiotyla* (Vain.) Riddle

Description: Brako (50: 1991); Elix (6: 2007); Mishra *et al.* (39: 2011); *Image:* Brako (44: 1991), Mishra *et al.* (41:2011).

Loja: Loc. 1, 2 and 3, this species was found in unmanaged and dense primary and secondary montane forests, at 2600-2850 m altitude, A. Benitez 277, 278 and 279.

In South America, it was previously known from Bolivia, Brazil, Costa Rica, and Venezuela, growing in montane forests at altitudes between 2000 and 3000 m (Brako 1991; Marcano *et al.* 1996; Umaña-Tenorio *et al.* 2002; Flackus *et al.* 2013). It is also known from North America (Brako 1991).

**Phyllopsora santensis* (Tuck.) Swinscow & Krog

Description: Timdal (357: 2008; 345: 2011a); *Image:* Timdal (website: 2011b)

Loja: Loc. 2, 3 and 4, this species has been found in primary evergreen dense forests, with an irregular and dense canopy layer, and in secondary forests, regrown after selective logging events on primary montane forest. A. Benitez 282, 283 and 284.

It was previously known from North America and Paraguay (Brako 1991; Elix 2006), and recently found in Cuba and Peru, between100 and 500 m altitude (Timdal 2008; 2011a).

**Porina internigrans* (Nyl.) Müll. Arg.

Description: Schumm & Aptroot (714: 2012); *Image:* Schumm & Aptroot (714-716: 2012).

Loja: Loc. 1 and 2, it has been found in two well-preserved and dense forest stands, at 2550-2850 m altitude, A. Benitez 288 and 289.

It usually grows together with *Herpothallon rubrocinctum* (Ehrenb.) Aptroot & Lücking, *Leptogium cochleatum* (Dicks.) P.M. Jørg. & P. James and *P. conoplea*. It was previously known from Brazil, growing in Atlantic forests (Cáceres *et al.* 2007).

**Pyrenula andina* Aptroot

Description: Aptroot *et al.* (91: 2008); *Image:* Aptroot *et al.* (90: 2008).

Loja: Loc. 3, this species has only been found in one locality in an unmanaged and dense secondary forest, A. Benitez 298.

It was previously known from Costa Rica and Cuba, occurring in primary and secondary forests, at altitudes between 1600 and 3100 m (Aptroot *et al.* 2008; Rosabal *et al.* 2012a).

**Pyrenula macrocarpa* A. Massal.

Description: Aptroot *et al.* (108: 2008), Rincón-Espitia *et al.* (341: 2011); *Image:* Aptroot *et al.* (107: 2008).

Loja: Loc. 1, 2, 3 and 4, this is a very common species growing on different trees and found at several localities of primary montane and secondary forests, at 2240-2830 m altitude, A. Benitez 300, 301, 302, 303.

It was previously known from Colombia, Costa Rica and Cuba, between 1500 and 2180 m altitude, in primary montane *Quercus* forests and moist lowland forests (Aptroot *et al.* 2008; Rincón-Espitia *et al.* 2011; Rosabal *et al.* 2012a).

**Pyrenula mastophoroides* (Nyl.) Zahlbr.

Description: Aptroot *et al.* (113: 2008); *Image:* Aptroot *et al.* (115:2008)

Loja: Loc. 6, it is a very rare species growing on bark of *A. acuminata* in an open and managed forest stand, found together with *G. ruiziana*, *Lobariella crenulata* (Hook.) Yoshim. and *Parmotrema exquisitum* (Kurok.) DePriest & B.W. Hale., A. Benitez 304.

It was previously known from Bolivia, Colombia and Costa Rica growing in primary and disturbed forests, at altitudes between 1140 and 2800 m (Aptroot *et al.* 2008; Sipman *et al.* 2008; Flackus *et al.* 2013).

**Pyrenula microcarpa* Mull. Arg.

Description: Aptroot et *al.* (113:2008); *Image:* Seavey & Seavey (www.seaveyfieldguides.com)

Loja: Loc. 1, this rare species has only been found in one locality of a well-preserved dense evergreen primary forest, growing together with *C. moniliforme*, *P. hispaniolae* and *S. tomentosa*, A. Benitez 305.

