UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
CAMPO DE CONOCIMIENTO: ECOLOGÍA

Ecología y conservación de las interacciones entre epífitas del género *Tillandsia* (Bromeliaceae), sus árboles hospederos y sus polinizadores en un bosque tropical seco

TESIS

QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS

PRESENTA:
M. en C. ROBERTO CARLOS SAYAGO LORENZANA

TUTOR PRINCIPAL DE TESIS: Dr. Mauricio Ricardo Quesada Avendaño
Instituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM
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MORELIA, MICH. JUNIO, 2016

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UNAM POSGRADO
Ciencias Biológicas

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C. P. AGUSTIN MERCADO
Director de Certificación y Control Documental
Dirección General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Subcomité de (Biología Evolutiva y Sistemática), del Posgrado en Ciencias Biológicas, celebrada el día 9 de diciembre de 2013, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **SÁYAGO LORENZANA ROBERTO CARLOS** con número de cuenta **503007704**, con la tesis titulada: **"Ecología y conservación de las interacciones entre epífitas del género *Tillandsia* (Bromeliaceae), sus árboles hospederos y sus polinizadores en un bosque tropical seco"**, bajo la dirección del **Dr. Mauricio Ricardo Quesada Avendaño.**

Presidente:	Dr. Alberto Ken Oyama Nakagawa
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Secretario:	Dr. Antonio González Rodríguez
Suplente:	Dra. Silvana Martén Rodríguez
Suplente:	Dr. Alfredo Mario Cascante Marín

Sin otro particular, quedo de usted.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F., a 1 de junio de 2016.

Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa

c.c.p. Expediente del interesado

AGRADECIMIENTOS INSTITUCIONALES

Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México por todas las facilidades y apoyo brindadas durante mi doctorado.

Al Instituto de Investigaciones en Ecosistemas y Sustentabilidad de la UNAM.

A la Estación Biológica de Chamela-Cuixmala por las facilidades brindadas para la realización de este estudio.

Al Consejo Nacional de Ciencia y Tecnología CONACYT por haberme brindalo la beca de manutención (Becario No. 42723) que hizo posible la realización del doctorado.

Al Museo Nacional de Costa Rica y la Escuela de Biología de la Universidad de Costa Rica, por haberme brindado la oportunidad de hacer una estancia de investigación en sus instalaciones.

A los proyectos hicieron posible la realización de este trabajo

- Manejo de bosques tropicales: bases científicas para la conservación, la restauración y el aprovechamiento de ecosistemas (MABOTRO) (CONACYT).
- Human, Ecological and Biophysical Dimensions of Tropical Dry Forest (TROPI-DRY)

- Fechas: 2007- a la fecha. The Inter-American Institute for Global Change Research (IAI) under their Collaborative Research Network (CRN-2) program.
- “Laboratorio Nacional de Análisis y Síntesis Ecológica para la Conservación de los Recursos Genéticos” (CONACYT Proyecto No. 250996).
- "Ecología y evolución floral del género Ipomoea subgen. quamoclit (Convolvulaceae): filogenia, sistemas de polinización y mecanismos de aseguramiento reproductivo.Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT IN212714-3)
- “Efecto de la fragmentación de bosques tropicales de Mesoamérica sobre la razón sexual, estructura y flujo genético de plantas dioicas” (CONACYT Proyecto No. 2009-131008).

A los miembros del jurado de la tesis los Dres. María del Coro Arizmendi ,Silvana Martén Rodriguez, Alfredo Cascante Marín, Alberto Ken Oyama Nakagawa y Antonio González Rodríguez.

A los miembros del comité tutoral los Dres. Maurico Quesada Avendaño, Antonio González Rodríguez y Jorge Humberto Vega Rivera

AGRADECIMIENTOS A TITULO PERSONAL

Al Dr. Mauricio Quesada Avendaño por ser uno de los maestros que más ha influenciado mi desarrollo profesional, por el apoyo que siempre me ha brindado y por motivarme a seguir adelante, pero sobre todo agradezco su confianza y amistad.

A la Dra. Martha Elena Lopezaraiza Mikel, por su amistad y por toda la enseñanza y apoyo para la realización y culminación de esta tesis.

A la Dra. Silvana Marten Rodríguez por su amistad, todos los consejos, enseñanza y apoyo brindado para la culminación de esta tesis.

A los Dres. Ramiro Aguilar, Lorena Ashworth, Germán Ávila y Jesús Bastida por las grandes aportaciones hechas a este trabajo de investigación.

Al Dr. Alfredo Cascante Marín por su apoyo y enseñanza durante la estancia de investigación en Costa Rica.

A Miguel Angel Toriz Meneses y Andrea Sabelli por todos los buenos momentos y apoyo en el trabajo de campo en la Reserva de la Biosfera Chamela Cuixmala.

A Lic. Lilia Espinosa por su confianza, amistad y apoyo.

Al Dr. Armando Rodríguez por toda su ayuda en los trámites administrativos para la obtención del grado.

A la Lic. Maria de Jesús Marquez Salazar y Lic. Lilia Jimenez Solis, por todo el apoyo que me brindaron durante mi estancia en el doctorado, pero sobre todo por su amistad.

A Dolores Rodríguez Guzman y Alejandro Rebollar por el apoyo administrativo pero sobre todo por su amistad y respaldo.

A todo el personal de la Estación de Biología de Chamela por su amabilidad y hospitalidad.

A Don Dagoberto Umaña, Doña Carmen Quesada, Guiselle Umaña, Alonso Umaña y Santiago Arce Umaña, por su hospitalidad y apoyo en la estancia de investigación en Costa Rica.

A mis amigos del laboratorio de Ecología y Evolución de Polinización y Sistemas Reproductivos de Plantas del Instituto de Investigaciones en Ecosistemas y Sustentabilidad Jacob, Marichuy, Balvino, Gloria, Luis Daniel, Mariana, José Miguel, Rogelio, Octavio, Víctor, Jesús y Fernando.

Al Biol. Gumersindo Sánchez Montoya por las facilidades logísticas.

DEDICATORIA

A mi mamá Juanita Lorenzana Rivera, por su amor, sacrificio y ejemplo de lucha. Madre gracias por todo lo que has hecho por mi.

A mi papá Dr. Saúl Sáyago Ríos, por su amor, su apoyo y su guia por buen camino, papá muchas gracias por todo tu amor no encuentro palabras para agradecertelo.

A mis hermanos Manuel Sáyago Lorenzana y Antonio Sáyago Lorenzana, gracias por todo su amor y confianza.

A mis cuñadas Susana Ramírez y Susana Valdespino y a mis sobrinos Antonio,Valeria, Diego y Susana, por todo su cariño.

A toda mi hermosa y gran familia.

A todos los alumnos de la Unidad Académica de Desarrollo Sustentable de la Universidad Autónoma de Guerrero.

A todos mis amigos y amigas que siempre han estado presente en toda mi vida, Irena, Pati, Claudia, Mari, Ana, Omar.

Al recuerdo de mis tías las Salinas, Leonor, Rafaela y Victoria.

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Resumen

Las plantas epífitas vasculares contribuyen con el 10% de la diversidad de especies de plantas vasculares en el mundo, siendo el Neotrópico la región con mayor diversidad de epífitas a nivel mundial. Bromeliaceae es una de las familias de plantas que aportan mayor diversidad a esta forma de crecimiento en el Neotrópico. En este trabajo estudié aspectos de la ecología y conservación de plantas epífitas de *Tillandsia* del bosque tropical seco, el género con mayor cantidad de especies de la familia Bromeliaceae cuyo centro de diversificación es México. En un primer estudio (Capítulo 2) evalué cuáles son los factores más importantes en estructurar la red de interacciones entre epífitas y sus árboles hospederos (forofitos). Considerando la presencia o ausencia de individuos de epífitas del género *Tillandsia* observados en los individuos de la flora leñosa de parcelas de bosque tropical seco contínuo, evalué si modelos de probabilidad de interacción entre las especies de epífitas y especies de flora leñosa explican la red de interacciones observada. La abundancia de las especies de epífitas y forófitos, su sobrelapamiento espacial y el tamaño del forofito en gran medida predijeron las interacciones observadas y varios valores de índices empleados para describir las redes de interacción. La densidad de la madera y la rugosidad de la corteza de las especies leñosas también contribuyeron para explicar la estructura de la red epífita –forofito observada. Los resultados muestran que las epífitas fueron más comunes en los árboles de gran tamaño, en las especies de flora leñosa más abundantes, con madera más dura y/o con corteza más rugosa. La importancia del tamaño de los forofitos en el establecimiento de las interacciones implica que los bosques maduros son necesarios para la conservación de lacomunidad de epífitas, considerada como la forma de crecimiento más vulnerable a los disturbios antropogénicos.

En un segundo estudio (capítulo 3) evalué la recuperación de la comunidad epífita de la familia Bromeliaceae en un gradiente sucesional de bosque tropical seco. Además modelé la respuesta de la comunidad de epífitas a la intensidad y frecuencia de distintos escenarios de disturbios, incluyendo la tala selectiva de la flora leñosa de acuerdo al tamaño de los individuos y a la abundancia de las especies. Encontré que la abundancia de epífitas y forofitos son significativamente menores en los estadios sucesionales temprano e intermedio comparados con el estadio sucesional tardío. En los estadios sucesionales temprano e intermedio el número de especies de forofitos y la intensidad de las interacciones se ven afectados negativamente, lo que resulta en una mayor asimetría de la red, y un menor número de especies de forofitos por especie de epífita y menor anidamiento en los estadios sucesionales temprano e intermedio que en el estadio sucesional tardío. Las diferencias en la estructura de las redes de interacciones no fueron explicadas por las diferencias en el número de especies leñosas o por el número de individuos de flora leñosa (forofitos potenciales) disponibles en los sitios. Las secuencias de remoción de flora leñosa de mayor a menor tamaño y de mayor a menor abundancia de especies mostraron un alto impacto en la comunidad de epifitas, mayor que lo esperado por el azar. Además, las red de interacciones epífita –forofito del bosque maduro es más robusta que las redes de los estadios sucesionales temprano e intermedio. Este resultado indica que la comunidad de plantas epífitas es propensa a que ocurra extinción local de especies de epífitas ante escenarios de explotación cuando los ciclos de disturbio son cortos. Este estudio demuestra que los bosques tropicales secos no se recuperan florísticamente en pocos años después de un disturbio, y que la forma de crecimiento epífita debe ser considerada en las prácticas de manejo de los bosques. Los resultados tienen implicaciones para la conservación de las

comunidades de epífitas a nivel mundial, debido a que incluso un grupo de epífitas considerado como resiliente a disturbios antropogénicos resulta altamente impactado.

Finalmente en un tercer estudio (capítulo 4) evalué los efectos de la fragmentación del hábitat sobre la reproducción de dos especies de epífitas con estrategias reproductivas contrastantes, *T. intermedia* especie policárpica y *T. makoyana* especie monocárpica, en sitios de bosque tropical seco continuo y fragmentado, durante tres años consecutivos. Mi hipótesis fue que la estrategia monocárpica junto con la forma de crecimiento epífita resultan en una mayor vulnerabilidad a extincionesl locales en hábitats que han sufrido disturbios antropogénicos. Encontré que ambas especies se reproducen anualmente, que la especie policárpica es auto-incompatible y la especie monocárpica es auto-compatible, y que ambas especies son polinizadas por colibríes. En bosques fragmentados existe una mayor cantidad de visitas florales y mayor proporción de flores que produjeron frutos que en el bosque contínuo en la especie policárpica *T. intermedia*, mientras que no encontré estas diferencias significativas para la especie monocárpica *T. makoyana*. Sin embargo, en sitios con bosques fragmentados *T. makoyana* produjo menos flores y abortó más semillas. Debido a que las poblaciones de plantas epífitas tienden a ser muy afectadas por la fragmentación del hábitat, planteo la hipótesis de que las poblaciones de especies de epífitas en los fragmentos de bosques deben de estar limitadas por la disponibilidad de árboles hospederos para el establecimiento de las semillas.

Palabras clave: Comensalismo, Epífitas Vasculares, Forofito, Fragmentación del Hábitat, Interacciones Ecológicas, Polinización, Reserva de la Biosfera Chamela-Cuixmala, Sucesión Ecológica.

Abstract

Vascular epiphytes account for 10% of the diversity of vascular plants, being the Neotropics the region with the highest diversity worldwide. Bromeliaceae is one of the plant families that contributes the most to this diversity in the Neotropics. In this work I studied aspects of the ecology and conservation of *Tillandsia* epiphytic plants of a tropical dry forest, the genus most species rich of the Bromeliaceae whose center of diversification is Mexico. In a fist work (Chaper 2) I studied the factors that affect the assembly of the commensalistic interactions between vascular epiphytes and their host plants. I used an analytical approach that considers all individuals and species of epiphytic bromeliads and woody hosts and non-hosts at study plots. I built models of interaction probabilities among species to assess if host traits and abundance and spatial overlap of species predict the quantitative epiphyte– host network. Species abundance, species spatial overlap and host size largely predicted pairwise interactions and several network metrics. Wood density and bark texture of hosts also contributed to explain network structure. Epiphytes were more common on large hosts, on abundant woody species, with denser wood and/or rougher bark. The effect of host size on the establishment of epiphytes indicates that mature forests are necessary to preserve epiphytic plant communities, the most vulnerable group before antropogenic disturbances.

In a second work (Chapter 3) I used a network approach to evaluate the recovery of the epiphytic community of Bromeliaceae along a secondary successional gradient of tropical dry forest in western Mexico. I further model the response of epiphytes to the intensity and frequency of different scenarios of disturbance, including selective logging by removing individual trees according to their size, and tree species according to their

abundance. Epiphyte and phorophyte abundance are significantly lower at early and intermediate compared to the late stages of succession. Phorophyte species number and interaction strength are negatively affected, resulting in a higher web asymmetry, and lower number of phorophyte species per epiphyte species and nestedness. Differences in network structure were not explained by differences in the number of woody species or individuals (potential phorophytes) available at sites. Simulations of tree removal show higher impact for removal scenarios of large trees and abundant species than random removals, and lower network robustness of recovering communities compared to mature forests. This result indicates that short cycles of forest exploitation will lead to the local extinction of epiphyte species. Our study highlights the importance of management practices that consider this life form and shows that tropical dry forests do not recover floristically in few years after disturbance. Epiphyte communities may be endangered worldwide, as even an epiphytic group regarded as resilient to disturbance is highly impacted.

Finally, in a third work (Chapter 4) I evaluated the effects of habitat fragmentation on the reproduction and recruitment of epiphytic plants from tropical dry forests. I studied the phenology, pollinator visitation and reproductive success of two epiphytic *Tillandsia* species with contrasting reproductive strategies (polycarpic *T. intermedia* and monocarpic *T. makoyana*) in continuous and fragmented habitats in Chamela, Mexico over three consecutive years. I predicted that monocarpism together with epiphytism should lead to a greater vulnerability to local extinction in habitats that have been disturbed by human activities. I found that both study species reproduce annually, the polycarpic species is self-incompatible and the monocarpic species is self-compatible, and both are primarily pollinated by hummingbirds. I found greater pollinator visitation and fruit set in fragmented conditions for polycarpic *T. intermedia*, while no differences among habitat conditions

were detected for these traits in monocarpic *T. makoyana*. However, this latter species had lower flower production and higher seed abortion in forest fragments than continuous forest. Given that epiphytic plant populations tend to be highly affected by habitat disturbance, I hypothesize that populations of these species should be limited by availability of host trees for seedling establishment.

Keywords: Biosphere Reserve Chamela-Cuixmala, Commensalism, Ecological Interactions, Ecological Succession, Habitat Fragmentation, Phorophyte, Pollination, Vascular Epiphytes.

CAPÍTULO UNO

Introducción General

Capítulo Uno

INTRODUCCION GENERAL

Las plantas epífitas vasculares (a partir de este momento “epífitas”), es una forma de crecimiento que depende de una relación comensalista, sus raíces no están en contacto con el suelo y crecen sobre otras plantas sin parasitarlas, son un componente importante de los bosques tropicales debido a su diversidad y a que han establecido gran cantidad de interacciones con diversos taxa, *e.g.* representan recursos alimenticios para los polinizadores, materiales para construcción de nidos de aves y microhábitats para insectos y vertebrados (Benzing 1990). El marco conceptual de redes de interacción permite evaluar los factores que estructuran la relación epífita-árbol hospedero (forofito) (Burns y Zotz 2010, Blick y Burns 2009, Silva *et al.* 2010, Burns 2007, Sayago *et al.* 2013), aspecto fundamental de entender, debido a que se considera que las epífitas es la forma de crecimiento más vulnerable ante disturbios antropogénicos, *e.g.* agricultura y ganadería (Turner *et al.* 1994, Hietz 1998, Barthlott *et al.* 2001, Flores-Palacios y García-Franco 2004, Padmawathe *et al.* 2004, Martin *et al.* 2004, Benavides *et al.* 2006). Se han reportado grupos de epífitas que aparentemente son beneficiadas por los disturbios antropogénicos *e.g. Tillandsia* (Bromeliaceae) (Barthlott *et al.* 2001, Flores-Palacios y García-Franco 2004), pero aún no se ha evaluado cómo responden las epífitas a la frecuencia de los disturbios antropogénicos, aspecto que necesariamente tiene que ser considerado para poder tener un panorama integral y así comprender la dinámica de esta comunidad, y poder vislumbrar la respuesta de este grupo de plantas a los disturbios antropogénicos (Hietz 1998, Barthlott 2001, Padmawathe *et al.* 2004, Benavides *et al.* 2006). Principalmente para el género *Tillandsia* ya que aporta a México la mayor riqueza de la familia Bromeliaceae con un componente importante de endemismo, siendo los bosques tropicales secos de México cruciales para este género debido a que el 50% de las especies de *Tillandsia* de México están presentes en los bosques tropicales secos (Espejo-Serna *et al.* 2004). Los bosques tropicales secos no se encuentran representados de forma adecuada en las áreas naturales protegidas de México a pesar de que este tipo de vegetación presenta gran diversidad biológica de diversos grupos, alta proporción de endemismo y por tener altas tasas de deforestación causadas por actividades antropogénicas (Trejo y Dirzo 2000, Quesada y Stoner 2004).

Una de las características que vuelve frágil a las epífitas ante los disturbios antropogénicos es que presentan ciclo de vida largo, *e.g.* el primer evento reproductivo sexual puede tomar décadas para ciertas especies de la familia Bromeliaceae (Benzing 1990, 2000). Además se han registrado especies del género *Tillandsia* que presentan dispersión limitada (Cascante-Marín *et al.* 2009), aspecto que potencialmente hace que los individuos remanentes, si son capaces de sobrevivir, tenga un papel crucial como fuente de propágulos, por lo que es necesario conocer el sistema de apareamiento y la respuesta de los polinizadores ante disturbios antropogénicos, aspectos que se ha evaluado principalmente con árboles policárpicos, mientras que la forma de crecimiento epífita prácticamente ha sido ignorada (Aguilar *et al.* 2006). Un aspecto crucial es que existen especies del género *Tillandsia* que son monocárpicas y muchas especies de *Tillandsia* son polinizadas por colibríes, grupo que potencialmente puede verse perjudicado por los disturbios antropogénicos pero que aún no se conoce cómo es que responde ante los disturbios antropogéncios (Winfree *et al.* 2011, Hadley y Betts 2009). Lo que ofrece una oportunidad única para evaluar el efecto de la fragmentación del hábitat en la reproducción de individuos en sitios que han tenido disturbios antropogénicos, y así poder entender cuál es el papel potencial que tienen los individuos remanentes como fuente de propágulos debido a que la estrategia reproductiva de monocarpismo puede incrementar el riesgo a la extinción en especies de epífitas por el tiempo que tardan en completar su ciclo de vida (20 años o más) y por que el reclutamiento de individuos de las especies monocarpicas es exclusivamente vía semillas, para las epífitas el reclutamiento es la fase más crítica en el ciclo de vida (Benzing 1990, 2000).

Plantas epífitas vasculares

Las plantas epífitas vasculares es una forma de crecimiento que utiliza como sustrato a otras plantas sin parasitarlas y sus raíces no se encuentran en contacto permanente con el suelo (Benzing 1990). De acuerdo con el ciclo de vida las epífitas se clasifican como holo-epífitas y hemi-epífitas, son holo-epífitas las especies que todo su ciclo de vida lo realizan sin tener contacto con el suelo y las hemi-epífitas en alguna parte de su ciclo de vida no tienen contacto con el suelo, este grupo a la vez se subdivide en hemi-epífitas primarias y secundarias. Las hemi-epífitas primarias son las especies que nacen en el dosel y después sus raíces llegan al suelo *e.g. Ficus cotinifolia*, y las hemi-epífitas secundarias son las especies que nacen en el suelo, suben al dosel y con el tiempo pierden contacto con este *e.g. Philodendron spp.* (Benzing, 1973, 1990, Nadkarni *et al.* 2001, Nieder *et al.* 2001).

Las epífitas viven en condiciones ambientales extremas debido a la poca disponibilidad de agua en el dosel, la gran intensidad de luz y la falta de nutrientes, por lo que existen adaptaciones que permiten que las epífitas puedan existir bajo estas circunstancias, como son una gran eficiencia en el uso de agua y de los minerales, metabolismo del ácido crasuláceo (CAM), una baja relación superficie volumen, tasas bajas de crecimiento, dispersión de las semillas por el viento, reproducción asexual y estructuras de fijación. Sin embargo, ninguna de las adaptaciones anteriores se considera distintiva de esta forma de crecimiento ni necesariamente todas las epífitas tienen todas las adaptaciones anteriores (Benzing 1973, Nadkarni *et al.* 2001).

La forma de crecimiento epífita es muy importante debido a que contribuye con el 10% de la diversidad de especies de plantas vasculares del mundo (Kress 1986). La distribución mundial de las epífitas no es homogénea y varía de acuerdo con los hábitats, la latitud y la altitud sobre el nivel del mar. Además se ha observado que existen diferencias importantes en la diversidad de especies entre los distintos continentes del planeta, siendo América y específicamente el Neotrópico el área del globo terráqueo con mayor diversidad de especies de epífitas (Ibisch *et al.* 1996, Nieder *et al.* 2001, Zotz 2005). Sin embargo, no existe gran cantidad de trabajos que expliquen el porqué se da este patrón. Gentry y Dobson (1987) sugieren que esto ocurre por que ha existido una explosión en la especiación de especies de epífitas en el Neotrópico, mientras que Madison (1977) y Benzing (1990) atribuyen este patrón a la presencia de ciertas familias entre las que destacan las Cactaceae y Bromeliaceae, debido a que aportan gran diversidad de especies con esta forma de crecimiento y además son prácticamente endémicas del continente americano (Benzing 1990).

Relación epífita-forofito

La relación de las epífitas con los árboles hospederos (forofitos) se ha tratado de entender con varios enfoques y las variables que se han tomado en cuenta de los forofitos son: la especie, la altura, la estructura, el diámetro a la altura del pecho, la tasa de crecimiento y la edad, mientras que de la corteza se ha considerado la capacidad de retención de agua, la química, la ornamentación y la porosidad, y de la rama los estudios consideran la estabilidad, el grosor y la calidad del suelo retenido en estas. También han sido consideradas relaciones bióticas que presentan los forofitos con otras especies *e.g.* la presencia de nidos de hormigas, termiteros, epífitas no vasculares y el comportamiento de los dispersores figuran dentro de los aspectos más importantes que se han considerado hasta el momento (Pittendrigh 1948, Frei y Dodson 1972, Johansson 1974, Schlesinger y Marks 1977, Todzia 1986, Cattling y Lefkovich 1989, ter Steege y Cornelissen 1989, Benzing 1990, Wolf 1994, Freiberg 1996, Zapfack *et al.* 1986, Nieder *et al.* 2000, Callaway *et al.* 2002, Moran *et al.* 2003, Kelly *et al.* 2004, Mehltreter *et al.* 2005, Cascante-Marín *et al.* 2006, Cardelús 2006, Laube y Zotz 2006).

Redes de interacción

Las redes de interacción es una herramienta integradora que permite analizar datos biológicos complejos de cualquier tipo de interacción ecológica (mutualismo, depredación, competencia, parasitismo y comensalismo) se ha empleado para entender la estructura y dinámica de las redes de interacción observadas (Bascompte *et al.* 2003, Berlow *et al.* 2004, Blick y Burns 2009, Burns y Zotz 2010, Silva *et al.* 2010, Burns 2007). Permiten obtener medidas útiles, *e.g.* conectancia, definida como la proporción de todas las interacciones posibles y las interacciones que sí ocurren entre las especies, el anidamiento definido como la tendencia de las especies especialistas de interactuar con un subgrupo de especies generalistas, la especialización definido como el número de especies con la que una especie está interactuando en la red. Además puede evaluarse el papel de la “neutralidad” y de las “relaciones prohibidas” en la estructuración de las redes observadas (Vázquez *et al.* 2009a). La neutralidad se refiere a que las interacciones observadas resultan del encuentro aleatorio entre los individuos, de forma que todos los individuos tienen la misma probabilidad de asociarse con otros individuos sin importar su identidad taxonómica, así es que las especies más abundantes tendrán mayor cantidad de interacciones, mientras que el papel de las “relaciones prohibidas” se refiere a que existen características específicas de las especies que permiten el establecimiento de las interacciones observadas *e.g.* tipo de corteza de las especies de forofitos con estructuras de fijación de las semillas (Vázquez *et al.* 2009b). Conocer los factores que contribuyen en el establecimiento de las interacciones biológica permite simular cómo afectan los distintos tipos de disturbio y la intensidad de estos en las redes de interacciones biológicas (Memmott *et al.* 2004), y también nos permite simular la frecuencia de los disturbios, un aspecto que no se ha evaluado en plantas epífitas.

Familia Bromeliaceae

La familia Bromeliaceae es monofilética y pertenece a las monocotiledóneas, presenta hojas opuestas y xerófilas, casi todas las especies presentan tricomas, son plantas perennes, terrestres y epífitas, se distribuyen en una gran cantidad de hábitats que van desde los bosques tropicales lluviosos hasta las zonas alpinas de Sudamérica. La familia Bromeliaceae se ha clasificado en tres subfamilias: Bromelioideae, Pitcairniodeae y Tillandsioideae, en total existen 54 géneros y hasta el momento se han descrito 2,742 especies, sin embargo la clasificación taxonómica de la familia aún está cambiando constantemente. Los países que presentan mayor diversidad de especies de la familia Bromeliaceae son Perú con 411 especies, Colombia con 391 especies y Ecuador con 368 especies (Benzing 2000). En México, se han reportado 342 especies de la familia Bromeliaceae siendo 233 especies endémicas al país, atributo dado principalmente a la familia por el género *Tillandsia* ya que cuenta con 192 especies de las cuales 133 son endémicas de México (Espejo-Serna *et al.* 2004).

Aspectos reproductivos de la familia Bromeliaceae que han sido estudiados parcialmente son el sistema de apareamiento, y se ha reportado que pueden existir diferencias en el sistema de apareamiento entre distintas poblaciones, existiendo poblaciones que son auto-compatibles y auto-incompatibles en distintas áreas de distribución geográfica de las especies *e.g. T. caput-medusae, T. dasylirifolia* y *T. paucifolia*. Inclusive se tiene evidencia de poblaciones que son dioicas en algunos sitios mientras que en otras áreas de distribución las poblaciones son hermafroditas *e.g. Catopsis nutans* (Benzing 2000). Respecto a la dispersión en el género *Tillandsia* prevalece la dispersión por viento considerado demasiado estocástico, por lo que se requiere de gran cantidad de semillas para que pueda lograrse el reclutamiento de individuos (Benzing 1990, 2000). Finalmente en cuanto estrategias reproductivas a la familia Bromeliaceae se les clasifica en tres patrones: Tipo “A” se tienen especies policárpicas que presentan producción de ramets y el individuo tiene un crecimiento simpódico; Tipo “B” se presentan especies monocárpicas sin reproducción asexual; y Tipo “C” especies policárpicas con la formación de ramets y un crecimiento monopódico (Benzing 2000).

Estrategias reproductivas

Existen dos estrategias reproductivas contrastantes, primero las especies policárpicas que son las que tienen múltiples eventos reproductivos y segundo las especies monocárpicas que son las que se caracterizan por tener exclusivamente un único evento reproductivo al final de su ciclo de vida (Begon *et al.* 1995). Muchas especies monocárpicas se asocian con estrategias de especies anuales (de Jong *et al.* 2000), sin embargo es posible encontrar esta estrategia reproductiva en todas las formas de crecimiento de las plantas vasculares, así pues, encontramos arbustos (*e.g. Erysimum mediohispanicum*), lianas (*e.g. Dioscerophyllum cumminsii*), árboles (*e.g. Tachigali versicolor*) y epífitas (*e.g. Tillandsia secunda*) (Benzing 2000, Obioh y Isichei 2007, Loveless *et al.* 1998). El ciclo de vida de las especies monocárpicas varia, muchas especies son anuales *e.g.* plantas herbáceas (de Jong *et al.* 2000), pero también puede tomar varias décadas, *e.g. T. versicolor* requiere de cuatro décadas para reproducirse (Zjhra y Kaplin 2004). El monocarpismo se ha identificado como una estrategia de especies pioneras, pero si consideramos a las especies monocarpicas con ciclo de vida largo estas pueden ser susceptibles ante disturbios antropogénicos, ya que sólo presentan una oportunidad reproductiva. También se incrementará la susceptibilidad de las especies si requieren de vectores bióticos para poder producir frutos y semillas, si los polinizadores son afectados por los disturbios antropogénicos.

Familia Trochillidae

La familia Trochilidae endémica de América con cerca de 300 especies, es por excelencia polinizadora y la que tiene mayor diversidad de especies de aves con este servicio, tienen la capacidad de revolotear y volar hacia atrás, y un alto consumo de energía por lo que visitan gran cantidad de flores y además presentan constancia en las especies de las que se alimentan (Feinsinger 1976). Las flores de las especies de plantas que consumen los colibríes tienden a ser rojas, naranjas o amarillas. Una revisión de la literatura indica que, 43 especies de la familia Trochilidae polinizan a 220 especies de plantas de 49 familias, siendo la familia Bromeliaceae la que encabeza la lista con 48 especies (Wolf 1970, Stiles 1975, Toledo 1975, Neil 1987, Arizmendi y Ornelas 1990, Buzato *et al.* 2000, Canela y Sazima 2003, Kaehler *et al.* 2005).

Reserva de la Biosfera Chamela-Cuixmala

La Reserva de la Biosfera Chamela Cuixmala es una de las pocas áreas naturales protegidas que principalmente tiene bosque tropical seco, para diversos grupos taxonómicos *e.g.* plantas y aves en esta reserva se representa una gran riqueza de especies con un alto componente endémico (Arizmendi *et al.* 1990, Arizmendi *et al.* 2002, Lott 2002, Lott y Atkinson 2002, Noguera *et al.* 2002). Se ha documentado que áreas aledañas a la reserva han tenido disturbios antropogénicos *e.g.* agricultura y ganadería, que han transformado el bosque tropical seco continuo en un mosaico de vegetación secundaria y fragmentada. Además se reporta que el número de fragmentos aumenta y su tamaño disminuye con el incremento de la distancia a la reserva (Sánchez-Azofeifa *et al.* 2008).

La familia Bromeliaceae representa un recurso importante en el bosque tropical seco de la reserva de la biosfera Chamela Cuixmala para la familia Trochillidae debido a que en cualquier época del año tienen recursos alimenticios que pueden ser explotados por sus polinizadores (Lott 2002) (Tabla 1.1). Por otro lado la mayoría de las especies de la familia Bromeliaceae son epífitas representando el 65.6% de la diversidad de esta forma de crecimiento en la región de Chamela (Lott 2002, Lott y Atkinson 2002). Arizmendi y Ornelas (1990) documentaron que de las nueve especies de colibríes reportadas en la Reserva, *Amazilia rutila, Heliomaster constantii* y *Chlorostilbon auriceps* son las principales especies polinizadoras de *T. bartramii*, *T. paucifolia* y *T. dasyliriifolia*.

Tabla 1.1 Fenología floral de las especies de la familia Bromeliaceae registradas en la Reserva de la Biosfera Chamela-Cuixmala de acuerdo con Lott (2002). Meses de floración por especie por año (Verde 1-2, Azul 3-4, Rojo >4), Número de especies con recursos florales por mes (Verde 3-4, Azul 5-7, Rojo >8).

Especie	**Enero**	**Febrero**	**Marzo**	**Abril**	**Mayo**	**Junio**	**Julio**	**Agosto**	**Septiembre**	**Octubre**	**Noviembre**	**Diciembre**
Aechmea bracteata	1	0	0	0	0	0	0	0	0	0	0	0
Aechmea mexicana	1	1	0	0	0	0	0	0	0	0	0	0
Thillandsia makoyana	1	0	1	0	1	0	1	0	1	0	1	0
Thillandsia. balbisiana	1	0	0	0	1	0	0	0	0	1	1	1
Thillandsia intermedia	1	1	1	1	1	0	0	0	0	0	1	1
Thillandsia polystachia	1	1	1	1	1	0	0	0	0	0	0	1
Thillandsia caput-medusae	0	0	1	1	1	0	0	0	0	0	0	0
Thillandsia schiedeana	0	0	1	1	1	1	1	0	0	0	0	0
Bromelia sp. 1.	0	0	0	0	1	0	0	0	0	0	0	0
Thillandsia bartramii	0	0	0	0	1	0	0	0	0	0	0	0
Thillandsia diguettii	0	0	0	0	1	0	0	0	0	0	0	0
Thillandsia sp. 1.	0	0	0	0	1	0	0	0	0	0	0	0
Thillandsia pseudobaileyi	0	0	0	0	1	1	0	0	0	0	0	0
Thillandsia ionantha	0	0	0	0	1	1	1	0	0	0	0	0
Thillandsia setacea	0	0	0	0	1	1	1	0	0	0	0	0
Bromelia plumieri	0	0	0	0	1	1	1	1	0	0	0	0
Bromelia palmeri	0	0	0	0	0	1	1	1	0	0	0	0
Bromelia pinguin	0	0	0	0	0	0	1	0	0	0	0	0
Hechtia jaliscana	0	0	0	0	0	0	1	1	0	0	0	0
Thillandsia rothii	0	0	0	0	0	0	1	1	1	1	1	1
Billbergia pallidiflora	0	0	0	0	0	0	0	1	0	0	0	0
Thillandsia usneoides	0	0	0	0	0	0	0	1	1	0	0	0
Thillandsia juncea	0	0	0	0	0	0	0	0	0	1	0	0
Catopsis nutans	0	0	0	0	0	0	0	0	0	1	1	1
Thillandsia jaliscomonticola	0	0	0	0	0	0	0	0	0	1	1	1
Thillandsia recurvata	0	0	0	0	0	0	0	0	0	0	0	1
No. Especies que florecen	6	3	5	4	14	6	9	6	3	5	6	7

Disturbios antropogénicos y reproducción de los individuos remanentes de plantas

Los disturbios antropogénicos como la agricultura y ganadería causan cambio de uso de suelo en los ecosistemas, pueden producir la disminución del número de individuos o la extinción local de ciertas especies de plantas silvestres promoviendo la fragmentación del hábitat y el establecimiento de vegetación secundaria, tanto en los fragmentos como en los sitios adyacentes (Murcia 1995, Chazdon *et al.* 2003, Bawa *et al.* 2003, Fahrig 2003, Kang y Bawa 2003, Sanchez-Azofeifa *et al.* 2003, Reich *et al.* 2004, Fuchs 2003, Cascante-Marin 2006, Herrerías-Diego *et al.* 2006). Es importante tener en cuenta que la fragmentación de hábitat y la sucesión ecológica son conceptos que no ocurren de forma aislada uno de otro y que el entendimiento de estos se relaciona con las escalas de estudios (espacial, temporal y taxonómica).

Los trabajos que estudian el efecto de la fragmentación del hábitat sobre la polinización en especies de plantas que requieren de vectores bióticos para transferir el polen a otros individuos de su misma especie, han documentado que la fragmentación en términos generales tiene consecuencias negativas en el movimiento de polen en poblaciones que han quedado aisladas y que se pudiera estar promoviendo la endogamia y la deriva génica, estos trabajos se han realizado principalmente con árboles policárpicos mientras que las plantas epífitas vasculares ha sido un grupo poco estudiado (*e.g.* Quesada *et al.* 2003, Ashworth *et al.* 2004, Johnson *et al.* 2004, Quesada *et al.* 2004, Aguilar *et al.* 2006). Aún no hay trabajos que evalúen para las epífitas de la familia Bromeliaceae el mantenimiento de poblaciones viables a largo plazo en sitios fragmentados por disturbios antropogénicos.

OBJETIVO GENERAL

Evaluar los factores que predicen la estructura en una red comensalista epífita-forofito en un bosque tropical seco continuo para poder simular la frecuencia de disturbios antropogénicos con el marco conceptual de redes de interacción. Evaluar redes de interacción Bromeliaceae-forofito en un gradiente de sucesión ecológica secundaria de un bosque tropical seco de la Costa del Pacífico del oeste de México. Evaluar la fenología reproductiva y el esfuerzo reproductivo en dos especies de *Tillandsia* con estrategias de vida contrastantes (monocarpismo-policarpismo) en bosque tropical seco continuo y en sitios que han sido fragmentados por actividades antropogénicas (*e.g.* ganadería y agricultura) en un bosque tropical seco del oeste de México.

Estructura de la tesis

La tesis se encuentra dividida en cinco capítulos. El capítulo I es la introducción general. En el capítulo II empleamos un análisis novedoso que considera a todos los individuos y especies de epífitas y de flora leñosa observadas en las parcelas de estudio para construir modelos de probabilidad de interacción. Se evalúan la contribución de distintos factores para explicar la red epífita-forofito observada en un bosque tropical seco continuo y se realizó un análisis para evaluar si existe relación filogenética en la red comensalista.

En el capítulo III también se emplea un enfoque de redes para evaluar la recuperación de la comunidad epífita-forofito a lo largo de un gradiente de sucesión secundaria en un bosque tropical seco del oeste de México, además empleando simulaciones de extinción se evalúa la respuesta de la red epífita-forofito a la magnitud y frecuencia de los diferentes escenarios de perturbación, incluyendo la tala selectiva mediante la eliminación de árboles individuales de acuerdo a su especie y tamaño de los árboles en función de su abundancia.

En el Capítulo IV se evalúan aspectos reproductivos de *Tillandsia makoyana* y *T. intermedia* especies con estrategias de vida contrastantes (monocarpismo-policarpismo), se describe la fenología reproductiva y el éxito reproductivo femenino medido como número de frutos, cantidad de semillas, proporción de frutos y proporción de semillas en sitios con bosque tropical seco continuo y sitios con bosque tropical seco fragmentado por disturbios antropogénicos durante tres años de muestreo. Finalmente el capítulo V es la discusión general.

Capítulo Dos. Evaluación de factores que predicen la estructura de una red comensalista epífita forofito.

En este capítulo evaluamos el papel que tienen distintos factores para predecir la estructura de una red cuantitativa epífita-forofito en un bosque tropical seco continuo del oeste de México. Nuestra hipótesis es que la textura de la corteza, el tamaño de los individuos leñosos, junto con su abundancia, la densidad de la madera de las especies de flora leñosa y el sobrelapamiento espacial de las especies, determinan en una red de interacción epífita-forofito los patrones de interacción de las especies y su especialización. Evaluamos la contribución relativa de estos factores para estructurar la red epífita-forofito y si los patrones de interacción presentan señal filogenética que expliquen la red comensalista epífita-forofito.

Capítulo Tres. Fragilidad de las redes de epífitas-forofito en un gradiente de bosque tropical seco.

En este capítulo estudiamos las redes Bromeliaceae-forofitos en un gradiente de sucesión ecológica secundaria de un bosque tropical seco de la Costa del Pacífico del oeste de México. Los objetivos son (1) evaluar la recuperación de la comunidad de epífitas en una cronosecuencia en un gradiente sucesional de bosque tropical seco en sitios después de haber sido utilizados para la agricultura y ganadería, (2) evaluar si las diferencias en la estructura de las redes epífita-forofito a lo largo del gradiente sucesional pueden ser explicadas por las diferencias en la riqueza de flora leñosa y abundancia, (3) Modelar diferentes escenarios de explotación forestal y deforestación para evaluar la vulnerabilidad absoluta y relativa de las redes de interacción epífita-forofito en escenarios de sucesión ecológica, (4) Evaluar los efectos de la frecuencia de disturbios en la comunidad epífita entre estadios sucesionales y bosque maduro. Nuestra hipótesis es que la estructura de la red difiere a lo largo de los estadios sucesionales, y que tienen mayor anidamiento y es más robusta en bosques primarios, y que la frecuencia de disturbios afecta drásticamente a la comunidad de epífitas, mientras que la recuperación de la estructura y la composición de especies de la flora leñosa puede recuperarse en menos de dos décadas después de que ha ocurrido en los sitios agricultura y ganadería.

Capítulo Cuatro. Efecto de la fragmentación del bosque tropical seco en el esfuerzo reproductivo femenino en plantas epífitas vasculares con estrategias reproductivas contrastantes.