It was previously known from Costa Rica growing in coastal areas, and in montane and moist lowland forests (Breuss 2006; Aptroot *et al.* 2008).

***Pyrenula psoriformis* Zahlbr.

Description: Aptroot *et al.* (34: 2012); *Image:* JSTOR (plants.jstor.org).

El Oro: Loc. 7 and 8, this is a very rare epiphytic species found exclusively on rugose bark of *Jacquinia sprucei* Mez of deciduous dry forest at 40-70 m altitude, A. Benitez 464 and 465.

This neotropical lichen is known only from Puerto Rico in Central America (Aptroot *et al.* 2012).

**Pyrenula tenuisepta* R. C. Harris

Description: Aptroot *et al.* (128:2008), Rincón-Espitia *et al.* (341:2011); *Image:* Aptroot *et al.* (129:2008)

Loja: Loc.1, 2, 3 and 4, it has been found in unmanaged primary and secondary forests, at 2300-2840 m altitude, A. Benitez 307, 308, 309 and 310.

It was previously known from Costa Rica, Colombia and Cuba growing in primary and lowland managed secondary forests and in coastal zones, between 100 and 239 m altitude (Aptroot et al. 2008; Rincón-Espitia *et al.* 2011; Rosabal *et al.* 2012b).

**Squamacidia janeirensis* (Müll. Arg.) Brako

Description: Cáceres (148:2007); *Image:* Cáceres (150:2007)

Loja: Loc. 1 and 2, this species has only been found in two well-preserved and dense primary evergreen montane forests, at altitudes between 2550 and 2780 m, growing together with *Pannaria mosenii* C.W. Dodge, *P. parvifoliella* and *Sticta humboldtii* Hook., A. Benitez 327 and 328.

It was previously known from Brazil, growing in Atlantic forests at 50 m altitude (Cáceres 2007).

**Sticta lobarioides* Moncada & Coca *Description:* Moncada *et al.* (170, 196: 2013); *Image:* Moncada *et al.* (171-172: 2013).

Loja: Loc. 1, 2, 3 and 4, this species has been found in several localities of primary evergreen montane forests and dense secondary forests, at altitudes between 2400 and 2850 m, A. Benitez 335, 336, 337 and 338.

It was previously known from Colombia, growing in montane forest and páramo, at altitudes between 1450 and 3500 m (Moncada *et al.* 2013).

**Sticta neolinita* Gyeln*.*

Description: Moncada (133: 2012), Moncada *et al.* (195: 2013); *Image:* Moncada (263: 2012).

Loja: Loc. 1, 2, 3 and 4, this species have been found in sever in of dense montane evergreen primary forests and secondary forests, A. Benitez 339, 340, 341, and 342.

It was previously known from Colombia, growing in Andean to subandean forests and páramos, at altitudes between 2000 and 3750 m (Moncada 2012).

**Sticta neopulmonarioides* Moncada & Coca

Description: Moncada *et al.* (178, 195: 2013); *Image:* Moncada *et al.* (179-180: 2013).

Loja: Loc. 1 and 2, this species has only been found in two well-preserved and dense evergreen primary forests. It usually appears together with *Lobaria tenuis* Vain., *Parmeliella delicata* P.M. Jørg. & Arv. and *Sticta andensis* (Nyl.) Trevis., A. Benitez 343 and 344.

It was previously known from Colombia, from montane forests at altitudes between 2290 and 3500 m (Moncada *et al.* 2013).

**Stigmatochroma gerontoides* (Stirt.) Marbach

Description: Makhija & Adawadkar (182: 2007), *Image*: Aptroot (www.tropicallichens.net)

El Oro: Loc. 7, at present this species was found growing on bark of *Cochlospermum vitifolium* tree in tropical dry deciduous forests. It usually appears together with *Schismatomma spierii* Aptroot & Sparrius and *Syncesia effusa* (Fée) Tehle. A. Benitez 476.

The species was previously known from Brazil; Thailand and Venezuela, occurring in upper montane and cloud forests (Marbach 2000; Neuwirth 2008; Menezes *et al.* 2011; van den Boom et *al.* 2014).

**Syncesia effusa* (Fée) Tehler

Description: Tehler (24:1997); *Image:* Ferraro & Michlig (743:2011).

El Oro: Loc. 7 and 8, this species has been found in two forest stands of deciduous forests, at 40-70 m altitude, together with *Cresponea flava* (Vain.) Egea & Torrente, *Graphis anfractuosa* (Eschw.) Eschw. and *Leucodecton occultum* (Eschw.) Frisch., A. Benitez 479 and 480.

It was previously known from Argentina, Brazil, Colombia, Jamaica, and North America (Tehler 1997; Cáceres 2007; Ferraro & Michlig 2011).

**Trichothelium horridulum* (Mull. Arg.) R. Sant.

Description: Lücking & Cáceres (553: 2004); *Image:* Lücking & Cáceres (552: 2004).

Loja: Loc. 1 and 2, this species was found in two well-preserved primary evergreen montane forests, with an irregular and dense canopy layer. Other co-occurring lichens in the community were *L. phyllocarpum*, *P. aurata* and *S. tomentosa*, A. Benitez 356 and 357.

It was previously known from Bolivia, Brazil, Costa Rica, Guyana, Paraguay, and Uruguay, growing in montane and lowland forests, and grassland, at altitudes between 10 and 2500 m (Lücking & Cáceres 2004; Flackus *et al*. 2013).

Acknowledgements

Financial support for this study was granted by the “Universidad Técnica Particular de Loja” (PROY_CCNN_941), the “Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación” of Ecuador and the “Ministerio de Ciencia e Innovación of Spain” (project EPICON, CGL2010-22049). We thank G. Cevallos for his help with fieldwork and Ministerio del Ambiente del Ecuador by providing access to the study areas.

References

Aguirre CJ, Rangel JO. 2007. Amenazas a la conservación de las especies de musgos y líquenes en Colombia. Una aproximación inicial. Caldasia 29 (2): 235–262.

Aptroot A. 2002. New and interesting lichens and lichenicolous fungi in Brazil. Fungal Diversity 9: 15–45.

Aptroot A. 2012. A world key to the species of Anthracothecium and Pyrenula. The Lichenologist 44(1): 5–53.

Aptroot A, Lücking R, Sipman HJM, Umaña L, Chaves JL. 2008. Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. Bibliotheca Lichenologica 94: 1–191.

Aptroot A, Menezes AA, Xavier-Leite AB, dos Santos VM, Alves MME, da Silva Caceres, ME. 2014. Revision of the corticolous Mazosia species, with a key to Mazosia species with 3-septate ascospores. The Lichenologist 46 (4): 563–572.

Aptroot A, Thor G, Lücking R, Elix JA, Chaves JJ. 2009. The lichen genus Herpothallon reinstated. Bibliotheca Lichenologica 99: 19–66.

Aragón G, Rosabal D. 2010. Líquenes epífitos en el matorral costero de la Reserva Ecológica Siboney-Juticí (Cuba). Botanica Complutensis 34: 21–25.

Benitez AR, Prieto M, González Y, Aragón G. 2012. Effects of tropical montane forest disturbance on epiphytic macrolichens. Science of the Total Environment 441: 169–175.

Brako L. 1991. Phyllopsora (Bacidiaceae). Flora Neotropica Monograph 55: 1–66.

Breuss O, Neuwirth G. 2007. Flechtenfunde im Bosque Esquinas, Costa Rica. Linzer Biologische Beiträge 39(1): 557–569.

Breuss O. 2006. Flechten aus Costa Rica IV. Bosque Esquinas (2). Linzer Biologische Beiträge 38(2): 1061–1069.

Brodo IM. 1991. Studies in the lichen genus Ochrolechia. 2. Corticolous species of North America. Canadian Journal of Botany 69: 733–772.

Brodo IM, Sharnoff SD, Sharnoff S. 2001. Lichens of North America. New Haven and London, Yale University Press.

Brodo IM, Culberson WL, Culberson ChF. 2008. Haematomma (Lecanoraceae) in North and Central America, including the West Indies. The Bryologist 111: 363–423.

Bungartz F, Ziemmeck F, Yánez-Ayabaca A, Nugra F, Aptroot A. 2013. CDF Checklist of Galapagos Lichenized Fungi - FCD Lista de especies de Hongos liquenizados Galápagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jiménez-Uzcátegui G, Ruiz D., Guézou, A, Ziemmeck, F. (eds.). Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin. Charles Darwin Foundation/ Fundación Charles Darwin, Puerto Ayora, Galapagos.