El objetivo del capítulo es evaluar el efecto de la fragmentación del bosque tropical seco en la fenología reproductiva, los visitantes florales y el éxito reproductivo en dos especies del género *Tillandsia* con estrategias reproductivas contrastantes (monocarpismo-policarpismo). Comparamos (1) los patrones de la fenología floral a nivel de individuo y de las flores, (2) el sistema de apareamiento y (3) los patrones de visitas a las flores y el éxito reproductivo femenino en hábitats continuos y fragmentados a través de tres años de muestreo. Nuestra hipótesis es que las especies monocarpicas epífitas son más vulnerables a la fragmentación del hábitat que las especies epífitas policárpicas debido a que el reclutamiento de individuos de la especie monocarpica es exclusivamente vía semillas y los individuos presentan un solo evento reproductivo sexual.

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Sáyago R., M. Lopezaraiza-Mikel, M. Quesada, M. Y. Álvarez-Añorve, A. Cascante-Marin y J. M. Bastida. 2013. Evaluating factors that predict the structure of a commensalistic epiphyte-phorophyte network. Proceedings of the Royal Society B. 280: 201222821. doi:10.1098/rspb,2012.2821.

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CAPÍTULO DOS

Evaluating factors that predict the structure of a commensalistic epiphyte – phorophyte network

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Proc. R. Soc. B 2013 **280**, 20122821, published 13 February 2013

PROCEEDINGS OF THE ROYAL SOCIETY B

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Evaluating factors that predict the structure of a commensalistic epiphyte–phorophyte network

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Research

Cite this article: Sáyago R, Lopezaraiza-Mikel M, Quesada M, Álvarez-Añorve MY, Cascante-Marín A, Bastida JM. 2013 Evaluating factors that predict the structure of a commensalistic epiphyte–phorophyte network. Proc R Soc B 280: 20122821.
http://dx.doi.org/10.1098/rspb.2012.2821

Received: 6 December 2012
Accepted: 21 January 2013

Subject Areas:
ecology, plant science

Keywords:
Bromeliaceae, Chamela-Cuixmala biosphere reserve, ecological interactions, Mexico, *Tillandsia*, tropical dry forest

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.2821 or via http://rspb.royalsocietypublishing.org.

A central issue in ecology is the understanding of the establishment of biotic interactions. We studied the factors that affect the assembly of the commensalistic interactions between vascular epiphytes and their host plants. We used an analytical approach that considers all individuals and species of epiphytic bromeliads and woody hosts and non-hosts at study plots. We built models of interaction probabilities among species to assess if host traits and abundance and spatial overlap of species predict the quantitative epiphyte–host network. Species abundance, species spatial overlap and host size largely predicted pairwise interactions and several network metrics. Wood density and bark texture of hosts also contributed to explain network structure. Epiphytes were more common on large hosts, on abundant woody species, with denser wood and/or rougher bark. The network had a low level of specialization, although several interactions were more frequent than expected by the models. We did not detect a phylogenetic signal on the network structure. The effect of host size on the establishment of epiphytes indicates that mature forests are necessary to preserve diverse bromeliad communities.

1. Introduction

An important aim in community ecology is to identify the factors that drive the establishment of species interactions. Mutualisms, antagonisms and more recently commensalisms have been depicted as complex networks [1–3], and have revealed patterns of community organization common in ecological systems, such as the tendency of species to interact with subsets of the interaction partners of more generalized species (nestedness, [4]). Quantitative differences in network properties among these interaction types have been identified [5–7], indicating differences in the underlying structuring factors. If interactions are neutral, the structure of the network is explained by the random interaction among individuals in the community and species abundance determines network patterns [8]. However, deterministic factors can also affect the structure of a network. There has been debate on whether neutral or biological factors such as complementarity in species phenotypes determine structural patterns of networks [9–12]. Phylogenetic analyses can help understand network topology because evolutionary history can influence ecological interactions [13,14]. Recent advances have been made in identifying the factors that influence network structure in mutualisms [12,15–17] and antagonisms [18–20], though there is a lag in the study of commensalistic interactions. Network structures may be the result of multiple, hierarchical, non-exclusive interactions among factors [21], but few studies have assessed several factors simultaneously [12,15,18]. Identifying the factors that structure interaction networks provides novel insights into the ecological and evolutionary processes at the community level that shape interactions, with possible implications for the management and conservation of species, particularly for groups with high vulnerability to extinction.

Vascular epiphytes (henceforth referred as epiphytes) are plants that establish obligate interactions with other plants (phorophytes) using them as a substrate without parasitizing them [22]. This makes them a vulnerable group to anthropogenic disturbance, together with their long life cycles, slow growth and the stressing environment in which they live [22]. Epiphytes represent 10 per cent of the diversity of living vascular plants [23] attaining their highest diversity in the Neotropics [24]. Studies of networks have found high values of nestedness [3,5,25]; no phylogenetic signal in species interaction patterns [26]; and the generalization of species partly or fully explained by species abundance [5,25]. However, no attempt has been made to incorporate other explanatory variables that might determine the structure of epiphyte–phorophyte networks. Certain host traits are associated with the presence of epiphytes. For example, bark ornamentation affects seed establishment [27,28]; bark porosity affects the humidity of the substrate [28,29]; and the production of secondary compounds can inhibit the germination of epiphytes [29,30]. Host tree size is related to epiphyte diversity and abundance [27,31,32]. Larger trees have more complex structures, providing more microhabitats and more substrate area for seeds to land. Tree size is also related to age, and older trees tend to have more epiphytes than younger trees because they have been exposed for a longer period of time to the seed rain of epiphytes. Additionally, bigger branches provide more stability, as these branches are less likely to fall [33,34]. Wood density is expected to affect epiphyte–phorophyte interactions because it influences branch stability, and because species with dense wood have slower growth rates [20] that affects the time of exposure to seed rain when tree size is considered. Thus, the combination of traits in a host species will influence the colonization, establishment and success of the interaction.

One of the main focuses in species interactions is their specialization. The observed specificity of epiphytes on host species may be owing to their specialization or to sampling effects posed by community attributes of the flora, such as species richness and abundance [21,22]. Low diversity forests have only few potential phorophyte species, and epiphytes may appear as highly specialized. On the other hand, species in forests with high alpha diversity have low densities, and rare species are seldom recorded, appearing more specialized than common species. Community studies have only considered common host, and sometimes epiphyte species even in network studies [3,25,31,35,36], and have used null models incorporating species abundance to overcome this problem when assessing specialization [3,25,31,36]. A further limitation to assess specialization (or neutrality) has been the exclusion of absence data, i.e. trees that do not bear epiphytes, because the real abundance of host species or species that lack epiphytes is not considered [22,37] (but see [31]).

Here, we assess which factors predict the structure of a quantitative epiphyte–phorophyte network in a tropical dry forest in western Mexico. We hypothesize that bark texture, size of woody individuals and wood density of woody species, together with the abundance and spatial overlap of species, determine network level patterns of species interactions and specialization. We evaluate the relative contribution of these factors to network structure, and whether patterns of interactions are conserved in the phylogeny of epiphytes and phorophytes.

2. Material and methods

Epiphyte–phorophyte networks in the tropical dry forest offer a great opportunity to investigate which factors contribute to emergent patterns of network organization because epiphyte and woody individuals can be easily recorded during the leafless season of this low canopy forest. This is an important advantage because excluding species and individuals that do not interact precludes the appropriate assessment of factors that may limit the establishment of interactions. We focus on the epiphytic bromeliads of a tropical dry forest in western Mexico. Rather than trying to document all possible interactions in the system, we focused on assessing if the factors considered can explain the network structure given the pool of individuals and species at the study sites.

(a) Study area and field data

The work was conducted in conserved tropical dry forest at the Chamela-Cuixmala Biosphere Reserve and its vicinity, in the central western coast of Mexico in the state of Jalisco (19°22′–19°35′ N, 104°56′–105°03′ W). The climate is very seasonal; the wet season occurs between July and October [38]. In this forest there are 421 woody species (potential phorophytes) reported and 29 vascular epiphyte species [39] distributed among the families Cactaceae (1 species), Orchidaceae (10 species) and Bromeliaceae (18 species). We focused on the Bromeliaceae, a monophyletic family of the monocots, which is the family with the highest epiphyte species richness and abundance in the region, and contributes importantly to the diversity of epiphytes in Neotropical forests [37].

We registered all interactions between bromeliad epiphytes and woody species at three 20 × 20 m plots (19°30.065′ N, 105°02.584′ W; 19°30.532′ N, 105°02.410′ W; 19°24.297′ N, 104°58.968′ W). We registered all epiphytes larger than approximately 3 cm in height, which can be confidently seen and identified from the ground using binoculars. Data on epiphytic bromeliads was collected during the dry season of 2007/2008 (from November to May) when the canopy is leafless and bromeliads are easy to observe. Two *Tillandsia* species have the potential of secondary dispersal by asexual means (*Tillandsia intermedia*, R. Sayago 2007, personal observation; *Tillandsia usneoides*, [37]) when ramets (clones) detach. We defined an individual as an epiphyte physically separated from other epiphytes.

All the woody plants at the plots with a diameter at 1.3 m above ground (trees and shrubs) or at the base (lianas) greater than 2.5 cm (DBH henceforth) were marked with an aluminium tag. For each marked individual we collected the following information: (i) DBH, (ii) species identity, and (iii) the abundance of each epiphytic bromeliad species. Leaf and reproductive samples were collected for each woody species. Plant identification was conducted by the authors and corroborated with herbarium specimens preserved at the Chamela Biological Station (Universidad Nacional Autonoma de Mexico). We refer to phorophytes only when referring to woody individuals bearing epiphytes, and to woody species to refer to all potential phorophytes present at the plots.

Bark texture for all woody species (see the electronic supplementary material, appendix S1) was recorded for at least one, and up to three of the largest individuals of each species based on four previously defined categories, from smooth (category 1) with lack of ornamentation (e.g. spines, lenticels, fissures) and including smooth exfoliating barks (e.g. some *Bursera* species), to rough (category 4) with coarse ornamentation (large lenticels and/or spines and/or deep fissures). Trees with rugose and ornamented bark are expected to have a greater load of epiphytes [22,29]. Data on wood density (specific gravity) of all tree species at the plots was obtained from the literature (see the electronic supplementary material, appendix S1).

(b) Observed interaction network

Ninety per cent of the bromeliad epiphytes were found on woody individuals with DBH greater than or equal to 5 cm, and we only considered these individuals for the network analyses. We constructed an interaction matrix **Y** describing the epiphyte–phorophyte network, pooling the data from the three sites. In this matrix the I rows correspond to woody species (all potential phorophytes) and the J columns to bromeliad species (epiphytes), and a cell y_{ij} is an integer that represents the number of interactions that occur between woody species i and bromeliad species j, i.e. the sum of all epiphyte individuals of species i at the three plots, recorded on individuals of woody species j. Any woody species i at the plots, whose individuals did not host bromeliads is present in this matrix with $\sum_i y_{i*} = 0$.

We use network statistics that characterize several aspects of network structure [40] to describe the observed network and to compare observed values with the values obtained from models of network determinants using functions in R [12,40–42] (see the electronic supplementary material, appendix S2): (i) connectance (C = number of links/IJ); (ii) nestedness [4], two metrics: $N = 100 - T$, where T is the matrix temperature [43], and nestedness based on overlap and decreasing fill (NODF) [44]; (iii) interaction evenness [45]; (iv) H'_2, a quantitative metric of specialization that controls for the interaction frequencies expected from the total observations per species, i.e. the effect of the differences in the abundance of species, that results in abundant species interacting more frequently and with more partners, is removed [46]; (v) generality and vulnerability, the weighted mean number of phorophyte species per epiphyte species, and epiphyte species per phorophyte species, respectively [47]; and (vi) the average interaction strength asymmetry for phorophytes and for epiphytes [8]. The first two statistics are based on unweighted links, whereas the remaining are based on weighted links. To allow for comparison, we assessed the significance of nestedness [43,48] using the equivalent of null model 2 of Bascompte *et al.* [4].

(c) Models of network determinants

We follow the conceptual and methodological framework proposed by Vázquez *et al.* [12], in which the observed matrix is a function of multiple interaction probability matrices determined by different factors. We built probability matrices from models that consider epiphyte and woody species abundance, bark texture and wood density of woody species, size (DBH) of woody individuals, and presence/absence of woody species and epiphytes species at each site (spatial overlap). In addition, we develop models that consider the joint effect of two or more factors, thus, all possible combinations (plant size is always assessed together with abundance, see below for details) of two, three and four factors, and a full model with the five factors are considered.

Consider a matrix **X** of the same size as **Y**, whose entries x_{ij} are given weights according to a particular model defined by the factors we are assessing. To calculate a probability matrix **P** from any matrix **X**, these weights are converted to probabilities of occurrence of pairwise interactions by normalizing the matrix so that all its elements sum to one. For the different models the calculation of x_{ij} is described in table 1. In the abundance model (A) interactions are determined by the abundance of species. The spatial overlap model (S) is based on the presence and absence of species on a local (site) scale, considering two species cannot interact if they do not co-occur at a site. The wood density model (W) weighs each species by its specific gravity. The model that considers bark texture (B) assigns higher probabilities of interaction to woody species with rougher bark texture. Model AD considers the joint influence of plant size and abundance. Because plant size is a trait of the individual and networks depict interactions among species, when considering the DBH of all individuals, the resulting probability matrix necessarily incorporates information on the abundance of each woody species. Models that consider the joint influence of spatial overlap and abundance are calculated so that not only presence/absence data are considered for each site, but the abundance of each species as well, thus incorporating the fine information on local abundance of this system. The performance of all models was compared to the performance of a null model that assumes that all interactions have the same probability to occur.

Two approaches are used to compare the performance of models in explaining the observed interaction network [12] (see the electronic supplementary material, appendix S2).

- The likelihood that a probability matrix explains the observed matrix is calculated assuming a multinomial distribution [12] and compared among models using the Akaike's information criterion (AIC) [49]. $\text{AIC} = -2\ \ln(L) + 2k$, where k is the number of parameters used to generate a probability matrix, which is the number of factors involved in the calculation of each probability matrix, except for plant size that involved two parameters (probability of presence and expected abundance). The model with the lowest ΔAIC, the difference in AIC between a given model and the AIC of matrix **Y** fitted to itself, indicates the model that better fits the data.
- A randomization algorithm [12] that assigns the total number of observed interactions (sum of elements in **Y**) to cells of a matrix of size **Y** with probabilities defined by a probability matrix is used to generate 1000 quantitative networks for each model; all network statistics are calculated for each generated network to obtain the 95% confidence intervals (CI) of the distribution of values of the statistics, against which the statistics of the observed network are compared. The only constraint of this algorithm [12] is to assign at least one interaction per species. To allow for empty rows, we did not use the constraint for woody species, though we left the constraint for epiphyte species. This simulates a scenario in which all woody species can potentially be colonized by epiphytes, and allows testing if the factors considered explain the absence of epiphytes on certain woody species. Network statistics are calculated excluding non-interacting woody species.

We identified the species with the predicted number of interactions that deviate the most from the observed values by assessing whether the observed value of each pairwise interaction falls outside the lower and upper 95% CI of 1000 runs of the algorithm.

(d) Phylogenetic signal in species associations

We evaluated the influence of evolutionary history on network patterns by assessing the presence of phylogenetic signal (i) on species degree (number of links per species); (ii) on species strength, a measure of the importance of a species to the partner's set that considers the relative frequency of the species on each partner [50]; and (iii) on the assemblage of interacting partners of the species (ecological similarity) [13]. Phylogenetic signal is assessed separately for epiphytes and for phorophytes, and was evaluated for the regional species pool (data from the three sites) and for the assemblages at each sampled plot. Phylogenetic hypotheses were constructed using PHYLOMATIC software [51] for host species, and MESQUITE v. 2.75 [52] for epiphyte assemblages, based on Barfuss *et al.* [53] and Chew *et al.* [54].

Table 1. Model calculation of pairwise interaction weights (x_{ij}). (Letters composing the model name indicate the factors that it considers: A, abundance; B, bark texture of woody species; D, plant size (DBH); S, spatial overlap of species; W, wood density of woody species.)

models	x_{ij} calculation	variables
null	$x_{ij} = 1/IJ$	I—total number of woody species
		J—total number of epiphyte species
A	$x_{ij} = a_i a_j$	a_i—number of individuals of species i
		a_j—number of individuals of species j
B	$x_{ij} = P(\text{presence of epiphytes}_i \mid \text{bark texture}_i)$	$P(\text{presence of epiphytes}) = e^z/(1+e^z)^{\text{a,b}}$
S	$x_{ij} = s$	s—number of sites in which species i and j co-occur
W	$x_{ij} = w_i$	w_i—woody species specific gravity
AD[c], ABD	$x_{ij} = \left(\sum_{m=1}^{M_i} P(\text{presence of epiphytes}_m \mid \text{DBH}_m)(n_m)\right)(a_j)$	M—total number of individuals of species i
		$P(\text{presence of epiphytes}) = e^z/(1+e^z)^{\text{a}}$
		$n_m = 10^{0.777\log(v1)}$, expected number of epiphytes for individual m[d]; v_1—DBH category of m
AS, ADS, ABDS	x_{ij} is calculated as for A, AD and ABD, respectively, but calculated for each of the three sites separately, and summing the three weights of x_{ij} obtained for each site.	
AB, BS, ABS	The respective probability matrices are calculated as the element-wise multiplication of the probability matrices **P** of models A and B, B and S, AS and B, respectively. The resulting matrices are normalized again to obtain **P**.	
AW, BW, SW, ADW, ABW, ASW, BSW, ABSW, ABDW, ADSW, ABDSW	The respective probability matrices are calculated as the element-wise multiplication of each of the probability matrices **P** of all models above (except W), and the probability matrix of model W. The resulting matrices are normalized again to obtain **P**.	

[a] e is the Napier's constant; z is calculated from a logistic regression equation that describes the log odds of presence of epiphytes on a tree, $z = \ln(\text{odds}(\text{presence of epiphyes}))$, in which bark category and DBH are the explaining variables. $z = b_0 + b_1 v_1 + b_2 v_2$, where b_0 is the intercept, v_1 is the DBH category of the tree, v_2 is the bark category of the species to which the tree belongs, and b_1 and b_2 are the regression coefficients (see the electronic supplementary material, appendix S2).

[b] In this model v_1 is held constant to five, the minimum DBH category size of the individuals considered.

[c] In this model v_2 is held constant to the intermediate category (two), the bark category to which most tree species belong (see the electronic supplementary material, appendix S1).

[d] n_m is the back-transformation of the log (expected number of epiphytes on a woody individual), calculated from the regression equation that describes the linear relation between log(DBH of phorophytes) and log(epiphyte abundance) (see the electronic supplementary material, appendix S2).

We transformed all branch lengths to 1, because branch length information is absent for the *Tillandsia* phylogeny. The amount of phylogenetic signal for (i) and (ii) was evaluated calculating the *K*-statistic [55], and for (iii) with Mantel tests comparing phylogenetic distance matrices with ecological distance matrices. Analyses were performed over 100 fully resolved trees. See full details in the electronic supplementary material, appendix S2.

3. Results

We recorded 363 woody individuals, of which 221 (DBH greater than or equal 5 cm) were included in the network analyses, belonging to 50 species and 20 plant families. The network included 1304 bromeliads recorded on 142 phorophytes (64% of woody individuals). We registered 151 links between 12 *Tillandsia* spp. and 36 (72%) woody species (figure 1). Five of these *Tillandsia* spp. are endemic to Mexico (see the electronic supplementary material, appendix S1). The observed network showed low levels of specialization, with $H_2' = 0.24$, connectance of 0.35, and a significantly nested structure ($N = 90.5$, mean for null matrices $= 62.21$, $p < 0.001$; NODF $= 62.89$, mean for null matrices $= 44.75$, $p < 0.01$). Epiphyte species interact on average with 8.8 phorophyte species (generality), and phorophyte species interact with 4.9 epiphyte species (vulnerability). Interaction evenness is high (0.82), indicating no dominance of few interactions. The average strength of interactions between epiphytes and their partners is close to symmetry (mean asymmetry for epiphytes is very low $= -0.023$), whereas phorophytes tend to experience stronger effects from their interaction partners (-0.389).