Rodriguez-Flakus P, Flakus A, Kukwa M, et al. 2014. Preliminary catalogue of lichens and lichenicolous fungi from Bolivia, Version 1.4. http://bio.botany.pl/lichens-bolivia/en,strona,home,1.html. 3 May. 2016.

Cáceres MES. 2007. Corticolous crustose and microfoliose lichens of northeastern Brazil. Libri Botanici 22: 1–168.

Calvelo S, Liberatore S. 2002. Catálogo de los Líquenes de la Argentina. Kurtziana 29 (2): 7–170.

Cevallos G. 2012. Checklist de líquenes y hongos liquenícolas de Ecuador Continental. Master Thesis, Universidad Rey Juan Carlos, España.

Dal-Forno M. 2009. A família Graphidaceae (Ascomycota Liquenizados) em Restinga em Pontal Do Sul, Pontal Do Paraná, Paraná. Master Thesis, Universidade Federal de Paraná, Brazil.

Egea JM, Torrente P. 1993. Cresponea, a new genus of lichenized fungi in the order Arthoniales (Ascomycotina). Mycotaxon 48: 301–31.

Elix J. 2007. Additional lichen records from Australia 62. Australasian Lichenology 60: 6–12.

Ferraro LI, Michlig A. 2011. Nuevos registros de microlíquenes para el norte de Argentina. Revista mexicana de biodiversidad 82(3): 739–746.

Feuerer T, Hawksworth D. 2007. Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan’s Floristic regions. Biodiversity and Conservation 16: 85–98.

Flakus A, Sipman HJ, Bach K, et al. 2013. Contribution to the knowledge of the lichen biota of Bolivia. 5. Polish Botanical Journal 58: 697–733.

Galloway DJ, Quilhot W. 1998. Checklist of Chilean lichen- forming and lichenicolous fungi. Gayana Botanica 55: 111–185.

Gatica A, Pereira Í, Vallejos O. 2011. Líquenes epífitos: una herramienta para estudiar la continuidad ecológica en Isla Mocha, Chile. Gayana Botanica 68(2): 226–235.

González-Román RD, López-Victoria M, Silverstone-Sopkin PA. 2014. Flora terrestre de la isla Malpelo (Colombia), Pacífico Oriental Tropical. Revista de Biología Tropical 62(1): 327–336.

Hafellner J. 1995. A new checklist of lichens and lichenicolous fungi of insular Laurimacaronesia including a lichenological bibliography for the area. Fritschiana 5: 1–132.

Hodkinson BP, Harris RC, Case MA. 2009. A checklist of Virginia lichens. Evansia 26(2): 64–88.

Joshi S, Jayalal U, Lökös L, et al. 2013. Leiorreuma exaltatum and Trapelia coarctata, new to Korean lichen flora. Mycobiology 41(1): 56–58.

Kukwa M, Schiefelbein U, Flakus A. 2013. A contribution to the lichen family Graphidaceae (Ostropales, Ascomycota) of Bolivia. Herzogia 26: 231–252.

Lendemer JC. 2010. Notes on the genus Graphis (Graphidaceae: lichenized Ascomycetes) in the coastal plain of southeastern North America. The Journal of the Torrey Botanical Society 137: 312–317.

Lücking R, Cáceres M. 2004. Corticolous species of Trichothelium (Ascomycota: Porinaceae). Mycological Research 108(5): 571–575.

Lücking R. 1999. Foliicolous lichens and their lichenicolous fungi from Ecuador, with a comparison of lowland and montane rain forest. Willdenowia 29: 299–335.

Lücking R, Archer AW, Aptroot A. 2009b. A world-wide key to the genus Graphis (Ostropales: Graphidaceae). The Lichenologist 41: 363–452.

Lücking R, Chaves JL, Sipman HJM, Umaña L, Aptroot A. 2008. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: The genus Graphis, with notes on the genus Hemithecium (Ascomycota : Ostropales : Graphidaceae). Fieldiana 46: 1–130.

Lücking R, Rivas E, Chaves JL, Umaña L, Sipman HJM. 2009a. How many tropical lichens are there… really?. Bibliotheca Lichenologica 100: 399–418.

Makhija U, Adawarkar B. 2007. Trans-septate species of Acanthothecis and Fissurina from India. The Lichenologist 39(2): 165–185.

Mangold A. 2008. Taxonomic studies on members of Thelotrematoid Ostropales (Lichenized Ascomycota) in Australia. PhD Thesis, Universität Duisburg-Essen, Germany.

Marbach B. 2000. Corticole und lignicole Arten der Flechtengattung Buellia sensu lato in den Subtropen und Tropen. Bibliotheca Lichenologica 74: 1–384.

Marcano V, Morales-Méndez A, Sipman HJM, Calderon L. 1996. A first checklist of the lichen-forming fungi of the Venezuelan Andes. Tropical Bryology 12: 193–235.

Mateus N, Lücking R, Aguirre-C J. 2011. Contribuciones a la biota liquénica foliícola de Colombia. I. Nuevos registros del género Coenogonium (Ascomycota-Ostropales: Coenogoniaceae). Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 35 (137): 425–430.

Menezes AAD, Leite ABX, Otsuka AY, Jesus LSD, Cáceres MEDS. 2011. New records of crustose and microfoliose corticicolous lichens in Caatinga vegetation of the semi-arid region in Alagoas. Acta Botanica Brasilica 25 (4): 885–889.

Messuti MI, de la Rosa IN. 2009. Notas sobre el género Haematomma (Ascomycota, Lecanoraceae) en Argentina. Darwiniana 47(2): 297–308.

Mishra KG, Upreti DK, Nayaka S, Haridas B. 2011. New taxa and new reports of Phyllopsora (lichenized Ascomycotina) from India. Mycotaxon 115: 29–44.

Moncada B. 2012. El género Sticta en Colombia: Taxonomía, Ecogeografía e Importancia. PhD Thesis, Universidad Nacional de Colombia, Colombia.

Moncada B, Coca LF, Lücking R. 2013. Neotropical members of Sticta (lichenized Ascomycota: Lobariaceae) forming photosymbiodemes, with the description of seven new species. The Bryologist 116(2): 169–200.

Nash IIITH, Ryan BD, Gries C, Bungartz F. 2002. Lichen Flora of the Greater Sonoran Desert Region, vol. I. Lichens Unlimited, Tempe, Arizona.

Nash IIITH, Ryan BD, Diederich P, Gries C, Bungartz F. 2004. Lichen Flora of the Greater Sonoran Desert Region. Vol. II. Lichen Unlimited: Tempe, Arizona.

Nash IIITH, Gries C, Bungartz F. 2007. Lichen Flora of the Greater Sonoran Desert Region. Vol. III. Lichens Unlimited, Tempe, Arizona.

Nelsen MP, Lücking R, Grube M, et al. 2009. Unravelling the phylogenetic relationships of lichenised fungi in Dothideomyceta. Studies in Mycology 64: 135–144.

Neuwirth G. 2008. Further studies on lichens from Venezuela with new and interesting records. Herzogia 21: 147–156.

Nöske NM, Mandl N, Sipman HJM. 2007. Lichens. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S. Ecuador). Ecotropical Monographs 4: 101–117.

Perlmutter GP, Lendemer JC, Guccion JC, et al. 2012. A provisional survey of lichen diversity in south-central South Carolina, U.S.A., from the 19th Tuckerman Lichen Workshop. Opuscula Philolichenum 11: 104–119.

Ramos D. 2014. Lista de especies de líquenes y hongos liquenícolas del Perú. Glalia 6(2): 1–49.

Rincón-Espitia A, Aguirre-C J, Lücking R. 2011. Líquenes corticícolas en el caribe Colombiano. Caldasia 33(2): 331–347.

Rivas-Plata E, Lücking R. 2013. High diversity of Graphidaceae (lichenized Ascomycota: Ostropales) in Amazonian Perú. Fungal Diversity 58: 13–52.

Rivas-Plata E, Lücking R, Aptroot A, et al. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus Coenogonium (Ostropales: Coenogoniaceae), with a world-wide key and checklist and a phenotype-based cladistic analysis. Fungal Diversity 23: 255–321.