In the likelihood analysis all the models tested had a better performance than the null matrix, and partially explained the observed patterns of pairwise interactions (figure 2). The full model (ABDSW, figure 1) was the best performing model, with $\Delta\text{AIC} = 1171.41$, which is 73.14 units away from the second lowest ΔAIC model (figure 2). Thus, the likelihood that the observed data are explained by model ABDSW is higher than for all other models. Abundance contributed the most to explain the observed patterns (figure 2, compare performance of models including one factor). The model that considers abundance and spatial overlap of woody species and epiphytes (i.e. local presence and abundance, model AS) is the model of two factors that better fits the observed data. Size of woody individuals is

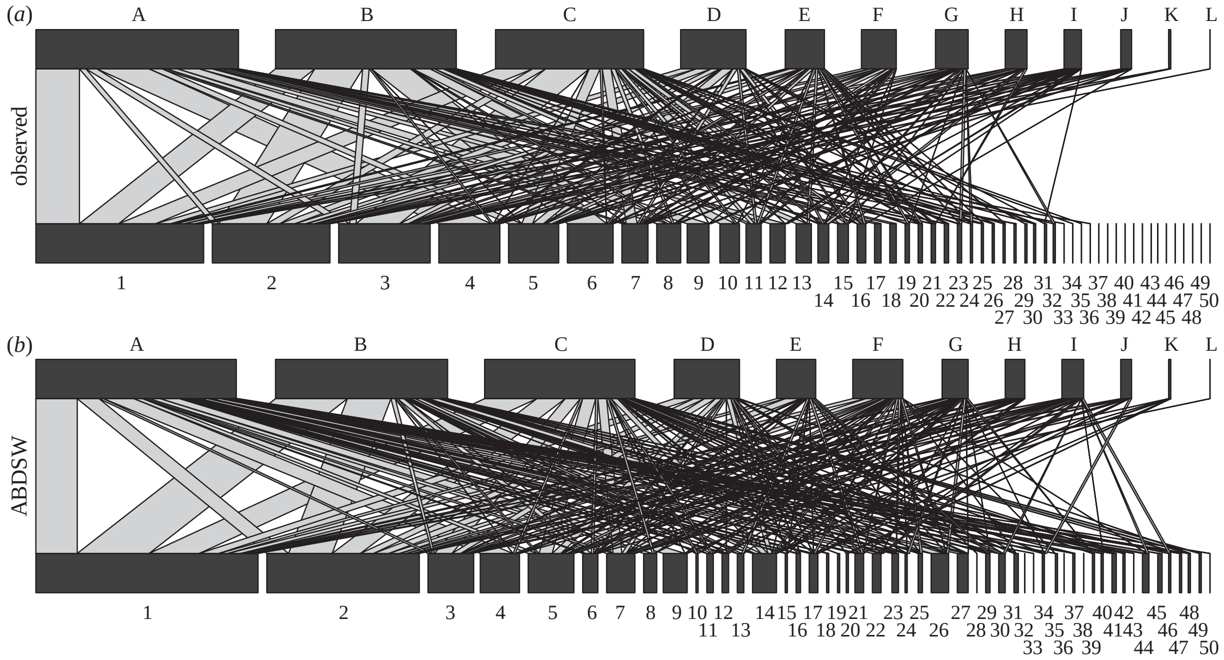

Figure 1. (*a*) The bromeliad–phorophyte network and (*b*) the network yielded by one run of the best performing model of network determinants, ABDSW. Widths of rectangles represent the relative interaction frequencies of bromeliad (*a*) and phorophyte (*b*) species. Links among species and their relative frequency are represented by the lines connecting the rectangles and their width, respectively. Networks are drawn to the same scale. Species order and code is the same at both networks. Species identity is shown in the electronic supplementary material, appendix S1.

the third factor in importance for explaining interactions between epiphytes and phorophytes, being ADS the model of three factors with lowest ΔAIC. Finally, wood density followed by bark texture contributed the least to explain the observed data (see figure 2 dark bars).

The models jointly including abundance, size of woody individuals and spatial overlap in general performed well for predicting network indices (figure 3 and electronic supplementary material, figure S1). In particular, connectance, interaction evenness, nestedness (NODF) and phorophyte interaction strength asymmetry were predicted by these models (figure 3 and electronic supplementary material, figure S1). Epiphyte interaction strength asymmetry was predicted or extremely close to the lower CI of models that incorporate abundance (figure 3). Similarly, nestedness (N) was predicted by models that incorporate abundance, and by model S (see the electronic supplementary material, figure S1).

No probability matrix predicted the values observed for indexes related to specialization; model matrices were more generalized. Epiphyte and phorophyte species interact with less species than predicted by any model (generality and vulnerability, electronic supplementary material, figure S1). Abundance, and to a lesser extent spatial overlap, contribute to explain vulnerability, being the models that include these factors the closest to the observed value, while all factors contribute to explain generality. The observed H_2' specialization is higher than predicted by any probability matrix. Incorporating information on the spatial heterogeneity of species abundance (models including AS) leads to higher values, yet lower than the observed (figure 3). The number of phorophyte species was overestimated by all models (see the electronic supplementary material, figure S1); ABDW (CI = 43–49) and ABDSW (CI = 44–49) yielded the matrices with the lowest number of phorophytes, yet more than the 36 observed.

The frequency of most links fell within the 95% CI of the frequencies predicted by the best performing models, i.e. models including ADS (mean = 92.4% of the links; electronic supplementary material, table S1 and figure S2). When links fell outside the 95% CI, more often, observed links were stronger than predicted by these models (see the electronic supplementary material, table S1). An improvement in the performance of the models can be observed, as the frequency of a larger number of interactions get closer to the line of best fit between mean values of a model and observed frequencies, and to the observed network (see the electronic supplementary material, figures S3 and S2, respectively). Finally, no significant phylogenetic signal was detected for the traits considered (*K*-statistic range for species degree and strength: 0.32–0.86; *p*-values $\geq$ 0.14 for the *z*-statistic for ecological similarity; electronic supplementary material, table S2 and figure S4).

4. Discussion

We found that individual traits (woody individual's size) and species traits (bark texture and wood density), and the abundance and spatial overlap of species contributed differentially to predict network metrics and the frequency of pairwise interactions in epiphytic bromeliads—woody species commensalisms in a tropical dry forest. Consistent with the finding that these ecological factors largely determine species–species interactions, and with the low specialization of epiphytes on host species, we did not detect a phylogenetic signal in the network, i.e. specialization, species strength and interaction partners are not conserved, neither in the phylogeny of epiphytes nor in the phylogeny of phorophytes.

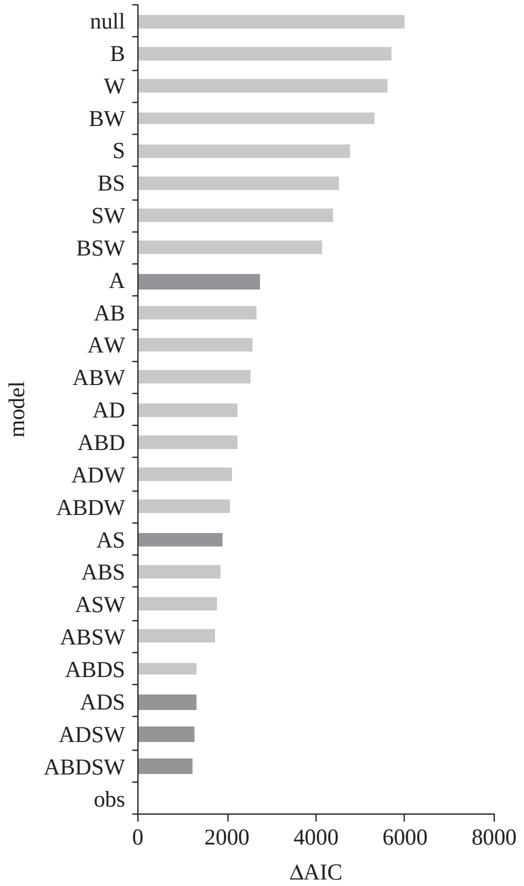

Figure 2. ΔAIC values for models of determinants of network structure that incorporate data on: A, species abundance; B, bark texture of woody species; D, plant size (DBH); S, spatial overlap; W, wood density and their combinations. obs, observed data; null, null model. The dark grey bars indicate the best performing models of one, two, three, four and five factors.

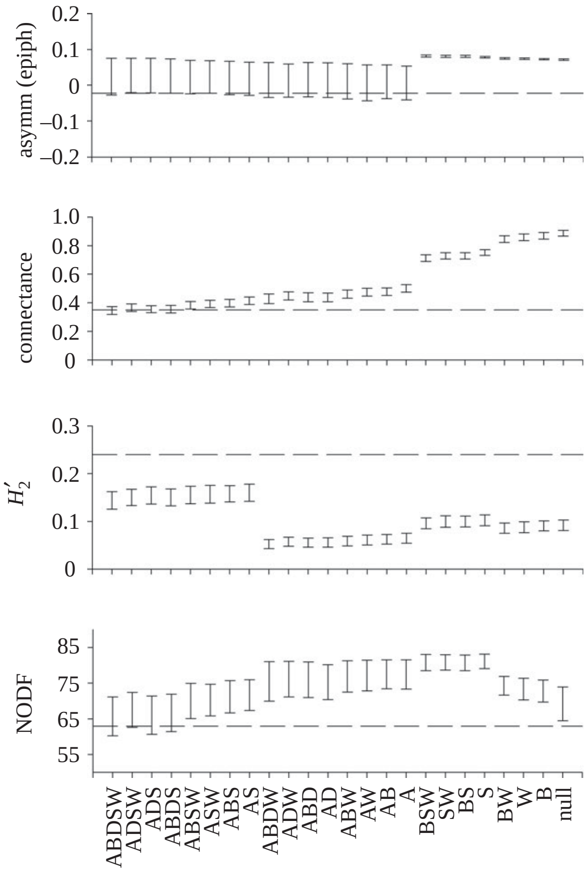

Figure 3. Network statistics for the observed epiphyte–phorophyte network and for networks yielded by models of determinants of network structure. Model names as in figure 2. The dashed line indicates the observed value. Interaction strength asymmetry of epiphytes, connectance, H_2' specialization and nestedness (NODF) are shown. Other statistics are reported in the electronic supplementary material, figure S1.

(a) Network structure

Our results are consistent with previous work which suggests that neutrality contributes to network structure [8,15,25]. Neutrality only partly accounted for the observed patterns (see performance of model A). Species abundance explains network patterns when neutrality determines the establishment of interactions, but this is a component of the community structure, which is influenced in a complex way by many biological factors (see causal model of Vazquez *et al.* [21]), among them, the spatial and temporal distribution of species. Once considering the constraints posed by the local spatial and temporal distribution of species (models including ADS, figure 3, and electronic supplementary material, figure S1), neutrality explained to a large extent network patterns. That is, network assembly, involving abundance, spatial overlap and phorophyte size (proxy for time of exposure to epiphyte seed rain) implies that networks are gradually built up by random encounters of individuals (regardless of the species to which they belong) concurring in space and time. However, it is clear that other biological factors also affect the establishment of interactions, including bark texture and wood density of hosts. The network specialization is comparable to ant-nectar plant ('low intimacy') and seed dispersal networks [56]. Ecological differences among epiphyte species may lead to differentiation in host use, e.g. if species differ in their susceptibility to nutrient, light or humidity levels and if substrate suitability varies among phorophyte species.

Clumped spatial distributions of woody species in tropical dry forests [57], and epiphyte communities (e.g. orchids and ferns [22]) may account for the unexplained network structure. Anemochory of *Tillandsia* can limit their dispersal kernel to a few metres resulting in spatial aggregation [28]. Asexual reproduction contributes for aggregated patterns when ramets detach and establish in the same or a neighbour host. Our models partly account for a clumped distribution: first, models that consider spatial overlap and abundance take into account differences in epiphyte abundances among plots. Second, when *Tillandsia* reproduces sexually or asexually, the probability of some progeny being established on the same host is large, influencing the epiphyte abundance–host size relation considered in the models (table 1).

Using a spatially explicit model, Morales & Vázquez [58] simulated the assembly of plant–frugivore networks using scenarios with varying levels of spatial autocorrelation of tree species and distances of bird foraging movements. Spatial structure and limited mobility affected the 'degree of mixing' in the system, imposing constraints to encounter probabilities [58]. A similar scenario could be found in our system with limited seed dispersal of *Tillandsia* and aggregated woody species. In Morales & Vázquez [58], a scenario analogous to our system (limited animal mobility and random individual tree spatial distribution), they show that with increasing spatial autocorrelation of tree identity, nestedness (N) varies slightly, connectance and evenness decrease, strength asymmetry increases, and unexpected presences/absences of interactions occur. Our findings agree with their results (figure 3 compare model A against AS, ADS and observed values which putatively increase in spatial structure), and the lower number of links, the many stronger interactions (see the electronic supplementary material, table S1, links above upper CI) and the absence of interactions in some woody species are evident in figure S2 (see the electronic supplementary material). This suggests that spatial processes contributed to structure the network.

We did not find evidence of a phylogenetic signal in the network structural patterns analysed, and the results were consistent across sites. A phylogenetic signal is not uncommon in mutualistic and antagonistic interactions [13,14,59]. Similar to our findings, the commensalistic networks between orchid epiphytes and their host trees do not show a phylogenetic signal [26]. The lack of phylogenetic signal could be related to the small size of the phylogenies [55]. Conversely, a phylogenetic signal may be present in other ways (e.g. in species roles [60], within or among compartments [61], within clades [59]). Evolutionary history may influence network structure at other scales and analysing a phylogenetically more diverse epiphyte community or a larger network might lead to the detection of a phylogenetic signal. Additionally, if traits important for species associations are phylogenetically conserved, then phylogeny will indirectly influence network structure [62,63]. Abundance does not show a phylogenetic signal in the epiphyte or phorophyte assemblage (see the electronic supplementary material, table S2 and figure S4). Wood density is highly conserved across the entire seed plant phylogeny [64]. Here our results showed a weak signal, and the contribution of wood density on the network structure is low.

(b) Pairwise interactions

Our results are consistent with previous epiphyte community reports that have found stronger observed interactions when compared with results from null models that consider phorophyte abundance [32,36]. When accounting for the effect of other factors, a higher percentage of the interactions is explained (see the electronic supplementary material, table S1; model ABDSW versus A). Nevertheless, several observed interactions remain stronger (more frequent) than expected by the full model. This is consistent with a higher observed than model yielded network specialization (H_2'). In our dataset, the most extreme case was that of *Caesalpinia sclerocarpa*, the only species in which all 12 *Tillandsia* species were registered. This is a timber species with dense wood (see the electronic supplementary material, appendix S1) and, therefore, more stable branches. A slower growth rate expected from dense wood also implies that size in this species represents older individuals than in other species. Despite considering all factors (ABDSW), five out of the 12 interactions were stronger than predicted. *Caesalpinia sclerocarpa*'s architecture, with ramifications high on the trunk and fairly horizontal branches may favour the establishment of epiphytes. Species with dense wood are capable of growing taller [65], and this is one of the tallest species in the forest; *Tillandsia* are light demanding [66] and may be more successful high in the canopy. By contrast, the most abundant woody species, *Apoplanesia paniculata*, interacted with 10 *Tillandsia* spp., but was found interacting less frequently than expected by its abundance, bark texture, wood density, spatial overlap and tree sizes, with two *Tillandsia* species.

Despite several weaker links than predicted by ABDSW (11 cases, electronic supplementary material, table S1), we found little evidence for axenic species (free of epiphytes). From the 14 species recorded with no epiphytes, only *Guazuma ulmifolia* and *Jacquinia pungens* were expected to interact with the most abundant epiphyte, *T. usneoides*. Overall, epiphytes tended to be absent or were less frequent on woody individuals that were young, on woody species with low abundance, present at a single site, and with smooth bark and/or soft wood. In the same way, less abundant epiphyte species tended to be hosted by a lower number of woody species.

(c) Conservation implications

Understanding community assembly will contribute to the conservation of interactions. Consequences of network structure for commensalistic interactions might be different than for other interactions where coevolution is involved. As other epiphyte–phorophyte networks [3,5,25], the bromeliad–phorophyte network showed high values of nestedness (N and NODF), higher than other types of interactions [5]. Several processes may lead to a nested pattern [63,67,68]. The specialization asymmetry implied in nestedness, suggested to arise through a coevolutionary process in other systems, with implications for extinction risk [4,63,69,70], seems to be here a consequence of the abundance and temporal and spatial distribution of species of a mostly generalized system. The one-way specialization of these bromeliads on an epiphytic life form but with low host specificity shows that many species can be adequate hosts, which in regard to host availability makes them less vulnerable to disturbance. However, hosts with suitable traits will give epiphytes higher probabilities of survival, with important implications for the conservation and management of this group.

Our analysis highlights the importance of time for the establishment of epiphyte communities. It takes at least one decade to the first reproduction of bromeliads [22,37], and the recruitment of species with different reproductive strategies (monocarpic versus polycarpic) may be affected differentially by disturbances. Epiphytes provide important resources for many taxa [22] and their disappearance will cascade through the ecosystem. *Tillandsia* is the richest genus of the Bromeliaceae, and Mexico is a centre of diversification for this genus, where 43 per cent of its species, most of which are endemic [37,71], occur. Our study contributes to understanding the processes that assemble ecological interaction networks in general and commensalistic networks in particular. Vascular epiphytes are the most vulnerable plant life form, and this study highlights ecological factors that shape their communities.

We are grateful to Andy Hector and two anonymous referees for their comments on the manuscript. We thank the Centro de Investigaciones en Ecosistemas and the Estación de Biología Chamela of the Universidad Nacional Autónoma de México (UNAM) for logistic support. Financial support was provided by grants to M.Q. from CONACyT-Mexico (grants nos. 2002-C01–0597, CB-2005-51043, 2009-C01-131008 and 2010-155016), Programa de Apoyo a

Proyectos de Investigación e Innovación Tecnológica (PAPIIT IN201011) and the *Inter-American Institute for Global Change Research* (IAI) Project CRN2-21. This paper constitutes a partial fulfilment of the Graduate Programme in Biological Sciences of UNAM. R.S. acknowledges the scholarship and financial support provided by CONACyT, and Posgrado en Ciencias Biológicas UNAM. CONACyT and UNAM financed M.L.'s postdoctoral position. M. Gargollo allowed us to work on her property. Technical assistance was provided by E. Castro, H. Ferreira, G. Sánchez-Montoya and A. Valencia-García.

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CAPÍTULO TRES

Fragility of epiphyte-phorophyte networks in a successional gradient of tropical dry forest

Running title: Epiphyte-phorophyte networks along succession.

Abstract

Vascular epiphytes comprise one of the plant groups most vulnerable to disturbance due to their life history traits. Here, using a network approach, we evaluate the recovery of the epiphytic community of Bromeliaceae along a secondary successional gradient of tropical dry forest in western Mexico. We further model the response of epiphytes to the intensity and frequency of different scenarios of disturbance, including selective logging by removing individual trees according to their size, and tree species according to their abundance. Epiphyte and phorophyte abundance per unit area are significantly lower at early and intermediate compared to the late stages of succession. In networks, epiphyte species richness is similar along the successional gradient, but phorophyte species number and interaction strength are negatively affected, resulting in a higher web asymmetry, and lower number of phorophyte species per epiphyte species and nestedness. Differences in network structure were not explained by differences in the number of woody species or individuals (potential phorophytes) available at sites. Simulations of tree removal show higher impact for removal scenarios of large trees and abundant species than random removals, and lower network robustness of recovering communities compared to mature forests. This result indicates that short cycles of forest exploitation will lead to the local extinction of epiphyte species. Our study highlights the importance of management practices that consider this life form and shows that tropical dry forests do not recover floristically in few years after disturbance. Epiphyte communities may be endangered worldwide, as even an epiphytic group regarded as resilient to disturbance is highly impacted.

Key words: Bromeliaceae, Chamela-Cuixmala Biosphere Reserve, commensalism, ecological networks, frequency of disturbance, *Tillandsia*, vascular epiphytes, Mexico.

INTRODUCTION

Human disturbances, and in particular habitat conversion and fragmentation negatively affect plant community structure and composition, and have resulted in the reduction of populations and extinction of plant species (Fahrig 2003). Most work in this topic is biased towards the study of trees, shrubs and herbs (Aguilar et al. 2006). In comparison, owing to methodological difficulties, the epiphytic life form has received much less attention (Zotz and Bader 2009). Epiphytes are plants that grow on other plants without parasitizing them, establishing a commensalistic relation with their host woody plants. Vascular epiphytes (hereafter "epiphytes") are an important component of the canopy of forests, representing 10% of the diversity of vascular living plants (Kress 1986). Tropical forests (Nieder et al. 2001) hold the highest species richness of epiphytes in the world (Freiberg and Freiberg 2000, Kreft et al. 2004); this growth form can contribute to up to 28-55% of the vascular plant species and ~50% of the individuals on a local scale (Gentry and Dodson 1987, Kelly et al. 1994, Martin et al. 2004). This pattern is partly attributed to the high epiphytic Orchidaceae species richness, and is exacerbated in neotropical forests by Bromeliaceae, a plant family endemic to America with a large proportion of epiphytic species (Benzing 1990). Epiphytes are an important part of a web of interactions in ecosystems, supporting other taxa by providing resources such as water, microhabitat and nectar (Benzing 1990).