Rivas-Plata E, Lücking R, Sipman HJ, Mangold A, Kalb K, Lumbsch HT. 2010. A world-wide key to the thelotremoid Graphidaceae, excluding the Ocellularia-Myriotrema-Stegobolus clade. The Lichenologist 42: 139 – 185.

Rosabal D, Burgaz AR, Reyes OJ. 2012a. Diversidad y distribución vertical de líquenes corticícolas en la pluvisilva montana de la Gran Piedra, Cuba. Botanica Complutensis 36: 19–30.

Rosabal D, Burgaz AR, Altamirano A, Aragón A. 2012b. Differences in diversity of corticolous lichens between interior and edge of the Monte Barranca semi-deciduous forest, Santiago de Cuba. The Bryologist 115: 333–340.

Schiefelbein U, Flakus A, Sipman HJM, Oset M, Kukwa M. 2014. A contribution to the lichen family Graphidaceae (Ostropales, Ascomycota) of Bolivia 2. Polish Botanical Journal 59(1): 85–96.

Schumm F, Aptroot A. 2012. A microscopical Atlas of some tropical Lichens from SE-Asia (Thailand, Cambodia, Philippines, Vietnam. Vol. II, Herstellung und Verlag, Norderstedt.

Seavey F, Seavey J, Hernández J, Lücking R. 2014. Three new Opegrapha species (Roccellaceae, Arthoniales) and several additions to the North American lichen mycota from Everglades National Park. The Bryologist 117: 62–71.

Sipman HJM, Aptroot A. 2001. Where are the missing lichens?. Mycological Research 105: 1433–1439.

Sipman HJM, Wolf JHD. 1998. Provisional checklist for lichens of Chiapas. Acta Botanica Mexicana 45: 1–29.

Sipman HJM. 2006. Diversity and biogeography of lichens in Neotropical montane oak forests. Ecological Studies 185: 69–81.

Sipman HJM. 2011. Diversity of lichenized fungi in the Tropical Andes. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen H. (eds.) Climate Change and Biodiversity in the Tropical Andes. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE). p. 220–223.

Sipman HJM, Hekking W, Aguirre-C J. 2008. Checklist of Lichenized and Lichenicolous Fungi from Colombia. Biblioteca José Jerónimo Triana No. 20. Instituto de

Ciencias Naturales, Facultad de Ciencias, Universidad Nacional de Colombia, Colombia.

Staiger B, Kalb K. 1995. Haematomma-studien: I. Dieflechtengattung Haematomma. Bibliotheca Lichenologica 59: 3–198.

Staiger B. 2002. Die Flechtenfamilie Graphidaceae. Studien in Richtung einer natürlicheren Gliederung. Bibliotheca Lichenologica 85: 1–526.

Tehler A. 1997. Syncesia (Arthoniales, Euascomycetidae). Flora Neotropica 74: 1–48.

Thor G. 1990. The lichen genus Chiodecton and five allied genera. Opera Botanica 103:1–92.

Timdal E, Krog H. 2001. Further studies on African species of the lichen genus Phyllopsora (Lecanorales). Mycotaxon 77: 57–89.

Timdal E. 2008. Studies on Phyllopsora (Ramalinaceae) in Peru. The Lichenologist 40(4): 337–362.

Timdal E. 2011a. The lichen genus Phyllopsora (Ramalinaceae) in the West Indies. Bibliotheca Lichenologica 106: 319–351.

Timdal E. 2011b. The Phyllopsora site. http://nhm2.uio.no/lichens/fl.php?p=ph. 3 May. 2015.

Umaña-Tenorio LU, Sipman HJM, Lücking R. 2002. Preliminary checklist of lichens from Costa Rica. Version 1.2. http://archive.fieldmuseum.org/ticolichen/checklist.html. 3 May. 2015.

Van den Boom PPG, Sipman HJM. 2013. Sixty-two species of lirelliform Graphidaceae (Ascomycota) new to Panama, including four species new to science. Herzogia 26: 9–20.

Van den Boom PPG, Giralt M, Moberg R. 2014. Lichen diversity of Physciaceae from Thailand. Graphis Scripta 26(1–2): 54–62.

Wirth M, Hale ME. 1978. Morden-Smithsonian Expedition to Dominica: the lichens (Graphidaceae). Smithsonian Contributions to Botany 40: 1–64.