Epiphytes are considered the most extinction-prone plant growth form (Benzing 1990, Turner et al. 1994, Martin et al. 2004, Padmawathe et al. 2004, Sodhi et al. 2008, Leao et al. 2014). Their dependence on adequate hosts, long life cycles and microclimatic requirements make them particularly vulnerable to habitat disturbance. Epiphytes are negatively affected by fragmentation and land use change, showing lower species richness, abundance and altered community composition on isolated remnant trees, disturbed forests, and plots under secondary succession (Turner et al. 1994, Barthlott et al. 2001, Borgo and Silva 2003, Flores Palacios and Garcia Franco 2004, Martin et al. 2004, Padmawathe et al. 2004, Benavides et al. 2006, Bonnet and Queiroz 2006, Cascante-Marin et al. 2006, Siqueira-Filho and Taberelli 2006). Frequent disturbances highly impact plant communities. Despite the impact of the frequency of disturbances in the ecology and conservation of communities, and its crucial role in natural resources management (Mackey and Currie 2001, Yeboah and Chen 2015), there has never been an attempt to evaluate its impact on epiphyte communities.

Some groups of epiphytes show higher vulnerability than others (Cogliatti-Carvalho and Rocha 2001, Bonnet and Queiroz 2006, Benavides et al. 2006). For example, Orchidaceae is highly affected by disturbance (Turner et al. 1994, Flores-Palacios and Garcia-Franco 2004, Martin et al. 2004), while Bromeliaceae is considered more resilient, with some species even increasing their abundances under disturbance (Barthlott et al. 2001, Flores Palacios and Garcia Franco 2004, Martin et al. 2004, Werner and Gradstein 2009). Bromeliaceae lower vulnerability to disturbance has been attributed to the ability of *Tillandsia*, the most species rich genus of the family (Benzing 2000), to survive following microclimatic changes associated to anthropogenic disturbances (Barthlott et al. 2001, Flores-Palacios and García-Franco 2004), such as an increase in wind incidence and sun radiation, and a decrease in relative humidity and rain interception (Fahrig 2003). *Tillandsia* spp. have been reported as drought tolerant, heliophilous and with CAM photosynthesis (Barthlott et al. 2001, Flores-Palacios and Garcia-Franco 2004, Reyes-Garcia et al. 2008); however, *Tillandsia* possesses traits that can, in the long term, make it susceptible to disturbance. *Tillandsia* spp. are very slow growing, having long life cycles with a first reproductive event estimated in 15 to 30 years. Some species are self-incompatible or monocarpic (semelparous, with a single reproductive event in life), and most species show specialized hummingbird pollination. All species are anemochorous, but limited evidence suggests that their dispersal is limited to a few meters (Bernal et al. 2005, Mondragón and Calvo-Irabien 2006, Cascante-Marin et al. 2009), and that they have extremely low recruitment (Benzing 1978, 1990, Mondragón et al. 1999).

Epiphytes form complex networks of interactions with their host plants. Woody species responses to disturbance are expected to largely influence epiphyte community recovery. Interaction networks are a tool to assess community structure and the response of communities to disturbance (Memmott 2009), and allow modeling different disturbance scenarios and testing the fragility of complex networks (Solé and Montoya 2001, Dunne et al. 2002, Memmott et al. 2004). Network studies of epiphyte communities report the highest nestedness levels among ecological networks (Burns 2007, Burns and Zotz 2010, Sayago et al. 2013, but see Silva et al. 2010), a structure that implies specialization asymmetry of interactions (Bascompte et al. 2003) and is related to network stability (e.g. Piazzon et al. 2011, Rohr et al. 2014). On the other hand, epiphyte network assembly is highly influenced by host size (Sáyago et al. 2013), suggesting that epiphyte community recovery may be slow and that mature forests are crucial for epiphyte community conservation. A study comparing epiphyte-tree networks between disturbed vs. old-growth forest found an association between nestedness and robustness, though it did not find topological or robustness differences between these forest conditions (Piazzon et al. 2011). Species loss may trigger secondary extinctions due to the loss of interactions. The proportional loss of species following primary extinctions has been used to measure and compare network robustness (*e.g.* Dunne et al. 2002, Memmott et al. 2004); however, when comparing sites within the same system, absolute loss should be a better indicator of robustness because community diversity and structure can be taken into account, particularly if considering a reference community. In such a case, relative robustness might result in misleading conclusions.

Here we study Bromeliaceae-host plant networks along a successional gradient of a tropical dry forest in the Pacific Coast of Mexico. Our objectives are a) to assess epiphyte community recovery after cattle and agriculture land use using a chronosequence in a successional gradient of tropical dry forest, b) to assess whether differences in epiphyte-phorophyte network structure along the successional gradient can be explained by differences in woody species richness and abundance, c) to model different scenarios of forest exploitation and deforestation and assess absolute and relative robustness of networks to them d) to model the effects of frequency of disturbance on the epiphyte community. We hypothesize that network structure differs along succession, with a higher nestedness and robustness at primary forests, and that frequent disturbances drastically affect epiphyte communities. While tree forest structure and composition has been studied in Tropical Dry Forests under succession after land use change to cattle or agriculture, epiphyte succession ecology is unstudied in this ecosystem (reviewed in Quesada et al. 2009). Bromeliaceae constitute the most important family of epiphytes in these forests (Lott 2002), and *Tillandsia* is the most important genus.

METHODS.

Study area

The study was conducted in a successional gradient of tropical dry forest at the Chamela-Cuixmala Biosphere Reserve (19°22´-19°35´N, 104°56´-105°03´W) and its vicinity, in the Pacific coast of Jalisco, Mexico. Rainfall is very seasonal, occurring between July and October (García-Oliva et al. 2002). In the tropical dry forest of the region there are 421 woody species (potential phorophytes) and 32 vascular epiphyte species reported (Lott 2002). Epiphytes belong to Cactaceae (1 sp.), Orchidaceae (10 spp.) and Bromeliaceae (21 spp. with 18 spp. in Tillandsioideae: *Tillandsia* spp. and *Catopsis nutans*). In this study we focused on the Bromeliaceae, a monophyletic family of the monocots with opposite and xeric leaves.

We used three categories in a successional gradient, according to the time elapsed since agriculture and cattle activities ceased at selected sites: a) Late successional stage sites (mature forest sites), where anthropogenic disturbances ceased at least 50 years prior to the study; b) intermediate successional stage sites, abandoned 11 to 15 years prior to the study; c) early successional stage sites, where human activities ceased six to eight years prior to the study. Three sites were selected for each category, and a 20 x 50 m plot was traced at each. Each plot was divided in ten 10 x 10 m sub-plots. For further details on site location and selection criteria see Avila-Cabadilla et al. (2009). At all, the nine sites, we sampled epiphyte-phorophyte interactions in four randomly selected 10 x 10 m sub-plots.

Field data

We marked all woody plants in the plots with a diameter at 1.3 m above ground (trees and shrubs) or at the base (lianas) greater than 5 cm (DBH henceforth) with an aluminum tag. We obtained the DBH and species identity of each woody individual. Leaf and reproductive samples were collected for each woody species and identification was corroborated with herbarium specimens preserved at the Chamela Biological Station (Universidad Nacional Autónoma de Mexico). Henceforth, when we refer to trees for simplicity, we refer to all woody plants marked at the plots, including lianas and shrubs.

We registered all interactions between bromeliad epiphytes and woody individuals during the dry season of 2007/2008 (from November to May) when the canopy is leafless and epiphytes are easily observed. At each woody individual, we searched for epiphytes with binoculars from the ground and registered all epiphyte individuals larger than 3cm in height, which can be confidently seen and identified to species level. Ramets (clones) of two *Tillandsia* species have the potential to detach and disperse (secondary dispersal by asexual means, *Tillandsia intermedia*, R. Sayago 2007, personal observation; *Tillandsia usneoides*, Benzing 2000). We defined an individual as an epiphyte physically separated from other epiphytes. We refer to phorophytes when woody individuals are bearing epiphytes.

Epiphyte-phorophyte community and network structure along the successional gradient

We compared the epiphyte-phorophyte communities among successional stages analyzing the following response variables at each of the 10 x 10 m sub-plots: woody and epiphyte number of species (species density), mean number of epiphyte species per phorophyte individual, epiphyte abundance, number of phorophytes and number of woody individuals. We used generalized linear models using proc GLIMMIX in SAS (SAS Institute 2008), with successional stage (early, intermediate, late) as fixed effect and site (1-3) nested within successional stage as random effect. For epiphyte abundance, a poisson distribution was specified (with a log function). The remaining variables did not require transformation. We analyzed differences in epiphyte community composition among stages using the information on the abundance of each epiphyte species at each site with non-metric multidimensional scaling (NMDS), based on a Bray-Curtis distance dissimilarity matrix. We used the function "metaMDS" of the vegan package of R (Oksanen et al. 2013, R Core Team 2015).

We constructed a quantitative epiphyte–phorophyte interaction network matrix for each site, with woody species as rows and epiphyte species as columns, and cells containing information on species interactions. Interactions were weighted by the number of bromeliad individuals that occur on each woody species (i.e. for each epiphyte species, epiphytes registered were summed across the woody individuals hosting them that belong to the same species). For some analyses, we constructed one network matrix for each successional stage pooling the datasets of the three sites of each successional stage.

To compare network structure among successional stages, for each network we calculated the following indices that describe several aspects of network structure (Dormann et al. 2009): a) connectance, the proportion of links that occur from the total possible (C= number of links/number of phorophyte species x number of epiphyte species); b) nestedness, the tendency of specialized species to interact with a subset of the interaction partners of more generalized species, using nestedness based on overlap and decreasing fill

(NODF, Almeida-Neto et al. 2008), that ranges from 0 to 100 with increasing nestedness; we computed and compared the *Z*-score (Ulrich et al. 2009) that quantifies the position of the observed metric within a simulated distribution from a null model (n=1000) in common units of standard deviation; c) web asymmetry, the balance between the number of epiphyte and phorophyte species (Blüthgen et al. 2007), with negative values indicating more phorophyte than epiphyte species; d) interaction evenness, the heterogeneity of the interaction frequencies in the network (Tylianakis et al. 2007); ranges with increasing evenness from 0 to 1; e) generality and vulnerability, the weighted mean number of phorophyte species per epiphyte species, and epiphyte species per phorophyte species, respectively (Bersier et al. 2002); f) network specialization H_2*'* (Blüthgen et al. 2006), that ranges from 0 to 1 with increasing specialization; g) specialization asymmetry, the difference in specialization between epiphyte and phorophyte species (calculated as proposed by Blüthgen et al. 2007), with positive values indicating epiphytes are more specialized than phorophytes. a), b) and c) are based on unweighted links (binary matrices), while the remaining are based on weighted links (considering frequencies of interaction). NODF and its *Z*-score were calculated using the functions oecosimu and nedtednodf (binary null model r1 that maintains row frequencies and uses column marginal frequencies as probabilities to fill presences, 1000 simulations) of the Vegan package of R (Oksanen et al. 2013). The other indices were calculated using the function networklevel of the Bipartite package of R (Dormann 2008, R Core Team 2015). The selected method for specialization asymmetry was “Bluethgen”, and for interaction evenness, “sum”).

To investigate differences in network structure among sites, we compared the network indices among successional stages with a general linear model using site as fixed factor, transforming data when needed (see Table 3.1) to meet the assumptions of the test.

We additionally compared network size, interaction strength, number of epiphyte and phorophyte species, and number of links among successional stages. To examine correlations among the indices, we also performed a Principal Component Analysis (PCA) using the "princomp" function of the stats package or R using a correlation matrix for the calculation.

We further assessed whether differences among networks can be directly explained by differences among successional stages in the number, abundance or biomass of woody species. For this, we compared structure between observed networks and networks resulting from randomly removing woody species or individuals from the mature forest dataset until the number of woody species, the number of woody individuals or the woody individual biomass recorded at the early and intermediate successional stages was reached. We randomly removed woody species when equaling number of species, and woody individuals when equaling number of individuals or biomass. We used the woody individuals' DBH as a proxy for biomass, and removed individuals until the target DBH summed across all remaining individuals was reached. In the intermediate stage *vs.* late stage comparison of woody species, the intermediate stage had more species (four species) than the mature forest; thus, we performed removals on the late stage dataset. For all other comparisons, the mature forest dataset had higher values. Removals (n=100 sequences) were carried out over the pooled datasets for a successional stage, considering all woody species and individuals at the plots (i.e. phorophytes and non-phorophytes). We built networks with the phorophytes and epiphytes that remained after removals (i.e. matrices contained only interacting species), and we computed the network indices for 100 generated networks. We assessed whether the observed network indices fall within the

95% confidence intervals of the distribution of network indices values resulting from the generated networks.

Simulation of disturbance scenarios on epiphyte communities

To assess epiphyte community robustness to species loss in terms of the secondary extinctions that follow primary extinctions (Dunne et al. 2002) under different disturbance scenarios and frequencies of forest exploitation, we first look at how an undisturbed epiphyte community responds to different scenarios of deforestation or forest exploitation using the mature forest network. We then compare the results to those of the same scenarios on early and intermediate successional stages to comparatively assess how the recovering epiphyte communities respond to deforestation. We performed network extinction simulation analyses (e.g. Memmott et al. 2004), removing woody species from the networks, simulating local "primary extinctions", and documenting the resulting "secondary extinctions" of epiphytes, i.e. the epiphyte species that become disconnected from the network following a primary extinction. In addition, we considered removal sequences of woody individuals for which we constructed network matrices with woody individuals as rows and epiphyte species as columns, each cell containing the number of epiphytes registered at each individual tree. Because we are looking at forest use and deforestation scenarios, at both removal levels we included phorophytes and non-phorophytes in the matrices from which removals were performed. The pooled datasets of the three sampled sites for the successional stages (i.e. one network per stage) were used.

We simulated different scenarios of forest exploitation and deforestation. In logging scenarios, it is likely that abundant species are more utilized, and that selected individuals are large, and both variables have been identified as important traits explaining network structure (Sáyago et al. 2013). In addition, considering species degree (number of links of a species) in removal sequences largely influences network robustness (Dunne et al. 2002) and this information can potentially benefit epiphyte communities if contemplated in forest management practices. Thus, we considered these traits in our removal scenarios.

For both levels of removal (individual and species) we simulated the following disturbance scenarios, performing one by one removal sequences: *a) random removal*: this represents the null model of removal; *b) selective logging*: we removed woody species according to their abundance at the sites from most to least and least to most abundant. We removed woody individuals according to their size, from largest to smallest and smallest to largest DBH; c*) number of links:* we removed from most to least and from least to most connected individuals and species; these scenarios are expected to result in the highest and lowest loss of epiphyte species and individuals (Solé and Montoya 2001, Dunne et al. 2002, Memmott et al. 2004, Kaiser-Bunbury et al. 2010). We use (a) and (c) as benchmarks with which to compare the impact of selective logging (b). At each step we registered the impact of a removal on network robustness as 1) epiphyte species richness (number of remaining species) and 2) network interaction strength (remaining epiphyte individuals, Kaiser-Bunbury et al. 2010). For (a) we calculated mean and 95% confidence intervals (n=1000 simulations) of both variables at each step.

Our standardized sampling design allows to compare absolute robustness among successional stages that reflect the real differences in epiphyte species richness and interaction strength among networks, which is the goal of the comparisons across the successional gradient. Relative robustness allows comparing results within a successional stage between response variables (species richness and interaction strength). Therefore, we compare results in relative terms (i.e. proportion of removals *vs.* proportion of remaining *Tillandsia* spp. or individuals), and in absolute terms (i.e. number of removals *vs.* remaining number of *Tillandsia* spp. or individuals). We used the area under the curve as a measure of robustness (Burgos et al. 2007). We used the function “robustness” of the bipartite package of R to calculate relative robustness and modified it to calculate absolute robustness.

RESULTS.

Overall, in the successional gradient of tropical dry forest we recorded 544 woody individuals with DBH > 5cm, belonging to 98 species of 65 genera and 29 families. We registered 195 different links between 1449 individuals of 13 bromeliad species belonging all to *Tillandsia* and 187 phorophytes belonging to 49 woody species of 35 genera and 17 families. We registered six Tillandsia species endemic to Mexico (Appendix SM-1).

Epiphyte-phorophyte community and network structure along the successional gradient

Epiphyte and woody species density did not significantly differ along the successional gradient. However, the density of woody, phorophyte and epiphyte individuals and epiphyte species richness per individual phorophyte were lower at the early than late successional stage, also differed between intermediate and late successional stages (Table 3.1). This resulted in a lower number of phorophyte species and total interaction strength at networks from the early and intermediate successional stages compared to networks from the late successional stage, although the total number of *Tillandsia* species and network size did not significantly differ among networks along the successional gradient (Table 3.1). The number of links tended to be higher at the late successional stage (Table 3.1).

Two sites of the early successional stage had only one phorophyte with one and two bromeliad individuals, which precluded their inclusion in further analyses. Therefore, we compared network indices and epiphyte community composition between successional sites (1 early, 3 intermediate, n=4) and mature forest sites (n=3). The NMDS of epiphyte community composition (stress = 0.08) shows differences in species composition among sites and separates the intermediate successional sites from the mature forest and the early successional site along axis 1, while axis 2 separates the early site from the intermediate and late successional sites (Figure 3.1A). *Tillandsia eistetteri, Tillandsia usneoides, Tillandsia scheriana* and *Tillandsia makoyana*, the most abundant species, were almost exclusively found at late successional sites; the presence and abundance of other *Tillandsia* spp. varies among sites (Figure 3.1A).

Several network indices tended to differ between successional sites and mature forest. Component 1 of PCA (Figure 3.1B) separates mature forest sites from successional sites (Table 3.1), and accounted for 68% of the variance, being more correlated to H_2' (0.45) and Z_{NODF} (-0.44). Web asymmetry, generality and nestedness were the indices that significantly differed between the successional sites and the mature forest sites (Table 3.1): the mature forest had more phorophyte than epiphyte species, in contrast to successional sites that tended to be more symmetrical; and the number of phorophyte species per epiphyte species and *Z-score* of NODF were significantly higher at the mature forest. Mature forest networks were significantly nested, while networks from successional sites were not (Table SM-1). Component 2 accounted for 20% of the variance and is more correlated to evenness (0.65) and connectance (-0.56), which did not differ along the successional gradient. Due to the sample size utilized (7 sites), only 7 indices could be included in the PCA and the PCA presented excludes vulnerability. Nevertheless, several indices are correlated and excluding other indices explains a similar proportion of variance (*e.g.* Figure SM-2). Interaction strength was positively correlated to generality, vulnerability and Z_{NODF}, and negatively correlated to web asymmetry (Figure SM-2, Table SM-2). Thus, underlying network structure differences among successional stages are partly explained by the effect of disturbance on interaction strength.

Network properties of the mature forest were mostly maintained after matching woody species number, woody individual number or biomass to that of the early and intermediate stage networks through the random removal of woody species and individuals (Figure 3.2 and SM-2). The number of phorophyte species, generality and specialization asymmetry tended to decrease, and web asymmetry to increase after removal, but confidence intervals did not overlap the network index values from the early and intermediate successional stages. Only H_2' from the early stage network (matching species and individuals) and specialization asymmetry from the intermediate stage network (matching individuals and DBH) fell within the 95% confidence intervals of the index values of the resulting networks after removal. Therefore, differences in network structure along the successional gradient were generally not explained by differences in woody species or individuals number, or in biomass among successional stages (Figure 3.2 and SM-2). This shows that network structure differs along succession and suggests that disassembly and assembly processes affect structure in different ways.

Simulation of disturbance scenarios on epiphyte communities

The comparison of deforestation and forest exploitation scenarios of the mature forest (Figures 3.3, 3.4A and 3.4B) shows for both response variables, epiphyte species richness and interaction strength, as expected, that systematically removing woody species or individuals according to their number of links results in the highest (when removals are from least to most connected) and lowest (when most to least connected) robustness of networks. Accordingly, selective logging scenarios had impacts close to latter removal scenarios, and the random removal scenario had mid impacts in robustness. Networks from early and intermediate successional stages showed the same general pattern for all scenarios as the late successional stage.

Frequency of disturbance strongly and negatively impacted network robustness: compared to the late successional stage, absolute robustness of remaining *Tillandsia* spp. was 44-83% lower at early and 20-70% lower at intermediate successional stages for the woody species removal scenarios (Figure 3.3A); and 55-89% lower at early and 36-88% lower at intermediate successional stages for the woody individuals removal scenarios (Figure 3.3B). The highest impact of frequency of disturbance was on interaction strength, in which for both, the woody species and the woody individuals removal scenarios, absolute robustness was 97-99% lower at early and 91-98% lower at intermediate successional stages (Figure 3.3C and 3.3D, note the log-scale). The impact of removals on interaction strength was consistently higher than on species richness (i.e. relative robustness is lower; Figure 3.3E, compare IS and SR for a scenario for the same successional stage). Notably, when comparing relative robustness among successional stages, some comparisons show opposite trends to the ones shown by absolute robustness.

DISCUSSION.

We found that the *Tillandsia* epiphyte community is highly vulnerable to anthropogenic disturbance, with a much lower abundance of epiphytes and phorophytes at successional sites compared to mature forests, and differences in community composition and network structure. A lower interaction strength and number of phorophyte species at early and intermediate successional sites impacted web asymmetry, generality and nestedness. The resulting network structure was not explained by differences in number of woody species, individuals or biomass between mature and successional forests. Logging scenarios showed that removing woody flora according to species abundance and individual's DBH causes a higher impact than the random removal of species, but the highest impact scenario was the removal of woody species and individuals according to their number of interactions (i. e. degree). Successional networks showed 20-98% lower robustness than the mature forest network, revealing the detrimental effects of frequent disturbances to the epiphyte community. Here we discuss possible processes affecting assembly and disassembly of epiphyte-phorophyte networks and the implications of our results to tropical dry forest management and conservation.

The *Tillandsia*-phorophyte networks have a low specialization level (Sáyago et al. 2013), and some *Tillandsia* spp. are even capable of growing on exotic species, rocks, and wire power lines (*e. g.* Catling and Lefkovitch 1989). However, generalization differed along the successional gradient. Rather than changes of epiphytes on this trait per se, the higher generality at the late successional stage must reflect a higher availability of woody species for establishment (resulting in higher web asymmetry) through time. Despite the similar woody species density and abundance at the intermediate stage compared to the late stage, the number of phorophyte species (and therefore web asymmetry) was lower. Species abundance and phorophyte size are among the traits that most explain network structure in mature forests (Sáyago et al. 2013), reflecting propagule and host availability, and time and microsites available for colonization. Therefore, at intermediate successional sites there may be limited microsites and propagule availability for the recovery of network structure. The lower nestedness found at the early and intermediate successional stages may imply a lower robustness to disturbance (Burgos et al. 2007), and indeed, these stages were less robust than the mature forest to extinctions. For example, *T. makoyana* was only found in mature forests and was almost absent from the early and intermendiate succesional sites.

Network assembly and disassembly

We show that *in silico* random disassembly of networks (removal of woody individuals and species) does not result in a similar network structure as the one resulting from the assembly processes operating during succession. In fact, network structure of the early and intermediate successional stages is similar to the structure resulting from the most detrimental scenarios of woody flora removal from the mature forest at the step that equals number of species or individuals (Figure SM-1). *Tillandsia* recovery has been documented at sites where anthropogenic disturbances ceased for at least for 40 years (Martin et al. 2004). The naturally slow assembly of these interactions is probably highly influenced by *Tillandsia*’s limited dispersal (Bernal et al. 2005, Mondragón and Calvo-Irabien 2006, Cascante-Marin et al. 2009), low reproductive rate (Benzing 1990) and low recruitment (Benzing 1978, 1990, Mondragón et al. 1999). However, network assembly during secondary succession must be even slower, as prior to these effects, the lack of phorophytes at the start of succession delays the network assembly process during the first years. Later on, the lower woody individual and species density of early successional sites may translate in a reduced recruitment due to a lower availability of hosts and microsites for the dispersed seeds. Once on a host, microclimatic conditions at earlier stages of succession, *e.g.* more light, temperature, less humidity (Barthlott et al. 2001), may also affect survival and recruitment (Goode and Allen 2009). These processes may greatly delay recovery and contribute to the differences in network structure among successional stages.

Dispersal distance and the number of dispersers can be the primary determinant of species persistence (Gadgil 1971, Hanski 1991). Few studies suggest that most seeds of anemochorous Bromeliaceae species are dispersed short distances, with ≤ 0.6% of the seeds dispersing up 10-15m (Bernal et al. 2005, Mondragón and Calvo-Irabien 2006, Cascante-Marin et al. 2009, Paggi et al. 2010). The lower number of phorophytes, epiphyte species richness per phorophyte, epiphyte abundance, number of links and interaction strength of networks at successional stages imply that population sizes are low. Increasing colonization distances due to large scale disturbances may result in small populations with low genetic diversity and limited gene flow, promoting inbreeding, and affecting long term viability of populations (Aguilar et al. 2008). Reproduction failure may occur due to the lack of partners in self-incompatible species (e.g. *T. intermedia*) or monocarpic species (e.g. *T. makoyana*) whose single reproductive event may not coincide with conspecifics'. In this respect, under limited pollen flow, species with asexual reproduction may avoid the negative effects of inbreeding while new individuals arrive. Large scale disturbances may already have eliminated epiphyte communities from forests where propagule sources are too distant.

Limited dispersal also contributes to the patchy and clumped distribution of epiphytes (Benzing 1981, Bennett 1986). Some woody individuals hold large numbers of *Tillandsia* species and individuals, resulting in a high vulnerability of networks to removal of the most connected woody species and individuals. However, this system differs from studied pollination networks (Kaiser-Bunbury et al. 2010) in that impact is higher on interaction strength than on species richness (Figure 3.3E), which may also be a consequence of the aggregated distribution of an epiphyte species on individual hosts.

Despite clear differences among successional stages in network structure, owing to epiphyte patchiness, we also found variation in network structure within successional sites (Figure 3.1). Part of the variation at early and intermediate successional sites is due to the presence of large remnant trees in the neighborhood that host epiphyte communities that were source of propagules to the successional sites. These trees can make large differences during network assembly; for example, two of the early sites had only one phorophyte hosting one *Tillandsia* species, while the third one had a much larger network. In the study region, certain tree species are maintained at pastures or agricultural sites for their shade, fruits or wood (*e.g. Cordia elaegnoides, Piranhea mexicana, Spondias purpurea*). Thus, remnants large old trees can play an important role for conserving *Tillandsia* richness *in situ* (Barthlott et al. 2001, Benavides et al. 2006, Köster et al. 2009).

Successional networks were less robust to disturbance (Figs. 3 A-D), already impoverished communities should suffer more from host removals. While this is evident when comparing absolute robustness, it is not so if comparing relative robustness (Fig. 3), which may explain the lack of a negative effect of disturbance on robustness reported by Piazzon et al. (2011). The fact that assembly of epiphyte-phorophyte networks is extremely slow implies that short cycles of forest exploitation will sweep away epiphyte communities from forests in a few cycles. This may already be the case in forests that appear less diverse in epiphyte communities. For example, tropical dry forest sites with a large history of human use are less diverse in epiphytes (tropical dry forests in Pacific Coast of Guerrero, personal observation). The annual rate of tropical dry forest loss in Mexico is dramatic (1.4% according to Trejo and Dirzo 2000; Sánchez-Azofeifa et al. 2008), and the turnover rate of logging slash and burn of sites is every 10 years or less, and is decreasing (Challenger 1998). This length of time does not allow *Tillandsia* community recovery and may be worsened by natural disturbances such as hurricanes. An example of massive epiphyte extinctions expected under these scenarios in Mexico was already experienced in Singapore due to anthropogenic disturbance where 62% of species were lost (185 of 297) in 200 years (Turner et al. 1994).

In addition to land use change, our data provides evidence that current management of forests for wood extraction are not sustainable for epiphyte biodiversity conservation. Our logging scenario based on tree size highly impacted network robustness. Large old trees that hold the greatest number of epiphyte individuals and species (Sáyago et al. 2013) are usually extracted by forest management practices. In our study sites, mature forests still contained large old trees of precious woods such as *Cordia eleagnoides, C. alliodora, Caesalpinia sclerocarpa, Piranhea mexicana* that are slow growing and thus, large specimens of these species have increased probabilities of holding a large diversity and abundance of epiphytes (Sáyago et al. 2013). Cycles of forest management often consider around 15 years, which does not allow epiphyte community recovery. To date, no forest management practices consider the epiphytic life form. Basing management decisions purely on studies of carbon sequestration or particular species will not guarantee biodiversity maintenance, and in particular of epiphytes. Further epiphyte-phorophyte network studies will shed light on responses of epiphyte communities of other ecosystems.

Conclusions

Our study shows that epiphyte communities are highly impacted by anthropogenic disturbance, even in a group regarded as resilient to disturbance. Mexico is center of diversification of *Tillandsia* (Lott 2002, Reyes-Garcia et al. 2008), which is present in nearly all terrestrial ecosystems of the country, holding 48% of the *Tillandsia* diversity of the world, and 28% of its species are endemic to Mexico (Benzing 2000, Espejo-Serna et al. 2004). Conservation management of this group is necessary under managed ecosystems, and mature forests will be key propagule sources for recovery. Epiphytes may serve as an indicator group for conservation status (habitat health) and appropriate forest management (Hietz 1999, Turner et al. 1994).

Acknowledgements

We thank the Instituto de Investigaciones en Ecosistemas y Sustentabilidad and the Estación de Biología Chamela of the Universidad Nacional Autónoma de México (UNAM) for logistical support. Financial support was provided by SEMARNAT-CONACyT, Mexico (Grants 2002-C01-0597 and CB-2005-51043) and the *Interamerican Institute of Climatic Change* (Tropi-Dry-CRN-21). This paper constitutes a partial fulfilment of the Graduate Program in Biological Sciences of the National Autonomous University of México (UNAM). R. S. acknowledges the scholarship and financial support provided by CONACyT, and Posgrado en Ciencias Biológicas UNAM. We would like to thank A. Sanchez-Azofeifa for valuable information that allowed the development of this project. Technical assistance was provided by E. Castro, H. Ferreira, G. Sánchez-Montoya, A. Valencia-García, A. Lopez-Maldonado. We would like to thank to M. Gargollo who allowed us to work on her property.

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Tables

Table 3.1. Community and network structure comparisons along a successional gradient of a tropical dry forest of western Mexico.

Network metric	*F-value*	*P-value*	d.f. (treatment,error)
Early, intermediate and late successional stages (9 sites)			
Sub-plot level			
woody individuals	6.44	0.032*	2, 6
woody species density	2.17	0.196	2, 6
epiphyte individuals	9.97	0.012*	2, 6
epiphyte species density	4.14	0.074	2, 6
phorophyte number	6.69	0.030*	2, 6
Plot level			
epiphyte species	2.192	0.193	2, 6
ln (interaction strength)	10.086	0.012*	2, 6
phorophyte species	5.546	0.043*	2, 6
sqrt (number of links)	5.075	0.051	2, 6
sqrt (network size)	3.874	0.083	2, 6
Successional sites vs. mature forest (7 sites)			
Plot level			
connectance	0.216	0.662	1, 5
generality	12.459	0.017*	1, 5
H_2'	2.984	0.145	1, 5
interaction evenness	1.301	0.306	1, 5
specialization asymmetry	2.269	0.192	1, 5
vulnerability	1.476	0.279	1, 5
web asymmetry	10.762	0.022*	1, 5
Z_{NODF}	7.483	0.041*	1, 5
component 1 scores of PCA	6.796	0.048*	1, 5

*statistically significant at P = 0.05

Figure legends

Figure 3.1. Ordinations of seven plots in a successional gradient of tropical dry forest in western Mexico. A- nonmetric multidimensional scaling of species composition (NMDS), B- principal component analysis (PCA) of network indices. Numbers indicate site identity. Site 1: early successional stage; sites 2-4: intermediate successional stage; sites 5-7: late successional stage (mature forest). C- connectance, E- interaction evenness, G- generality, H2- H_2´specialization, SA- specialization asymmetry, WA- web asymmetry, ZN- *Z-score* of *NODF*. Networks from two early successional sites contained only one link and were omitted. Species names and other ordinations are found in Appendix SM-1 and Fig SM-2 in Supplementary Material.

Figure 3.2. Mean index values ± 95% confidence intervals of networks generated by randomly removing tree species or individuals from the late successional stage network (n=100), matching the number of species, individuals and biomass (summed DBH across trees) of the successional stages. See text for details. Dotted line: observed value for early successional stage, dashed line: observed value for the intermediate successional stage, dotted-dashed line: observed value for the late successional stage. For other metrics see Figure SM-3 in Supplementary Material.

Figure 3.3. Robustness of networks from early, intermediate and late successional stages to the removal of tree species (A, C and left side of E) and individuals (B, D and right side of E). A-D show absolute robustness, E shows relative robustness. Robustness is shown for

the responses: i) *Tillandsia* species richness (SR) in A, B and SR of E and ii) *Tillandsia* individuals (i.e. network interaction strength, IS) in C, D and IS of E. Note the $\log_{10}$ scale in C and D. Scenarios for woody species and individuals removal of the x-axis are: random removal (random), from most to least connected (links+-), from least to most connected (links-+), from most to least abundant (abund+-), from least to most abundant (abund-+), from largest to smallest (dbh+-), and from smallest to largest (dbh-+); see main text for details.

Figure 3.4. Examples of robustness curves for different stages and scenarios. A, C, E- remaining *Tillandsia* individuals (i.e. network interaction strength) as a response for woody species removal scenarios. B, D, F- remaining *Tillandsia* species as a response for woody individuals removal scenarios. A and B show scenarios for the late stage network; scenarios in the legend are as in Figure 3.3 C-F show curves for one removal scenario comparing the early, intermediate and late successional stages; to account for different network size and strength, curves of successional stages are drawn to start at different steps of removal, aligned to their last removal. C shows the removal of woody species from the least to the most connected (links-+). D shows the random removal of woody individuals (random). E shows the removal of woody species from the most to the least abundant (abund+-). F shows the removal of woody individuals from the largest to the smallest (dbh+-).

Figures

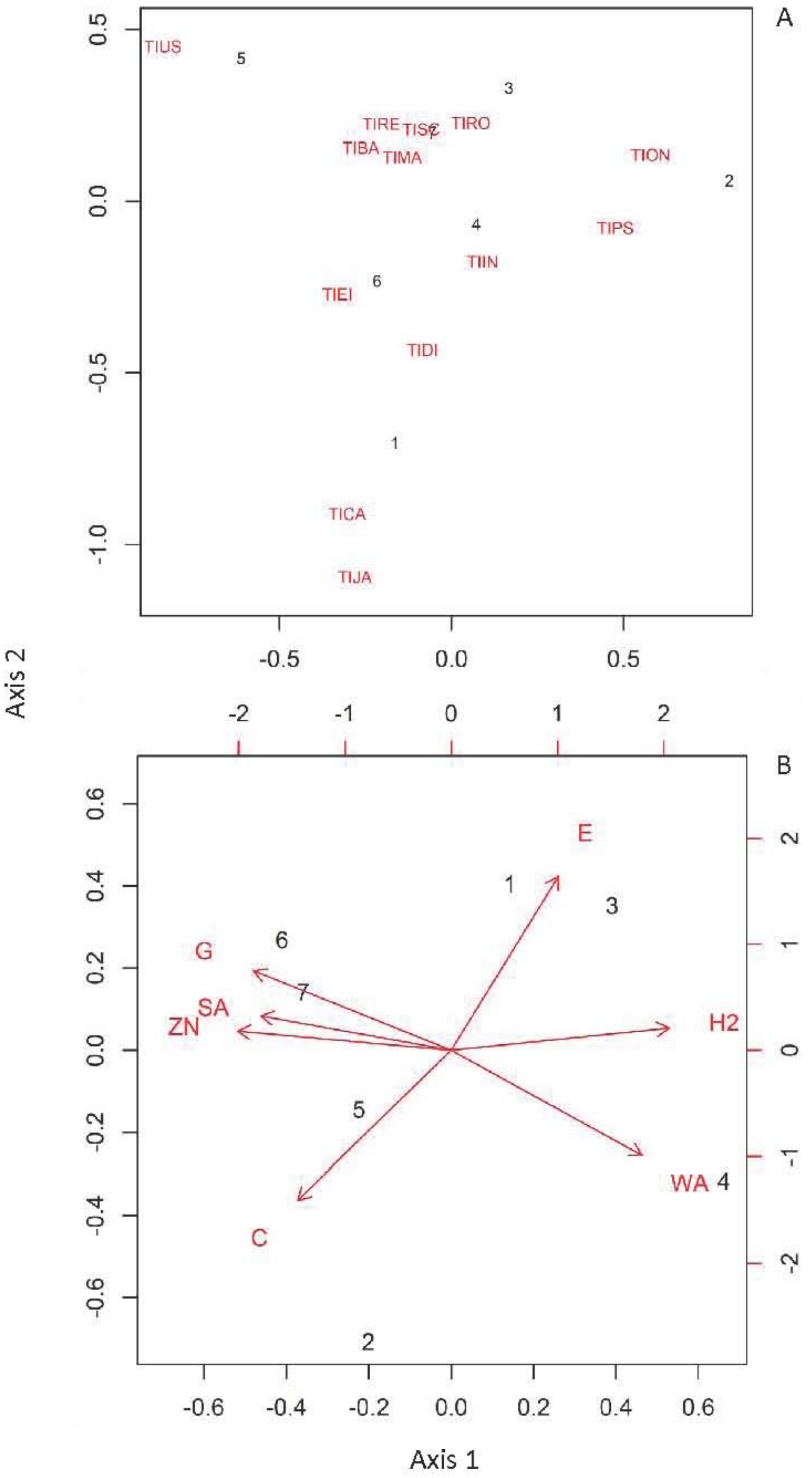
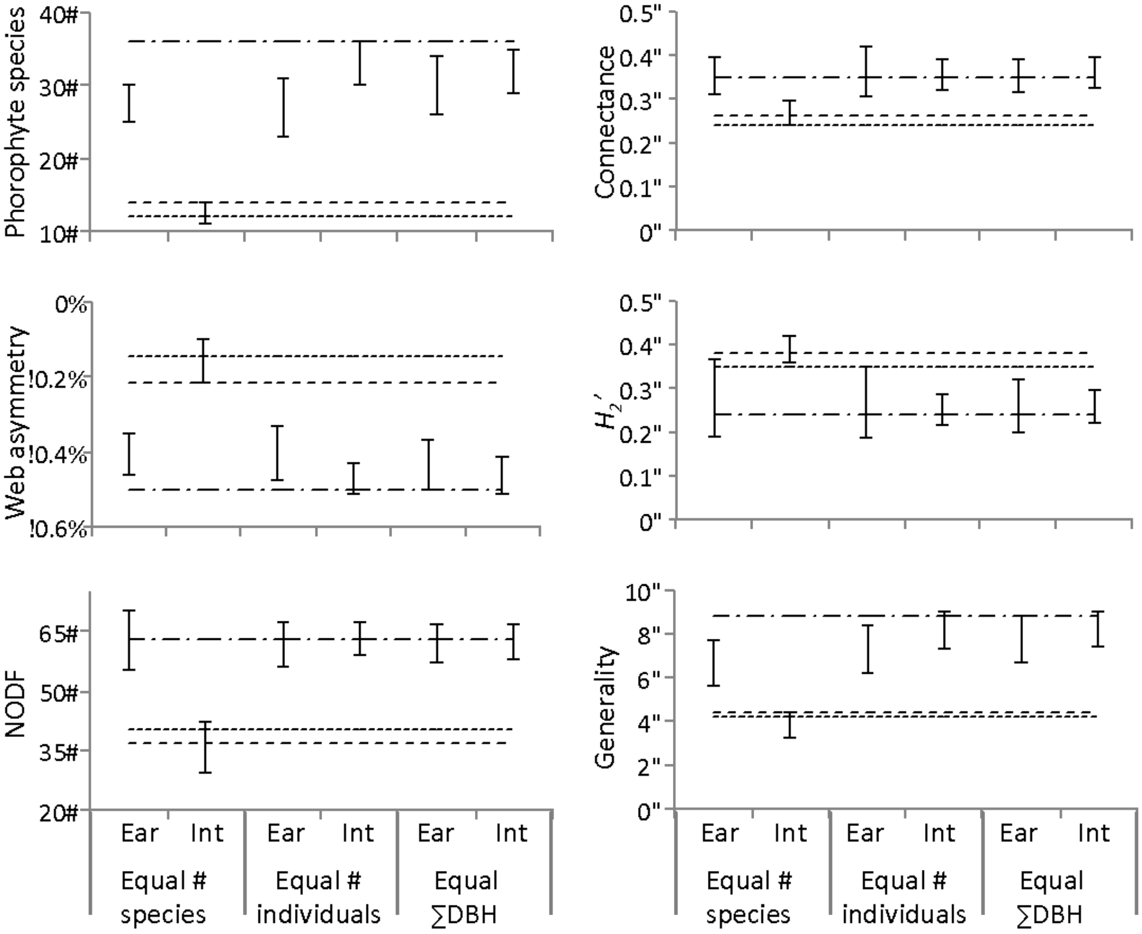


Figure 3.1



Phorophyte species
40#
30#
20#
10#
Connectance
0.5"
0.4"
0.3"
0.2"
0.1"
0"
Web asymmetry
0%
!0.2%
!0.4%
!0.6%
H_2'
0.5"
0.4"
0.3"
0.2"
0.1"
0"
NODF
65#
50#
35#
20#
Generality
10"
8"
6"
4"
2"
0"
Ear
Int
Ear
Int
Ear
Int
Equal # species
Equal # individuals
Equal ∑DBH
Ear
Int
Ear
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Ear
Int
Equal # species
Equal # individuals
Equal ∑DBH

Figure 3.2.

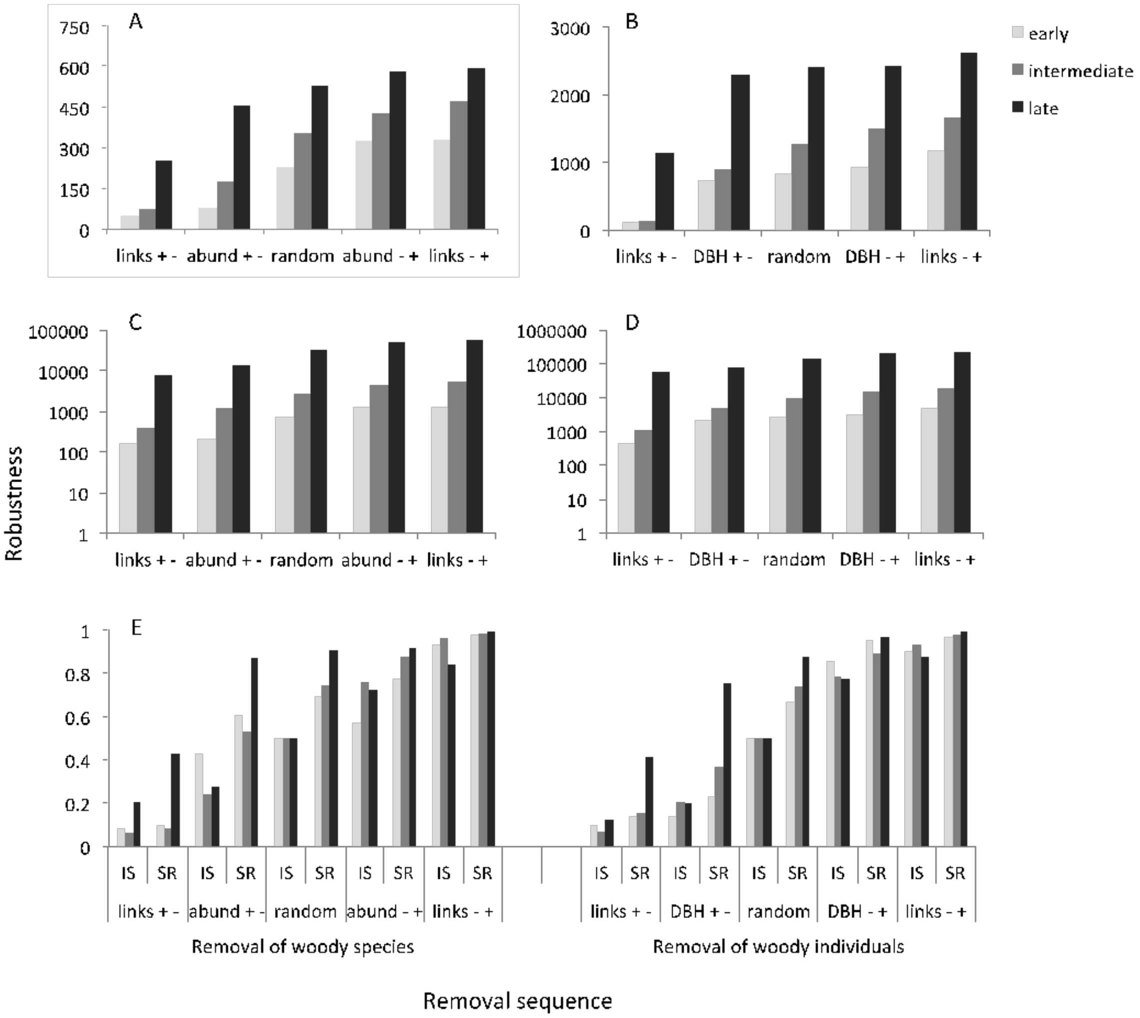
A
750
600
450
300
150
0
links + -
abund + -
random
abund - +
links - +
B
3000
2000
1000
0
links + -
DBH + -
random
DBH - +
links - +
early
intermediate
late
C
100000
10000
1000
100
10
1
D
1000000
100000
10000
1000
100
10
1
Robustness
E
1
0.8
0.6
0.4
0.2
0
IS
SR
Removal of woody species
Removal of woody individuals
Removal sequence

Figure 3.3

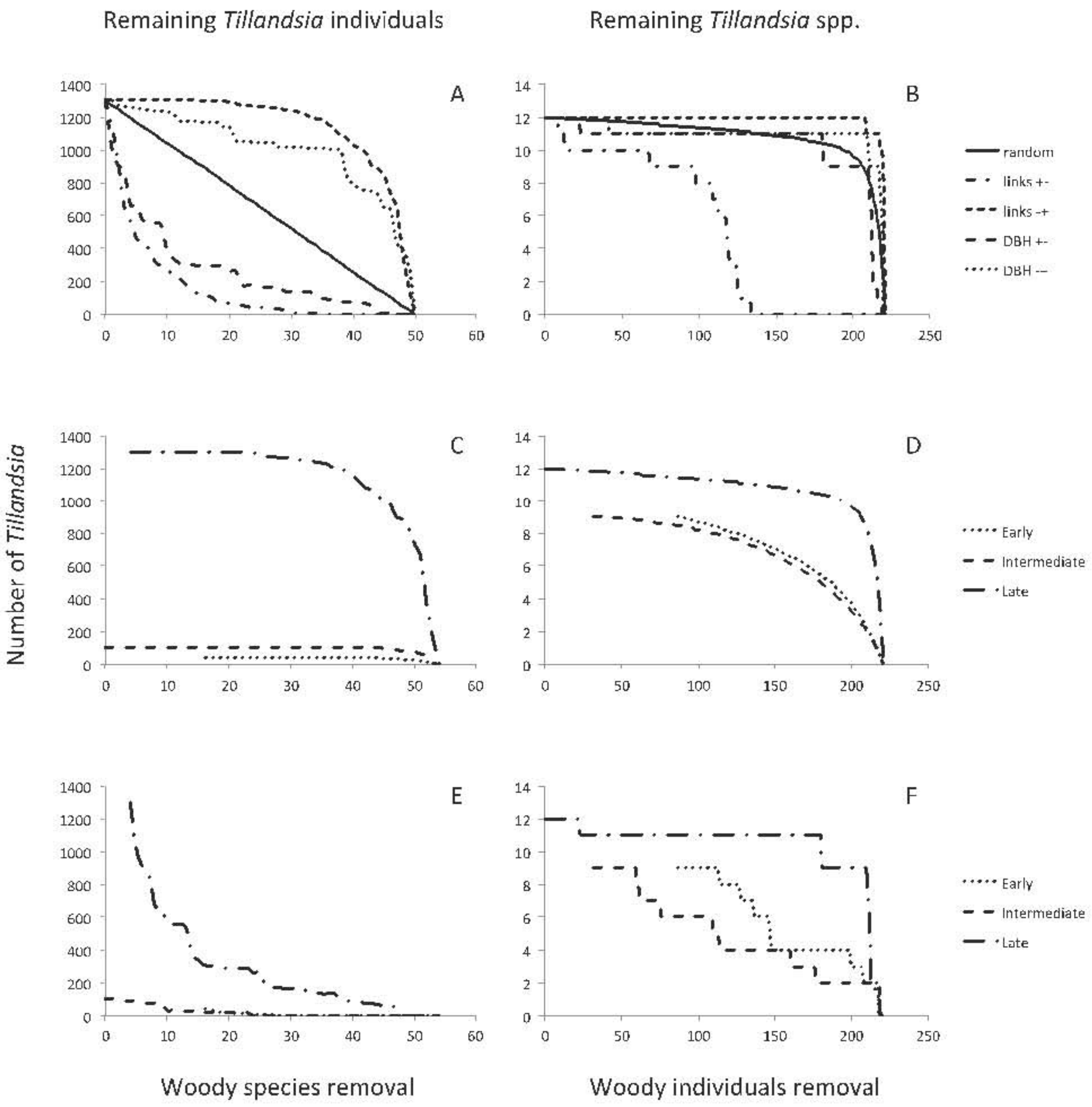
Remaining *Tillandsia* individuals
Remaining *Tillandsia* spp.
A
B
C
D
E
F
Number of *Tillandsia*
Woody species removal
Woody individuals removal
random
links +-
links -+
DBH +-
DBH --
Early
Intermediate
Late
0
200
400
600
800
1000
1200
1400
2
4
6
8
10
12
14
10
20
30
40
50
60
100
150
250

Figure 3.4

CAPÍTULO CUATRO

Alternative reproductive strategies in epiphytic bromeliads in fragmented and continuous Tropical Dry Forest habitats

Abstract

The effects of habitat fragmentation on pollination success have been documented in various groups of tropical plants; however, little is known about the effects of fragmentation on the reproduction and recruitment of epiphytic plants from tropical dry forests. We studied the phenology, pollinator visitation reproductive success of two epiphytic *Tillandsia* species with contrasting reproductive strategies (polycarpic *T. intermedia* and monocarpic *T. makoyana*) in continuous and fragmented habitats in Chamela, Mexico over three consecutive years. We predicted that monocarpism together with epiphytism should lead to a greater vulnerability to local extinction in habitats that have been disturbed by human activities. We found that both study species reproduce annually, the polycarpic species is self-incompatible and the monocarpic species is self-compatible, and both are primarily pollinated by hummingbirds. We found greater pollinator visitation and fruit set in fragmented conditions for polycarpic *T. intermedia*, while no differences among habitat conditions were detected for these traits in monocarpic *T. makoyana*. However, this latter species had lower flower production and higher seed abortion in forest fragments than continuous forest. Given that epiphytic plant populations tend to be highly affected by habitat disturbance, we hypothesize that populations of these species should be limited by availability of host trees for seedling establishment.

Key words: Bromeliaceae, Chamela-Cuixmala Biosphere Reserve, Tillandsia, Tropical Dry Forest, Monocarpic, Polycarpic, Reproductive strategy.

Introduction

Human disturbances like cattle and agriculture cause habitat loss that results in fragmentation at local and regional scales (Sanchez-Azofeifa et al. 2008). Anthropogenic disturbances can cause population reductions that may even result in local population extinctions. Several studies have evaluated the effect of habitat fragmentation on the reproductive success of tropical trees and other terrestrial species, but vascular epiphytes have been largely ignored (Aguilar et al. 2006). Epiphytes are non-parasitic plants that grow on other plants (phorophytes), and they are particularly diverse in the Neotropics (Benzing 1990). They are important elements of the forest due to their high taxonomic and physiological diversity, and their capacity to provide habitat and resources to other organisms (Kress 1986, Ibisch et al. 1996). Epiphytes are highly vulnerable to habitat disturbance because they have low growth rates, delayed sexual maturity, very limited seed dispersal and recruitment, and no seed bank (Benzing 1990, Turner et al. 1994, Hietz 1999, Martin et al. 2004, Cascante-Marin et al. 2009, Sáyago et al. 2013). In addition, epiphytes are highly dependent on the availability and fate of their phorophytes, which also need to provide particular microhabitats to allow successful colonization and establishment.

Anthropogenic disturbances, such as habitat fragmentation, imply environmental changes for remnant plant populations that may affect individual fitness due to abiotic microclimatic changes and biotic changes in pollinator diversity, abundance and behavior (Bawa 1990, Laurance 2002, Bawa et al. 2003, Chazdon et al. 2003, Fuchs et al. 2003, Kang and Bawa 2003, Lobo et al. 2003). Many bromeliads have distance-limited seed dispersal, thus colonization of disturbed habitats is challenging; therefore, reproductive mature epiphyte individuals surviving in forest fragments represent important sources of propagules for the long term persistence of populations in disturbed habitats (e.g., *Tillandsia*, Cascante-Marin et al. 2009). In order to fully understand the reproductive vulnerability of epiphytic species due to habitat disturbance, it is important to understand the patterns of pollinator visitation, plant breeding systems, reproductive success, recruitment and reproductive strategies of populations in fragmented and continuous habitats.

Knowledge of breeding systems is relevant because it allows inferring the ability of plants to produce selfed seeds in the absence of pollinators. For example, self-incompatible plants are more susceptible to habitat transformation because seed production directly depends on pollinator activity and on the availability of co-flowering conspecific individuals (Aguilar et al. 2006). For these species, anthropogenic disturbances often imply reductions in plant population density and pollinator visitation, diminishing pollen availability and cross-pollination events. Self-compatible plants could also be affected if they depended on animals for pollination (e.g. monoecious species), or if they experienced high levels of inbreeding depression after self-pollination (Angeloni et al. 2011).

Reproductive strategies in plants are related to the number of reproductive episodes that occur during the plant's life cycle. Polycarpic species have more than one reproductive event during a lifetime, while monocarpic species reproduce only once and die after reproduction. The number of propagules in a reproductive event is generally higher in monocarpic than in polycarpic species (Cole 1954). Monocarpic plants are often associated to annual herbs, but this reproductive strategy is present in all plant life forms. Monocarpic species show variation in reproductive synchrony and periodicity, time elapsed from germination to reproduction, and presence of asexual reproduction (Loveless et al. 1998, Zjhra and Kaplin 2004, Obioh and Isichei 2007). The impact of anthropogenic disturbance on plant reproductive success is expected to vary with the reproductive strategy of each species (e.g., Aguilar et al. 2006). For polycarpic species, *e.g.* trees, some reproductive episodes may be affected by anthropogenic disturbance. For monocarpic species, especially those with long life cycles, *e.g.* epiphytes, disturbance effects on particular reproductive events can affect population fitness more drastically. Until now the effects of human disturbances in plant reproduction has been studied mostly in polycarpic and annual monocarpic species, while long lived monocarpic species have been largely ignored (with the exception of some *Agave*; reviewed in Aguilar et al. 2006, Delgado-Lemus et al. 2014).

The main goal of this study is to evaluate the reproductive phenology, pollinator visitation and reproductive success of a monocarpic and a polycarpic epiphytic *Tillandsia* species in continuous and fragmented forest conditions. To accomplish this, we compared: (1) patterns of flowering phenology at the individual and flower levels, (2) breeding systems, and (3) patterns of pollinator visitation and female reproductive success in fragmented and continuous habitats across three years. We hypothesize that monocarpic epiphytic species are more vulnerable to habitat fragmentation than polycarpic epiphytic species.

Methods

Study area

The study was carried out in a tropical dry forest (TDF) in the region of the Chamela Cuixmala Biosphere Reserve, in the state of Jalisco Mexico. This region is characterized by its high species diversity, large proportion of endemic species, and the high degree to which it is threatened by anthropogenic disturbances (Ceballos and García 1995, Trejo and Dirzo 2000, Quesada and Stoner 2004, Miles 2006). Some areas around the reserve have been affected mainly by cattle ranching and agriculture, transforming continuous TDF into fragmented habitats (Sánchez-Azofeifa et al. 2008). The weather is $A(w_0i)$ in the Köppen classification system modified by Garcia (1988) with a coefficient of annual precipitation – temperature of 32 (P/T). It is a seasonal forest, the wet season occurring between July and October (Garcia-Oliva et al. 2002).

We sampled the two *Tillandsia* species at four sites in continuous TDF and three sites in fragmented TDF. The four continuous TDF sites were located around and inside the Biosphere reserve; these sites had not been used for cattle and agriculture at least for the last 50 y. The specific locations were: (1) Bosque de la enseñanza trail (19°29’55.58’’ N, 105°02’43.51’’ W), (2) Tejon trail (19°30’18.90’’ N, 105°02’34.52’’ W), (3) Ardilla trail (19°30’27.11’’ N, 105°02’23.45’’ W), and (4) Careyes Estuary (19°25’50.49’’N, 105°1’22.12’’ W). The three fragmented TDF sites were located around the biosphere reserve in forest fragments embedded within a matrix of anthropogenic disturbance. The specific sites were:(1) Arroyo Seco (19°21’45.91’’N, 104°56’16.05’’W), (2) Ranchitos (19°36’47.52’’N, 105°1’20.71’’W), and (3) Santa Cruz (19°36’11.32’’N, 105°2’45.71’’W). Reproductive individuals of *Tillandsia* in TDF fragmented conditions were anchored in large trees that had been left standing after disturbance.

Study species

The study species both belong to the genus *Tillandsia* subgenus *Tillandsia* and they were selected because they had the following characteristics: contrasting reproductive strategies (monocarpic vs. polycarpic), both shared pollination by hummingbirds, and similar flowering seasons. Monocarpic *T. makoyana* is a tank bromeliad with leaves that can reach up to 70 cm and produces a compound spyke with tubular purple, perfect flowers (Figure 4.1). Polycarpic *T. intermedia* is a species with hollow pseudobulbs formed by overlapping leaf bases; leaf blades are involute, long, and contorted. Inflorescences are spikes with pink tubular, perfect flowers (Figure 4.1). Both *Tillandsia* species flower from April to July (unpublished data).

Preliminary data indicates that for the monocarpic species (*T. makoyana*) an individual may take decades to achieve its reproduction event. In the case of the polycarpic species (*T. intermedia*) the first reproduction event can be achieved before a decade (Benzing 2000). *T. intermedia* also has the potential for secondary dispersal by asexual means when ramets (clones) detach (R. Sayago 2007 personal observations).

Floral Phenology

Phenological data were recorded in 2008 for both *T. intermedia* and *T. makoyana* in continuous forest. Before the study began, the flowering season was determined by recording individuals in flower once a month during the 12 months of the year. Flowering phenology at the individual level was evaluated by following 125 tagged individuals every two-three days for a period of one month for *T. intermedia* and 51 individuals for a period of two months for *T. makoyana*. Sampling periods allowed assessing the complete flowering period for each individual. Each day we recorded the number of flowers open per inflorescence to describe the pattern and length of flowering at the individual level. To document flowering phenology at the flower level, we recorded time of anthesis and stigma receptivity in 60 individuals for *T. intermedia* and in 51 individuals for *T. makoyana*. To determine time of anthesis and floral longevity, flowers were checked every hour for 25 hours, from 19:00 h to 20:00 h of the following day, when they began to wilt. On a different set of flowers, stigma receptivity was tested once, 2 hours before anthesis, using the H_2O_2 catalase activity method (Zeisler 1938). All flowers were receptive at this time, therefore, no further measurements of stigma receptivity were taken.

To characterize nectar production in both species we sampled 30 flowers on 19 individuals and took measurements of volume and sugar concentration every 2 hours starting at 6:00 h until flower wilting at 20:00 h. Flowers were bagged previous to anthesis and after every measurement to prevent pollinator visits. Nectar volume was measured with microcapillary tubes and nectar concentration was recorded with a pocket refractometer (Atago)

Breeding systems

Breeding system was assessed for *T. intermedia* during 2008 in plants located in continuous forest. Inflorescences on 98 individuals were bagged with mesh bags previous to anthesis and the following treatments were applied to individual flowers on each inflorescence: (1) Apomixis (emasculated bagged flowers) (2) manual self-pollination, (3) manual cross-pollination and (4) autonomous self-pollination (bagged flowers). Because individuals of *T. makoyana* were high in the canopy and it was difficult to conduct pollination treatments, we evaluated the potential for autonomous self-pollination under the complete absence of pollinators by bagging the inflorescences of 13 individuals found across three years (2008-2010). We also bagged whole inflorescences in 30 individuals of *T. intermedia* across the same three years for comparison.

Pollinator visitation

We conducted pollinator observations during three consecutive years (2008-2010) for 169 ramets of *T. intermedia* and 128 individuals of *T. makoyana* in the three fragmented and four continuous forest sites. Observations were conducted on 73 different days for a total of 526 hrs. Floral visitors were recorded with a Sony Digital Handycam DCR-PC 100. Cameras were focused on particular flowers to allow clear observation of anthers and stigmas. In 2008, we recorded visitation to flowers throughout the day and night; however, no pollinator visits were recorded during night time. Thus, on following years, we observed floral visitors during the day. We conducted video recordings for three consecutive hours and filmed all the flowers available on each inflorescence. For each visit we recorded the identity of the visitor, the duration of the visit and whether it contacted the stigma or anthers. To obtain pollinator visitation rates per inflorescence per hour, we divided the total number of visits to an inflorescence by the number of hours observed.

Female reproductive success

To test for differences in reproductive success between continuous and fragmented habitats, we quantified the number of flowers, fruits and the fruit set of both *Tillandsia* species under continuous and fragmented conditions. For both species we tagged inflorescences on 703 ramets of *T. intermedia* and 208 of *T. makoyana* and counted the number of flowers produced by each inflorescence in three consecutive years (2009-2011). We quantified fruit production 12 months after flowering and before seed dispersal. The fruit set of each plant was calculated as the total number of fruits divided by the total number of flowers produced by each inflorescence each year.

Seed production was quantified from fruits collected in 2011 from 68 individuals of *T. intermedia* and 56 individuals of *T. makoyana.* Seeds were counted on one to three fruits per individual, depending on fruit availability. We classified potentially viable seeds when they had a fully developed endosperm and coma (filamentous structure that allows dispersal and attachment to substrate). We identified aborted seeds that did not develop properly because they were smaller and had wrinkled endosperms. Seed set was calculated as the total number of seeds developed divided by the number of ovules in each ovary. The number of ovules was obtained by adding the number of viable and wrinkled seeds per fruit.

Statistical Analyses

Statistical analyses were conducted through generalized linear models using PROC GLIMMIX in SAS (SAS Institute 2008). As predictor variables we specified habitat condition (continuous vs. fragmented), year (2008-2010), and site nested within habitat condition. The interaction between habitat condition and year was initially included, but later eliminated because it was not significant for any variable. Response variables included the number of flowers, number of fruits, fruit set, number of ovules, number of seeds, seed set, number of aborted seeds and pollinator visitation rates. A Poisson distribution with a log link function was specified for the variables number of fruits and visitation rates; a binomial distribution with a logit link function was used for fruit set and seed set. The remaining variables did not require transformation. Back-transformed least square means were obtained using the ilink function. *P*-values for pairwise differences were Tukey adjusted. Below we report Least Square Means ± SEM for all variables.

Results

Phenology and nectar production

The populations of both species of *Tillandsia* flowered annually. The development of inflorescences for polycarpic *T. intermedia* started in February and for monocarpic *T. makoyana* started in December. Flowering occurred from April to early July for both species. Fruit initiation was evident seven weeks after flowering, but fruits were fully mature in one year. Seeds are wind dispersed and the dispersal period overlapped with the flowering season in both species.

Ramets of both species only develop one inflorescence. *Tillandsia intermedia* ramets flower only once, but individuals asexually produce one or two ramets per reproductive season. Each inflorescence produces in average 7± 0.1 flowers in mature forest habitats. Of 117 ramets followed in continuous forest, 25% and 71% of them reproduced sexually during the first and second year, respectively. In contrast, *T. makoyana* does not reproduce asexually. Each individual has a single inflorescence that develops within a period of 20 weeks; in mature forest habitats each inflorescence produces in average 84 ± 3.7 flowers. Senescence begins after flowering and most plants are dry by the time seeds are dispersed a year later.

Flower anthesis occurs acropetally (from the base to the apex) along inflorescences. Anthesis starts at midnight, and the flower lifetime is 20 hours for both species. For *T. intermedia*, the mean number of open flowers per day per inflorescence, on days with at least one open flower, was 1.0 (± 0.0; standard error of the mean, hereafter) in both continuous and fragmented forests (range: 1-2 flowers open per day, *N=166*). For *T.*

makoyana, the number of open flowers per day per inflorescence, on days with at least one open flower, was 1.8 (± 0.0) in both continuous (*N*=98) and fragmented (*N*= 72) forest (range: 1-7 flowers). In each inflorescence, individual flowers opened on average every 4.6 days (± 0.0, *N*=336) in *T. intermedia* and every 2.5 days (± 0.0, *N*=467) in *T. makoyana*.

In *T. intermedia* nectar production was very low and it was not possible to measure volume. A previous study carried out in the same area as the present study reported a mean nectar volume of 0.7 µl (± 0.7), and a sugar concentration of 26.7% for *T. intermedia* (Arizmendi and Ornelas 1990; syn. *T. paucifolia*). Nectar production started at sunrise in *T. makoyana*; mean nectar volume per day was 7.3 µl (± 0.19, *N*=30) and mean sugar concentration was 29.5% (± 0.25, *N*=27).

Breeding system

Fruit set for all these treatments was too low to conduct any statistical analyses. For *T. intermedia*, fruit set from hand outcrossed flowers was 12% and fruit set from open-pollinated flowers was 32%. The apomixis, manual self-pollination and autonomous self-pollination treatments did not produce fruits. None of the bagged inflorescences produced fruits either. These results indicate *T. intermedia* is self-incompatible. For *T. makoyana* mean fruit set of bagged inflorescences was 19%, indicating self-compatibility but a low potential for autonomous self-pollination.

Pollinator visitation

Floral visitors of *T. intermedia* and *T. makoyana* included hummingbirds, bees, butterflies, spiders and ants, both in continuous and fragmented forests. However, flowers were mainly visited by hummingbirds and Meliponinae bees (Tables 4.1, 4.2). In both *Tillandsia* species, hummingbirds generally visited flowers for seconds and they contacted both stigmas and anthers on every visit, while the Meliponinae bees spent on average 5.38 (± 2.83, N=344) minutes on the flowers, and contacted the reproductive structures on 87% of their visits. Hummingbird visitation was thwarted 45% of the times in which Meliponinae bees were already visiting a flower.

For *T. intermedia*, mean visitation rate (visits inflorescence^{-1} hour^{-1}) was lower in continuous (0.6 ± 0.2) than in fragmented forest (1.4 ± 0.1; $F_{(1,152)}$=9.26, P=0.003; Figure 4.2). There was also a temporal effect with significantly higher visitation in 2010 than in the previous two years ($F_{(2,152)}$=6.77, P=0.002; Figure 4.2). Visitation rates also differed among sites ($F_{(5,152)}=5.47$, $P=0.0001$). Visitation rates to the flowers of *T. makoyana* did not differ significantly between habitat conditions (continuous=3.8 ± 0.2, fragmented=4.1± 0.3; $F_{(1,167)}=1.07$, $P=0.303$; Figure 4.3), but there were significant differences among years ($F_{(2,167)}=11.96$, $P<0.0001$) and among sites ($F_{(4,167)}=6.83$, $P<0.0001$; Figure 4.3a).

Reproductive success

For *T. intermedia,* the mean number of flowers produced per inflorescence was similar between habitat conditions (continuous= 6.6 ± 0.1, fragmented= 6.3 ±0.1; $F_{1,695}=2.74$, $P=0.098$) and years ($F_{2,695}= 2.08$, $P=0.125$, Figure 4.2); however, there were significant differences among sites ($F_{4,695}= 9.46$, $P<0.0001$; Figure 4.2). The mean number of ovules per ovary was also similar between continuous (171 ± 7.8) and fragmented forest (169± 7.01; $\mathrm{F}_{1,58}=0.04$, $\mathrm{P}=0.851$), and among sites ($F_{4,58}=0.98$, $P=0.428$; Table 4.3).

For *T. makoyana*, the mean number of flowers produced per inflorescence was higher in continuous (83.7± 3.7) than in fragmented forest (66.7 ± 5.6; $F_{1,220}=6.93$, $P=0.0091$). There were also significant differences among years ($F_{2,220}= 8.20$, $P=0.0004$), and among sites ($F_{4,220}= 6.22$, $P<0.0001$; Figure 4.3). The number of ovules per ovary did not differ between continuous (173± 6.0) and fragmented forest (181±7.6; $F_{1,60}= 0.65$, $P=0.423$), or among sites ($F_{4,60}= 2.11$, $P=0.091$; Table 4.4).

The mean number of fruits produced per inflorescence by *T. intermedia* was lower in continuous (1.5 ± 0.07) than in fragmented forests (2.1 ± 2.0; $F_{1,695}=27.04$, $P<0.0001$), and it was higher in 2010 than in the previous two years ($F_{2,695}=17.95$, $P<0.0001$, Figure 4.2); there were also significant differences in number of fruits among sites ($F_{4,695}= 25.08$, $P=0.0001$, Figure 4.2). Likewise fruit set was lower in continuous (0.25 ± 0.026) than in fragmented forest (0.37 ± 0.027; $F_{1,695}$=9.69, P=0.0019), and highest in 2010 ($F_{2,695}$=5.78, P=0.0032); differences in fruit set among sites were also detected ($F_{4,695}$=4.72, P=0.0009; Fig 4.2).

The mean number of fruits produced per inflorescence by *T. makoyana* were similar between habitat conditions (continuous=27.1 ± 2.0; fragmented= 24.8 ± 3.1; $F_{1,220}$=0.41, P=0.530), and between years ($F_{2,220}$= 1.01, P=0.366), but there were significant differences among sites ($F_{4,220}$= 7.55, P<0.0001; Figure 4.3). Fruit set did not differ between habitat conditions (continuous=0.33 ± 0.047; fragmented= 0.37 ± 0.074; $F_{1,220}$=0.18, P=0.669), among years ($F_{2,220}$=0.81, P=0.447; Figure 4.3), or among sites ($F_{4,220}$=1.20, P=0.311; Figure 4.3).

For *T. intermedia,* the mean number of seeds per fruit did not differ between continuous and fragmented forest ($F_{1,58}$=0.01, P= 0.914; Table 4.3), or among sites ($F_{4,58}$=1.47, P=0.222). Likewise, the mean number of aborted seeds did not differ between conditions ($F_{1,57}$=0.11, P= 0.736), or sites ($F_{4,57}$=0.7, P=0.594). Seed set did not differ between habitat conditions $F_{1,58}$=0.58, P=0.448), or sites ($F_{4,58}$=0.32, P=0.866, Table 4.3).

For *T. makoyana* the mean number of seeds per fruit was similar between continuous and fragmented forest ($F_{1,60}$= 1.1, P=0.301, Table 4.4), but there were differences in the number of seeds among sites ($F_{4,60}$= 2.4, P=0.062). The number of aborted seeds per fruit was higher in fragmented than in continuous forest ($F_{1,59}$= 8.10, P=0.006) and there were no differences among sites ($F_{4,59}$= 1.04, P=0.393). Seed set did not differ between conditions ($F_{1,60}$=0.61, P=0.438), or sites ($F_{4,60}$=0.23, P=0.920, Table 4.4).

Discussion

The main hypothesis of this study, that monocarpism should be associated with greater vulnerability to habitat fragmentation was partly supported by the data, since *T. makoyana* produced fewer flowers per inflorescence and a larger number of aborted seeds /unfertilized ovules in fragmented conditions, while *T. intermedia* had increased floral visitation and fruit set in forest fragments. Below we discuss plant traits (e.g., phenology, breeding system, life history), plant-pollinator interactions and habitat conditions that may explain these results.

Phenology and pollinator visitation

Our results show that both monocarpic and polycarpic *Tillandsia* populations of these species reproduce annually and flower continuously from late April to early July, corresponding to the end of the dry season in the TDF of Chamela (García-Oliva et al. 2002). These are also months of low flowering intensity at the community level (Lopezaraiza *et al.* 2013); nevertheless, the study species flower along with 12 additional Bromeliaceae species during the month of May (Lott et al. 2002). Together, these bromeliads possibly provide an important floral resource for hummingbirds during one of the driest periods of the year. At the community level, the family Bromeliaceae in Chamela has 26 species that show a sequential pattern of flowering throughout the year, similar to what has been reported for the Bombacaceae and Heliconiaceae in other regions of the Neotropics (Lobo et al. 2003, Stiles 1975). This staggered flowering phenology ensures the availability of floral resources for pollinators across the year, particularly for vertebrate pollinators with high energy requirements (e.g., hummingbirds, Stiles 1975; bats, Lobo et al. 2003).

The two studied *Tillandsia* species are hummingbird-pollinated, as are most species in the family Bromeliaceae (Wolf 1970, Stiles 1975, Toledo 1975, Snow 1981, Neil 1987, Arizmendi and Ornelas 1990, Buzato *et al.* 2000, Canela and Sazima 2003, Kaehler *et al.* 2005). In the region of Chamela in particular, the main pollinator of *T. intermedia* and *T. makoyana* is the hummingbird *Amazilia rutila* (Trochilidae), a frequent and reliable flower visitor as indicated by the lack of among year variation in pollinator visitation documented in this study. *Amazilia rutila* is the most abundant hummingbird in the Chamela region and has been reported to visit 17 plant species, including several Bromeliads (Arizmendi and Ornelas 1990). *Tillandsia intermedia* and *T. makoyana* were also visited by two other hummingbird species and by stingless bees, particularly in forest fragments (Tables 4.1, 4.2); however, stingless bees are probably not highly effective pollinators of *Tillandsia*. They spend long periods taking pollen and nectar within each flower and they visit all open flowers in a plant, a behaviour that may cause geitonogamy in case of self-compatible species (De Jong et al. 1983) or stigma clogging in case of self-incompatible species. Furthermore, stingless bees were occasionally observed feeding on the reproductive structures of the flower; thus, acting as antagonistic floral visitors. The action of stingless bees as pollen thieves has been documented in various other species of tropical plant species (Hargreaves et al. 2009) including another hummingbird-pollinated bromeliad (Canela and Sazima 2005).

Breeding systems in relation to plant habitat

It has been proposed that self-pollination should be common in epiphytic plant species because they are frequent colonizers of unstable habitats, such as tree branches that break and fall frequently (Benzing 2000). Furthermore, self-pollination is expected to occur in monocarpic epiphytes as a reproductive assurance mechanism, given that these species only have one opportunity to reproduce (Cole 1954). Contrary to these expectations we found that both *Tillandsia* species are protogynous and self-pollination is negligible in *T. intermedia*, and low in *T. makoyana* (20% fruit set under pollinator exclusions). Both self-compatible and self-incompatible breeding systems have been described in the family Bromeliaceae (Benzing 2000, Ramírez *et al*. 2009), suggesting breeding system is a labile trait in this plant group. Since *T. intermedia* has clonal growth, an outcrossing breeding system should favour matings among different individuals to maintain genetic variation. In contrast *T. makoyana* has no clonal growth; thus, even a low potential for autonomous self-pollination may provide reproductive assurance in this monocarpic species.

Fragmentation effects on plant reproduction

Our study showed that habitat fragmentation affected the reproduction of the two *Tillandsia* species in different ways. *Tillandsia makoyana* has fewer flowers in fragmented conditions but fragmentation did not affect pollinator visitation, fruit production, fruit set or seed production in this species. Populations of *T. makoyana* are mainly found in mature forest and almost disappear in disturbed secondary growth habitats (Sayago et al. in prep). The reproductive success of the few individuals that persist under anthropogenic disturbance is similar to the plants found in mature forest, probably because *T. makoyana* is monocarpic, i.e., individuals invest all their energy into a single reproductive event and die off. In addition, the reproductive success of *T. makoyana* is expected to be similar in disturbed and mature forests because autonomous self-pollination should provide reproductive assurance under conditions of low pollinator visitation.

The benefits of reproductive assurance however, may be countered by inbreeding depression effects in the progeny produced via selfing (Herlihy and Eckert et al. 2002). The greater seed abortion of *T. makoyana* under fragmented habitat conditions suggests that the contribution of self-pollination (via autonomous selfing or geitonogamy) to seed set may be reduced by abortion of inbred seeds. Two lines of evidence support this view. First, *T. makoyana* is self-compatible; therefore, geitonogamous self-pollination -transfer of self-pollen within a plant- is possible in addition to some autonomous self-pollination. Second, the density of *T. makoyana* individuals is drastically reduced in fragmented and successional sites, associated with a reduction in the abundance of phorophytes in these habitats compared to the mature forest (Sayago et al. chapter 2); therefore, the chances of outcross pollen transfer are reduced in forest fragments. While these results support the view that selfing and inbreeding depression might be higher under disturbed conditions, studies that quantify these variables under natural conditions are not yet available.

In contrast to the case of *T. makoyana*, forest fragmentation was not negatively associated with reproductive success in polycarpic *T. intermedia*, where pollinator visitation rate and the number of fruits produced per inflorescence were lower in continuous than fragmented forests. The increase in floral visitation might reflect differences in pollinator assemblages between sites and forest conditions (Table 1,2, Figures. 4.1, 4.2). Interestingly, a single species of hummingbird was observed visiting both *T. intermedia* and *T. makoyana* in continuous forest, while three hummingbird species were observed in forest fragments (Tables 4.1, 4.2). Consistent with these findings, a study that recorded floral resources used by the community of hummingbirds in Chamela found that *C. latirostris* and *H. constantii* -only observed in forest fragments in this study- were rare visitors to flowers of *T. intermedia*, but common visitors of other ornithophilous plants in mature forest (Arizmendi and Ornelas 1990). Visitation of *C. latirostris* to flowers of *T. intermedia* possibly reflects a lower diversity or abundance of alternative floral resources under fragmented conditions, which might cause a shift in resource use. Additionally, stingless bees were almost three times more abundant in flowers of *T. intermedia* in fragmented than continuous forest (Table 4.1). In general, it has been observed that under fragmentation scenarios, pollinators change their foraging behaviour and may visit other plant species within the community (Ghazoul and McLeish 2001, Goverde et al. 2002), as may be the case of the hummingbird *C. latirostris*.

In conclusion, forest fragmentation had different effects on plant female reproductive success of two *Tillandsia* species with contrasting life history strategies, negatively affecting monocarpic *T. makoyana* and positively influencing polycarpic *T. intermedia*. However, fragmentation also affects other life stages of epiphytic bromeliads not measured in this study (e.g. Cascante et al. 2008). Given that habitat disturbance severely affects the abundance of phorophytes and epiphytic *Tillandsia* in the region of Chamela (Sayago et al. chapter 2), we hypothesize that the recruitment and establishment of both species should be limited by availability of suitable habitats and proper microclimatic conditions. To better understand the effects of fragmentation on the long term population persistence of *Tillandsia* epiphytes, it is necessary to quantify seed dispersal and viability, seedling establishment and plant survival of these species under the severe habitat disturbance that characterizes the TDF biome.

Acknowledgements

We thank the Centro de Investigaciones en Ecosistemas and the Estación de Biología Chamela of the Universidad Nacional Autónoma de México (UNAM) for logistical support. We would like to thank Miguel Angel Toriz Meneses and Andrea Sabelli too for valuable field assistance. Technical assistance was provided by H. Ferreira, G. Sánchez-Montoya, A. Valencia-García, A. Lopez-Maldonado. Funding was provided by SEMARNAT-CONACyT, Mexico (Grants 2002-C01-0597 and CB-2005-51043) and the *Interamerican Institute of Climatic Change* (Tropi-Dry-CRN-21). This paper constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the National Autonomous University of México (UNAM). R. S. acknowledges the scholarship and financial support provided by CONACyT, and Posgrado en Ciencias Biológicas UNAM.

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TABLES

Table 4.1. Percentage of visits to flowers of *Tillandsia intermedia* by different animals recorded during 2008-2010 at four continuous and three fragmented Tropical Dry Forest sites in the region of Chamela, Mexico.

	CONDITION		**SITES**						
			Continuous				*Fragmented*		
Visitant	*Continuous*	*Fragmented*	***Ardilla trail***	***Station***	***Tejón trail***	***Careyes Estuary***	***Arroyo Seco***	***Ranchitos***	***Santa Cruz***
Amazilia rutila	68.3	36.4	75	76.7	50	65	73.3	26	40.4
Cynanthus latiirostris	0	18.5	0	0	0	0	0	22.6	19.3
Heliomaster constantii	0	1.2	0	0	0	0	0	1.6	0.9
***Euglossa* sp.**	9.8	0	0	0	0	20	0	0	0
Meliponinae bees	15.8	41.3	25	23.3	50	2.5	25	45.9	39.4
Unidentified ants	4.9	2.6	0	0	0	10	1.7	3.9	0
Unidentified spider	1.2	0	0	0	0	2.5	0	0	0

Table 4.2. Percentage of visits to flowers of *Tillandsia makoyana* by different animals recorded during 2008-2010 at four continuous and three fragmented Tropical Dry Forest sites in the region of Chamela, Mexico.

	CONDITION		**SITES**					
			Continuous			*Fragmented*		
Visitant	*Continuous*	*Fragmented*	***Ardilla trail***	***Station***	***Tejón trail***	***Arroyo Seco***	***Ranchitos***	***Santa Cruz***
Amazilia rutila	74.6	79	71.4	76.7	74.2	92.8	33.9	67.5
Cynanthus latiirostris	1	2.1	0	2.1	0	0	14.3	2.9
Heliomaster constantii	0.3	3.8	0	0.6	0	0.2	12.5	7.4
Apis mellifera	0.4	0	0	0.8	0	0	0	0
Meliponinae bees	21.8	14.8	26.8	17.7	24.2	6.8	39.3	21.8
Unidentified ants	1.7	0.3	1.8	1.9	1.3	0.2	0	0.4
Unidentified butterfly	0.1	0	0	0	0.3	0	0	0
Unidentified spider	0.1	0	0	0.2	0	0	0	0

Table 4.3. Mean number of ovules; viable and aborted seeds, aborted/ovules and seed set (± SE) obtained during 2010 for *Tillandsia intermedia* in Tropical Dry Forest continuous and fragmented sites western Mexico.

	CONDITION		**SITES**					
			Continuous			*Fragmented*		
Variable	*Continuous*	*Fragmented*	*Ardilla trail*	*Station*	*Tejón trail*	*Arroyo Seco*	*Ranchitos*	*Santa Cruz*
Ovules	171 (7.8)	169 (7.0)	169 (8.6)	176 (6.5)	168 (21.0)	154 (7.2)	173 (9.9)	181 (17.1)
Viable Seeds	134 (8.5)	135 (7.6)	122 (9.3)	146 (7.0)	132 (22.8)	125 (7.8)	130 (10.7)	150 (18.6)
Aborted Seeds	40 (7.3)	37 (3.0)	51 (9.9)	36 (5.4)	36 (17.3)	37 (6.2)	46 (10.4)	31 (12.2)
Seed set	0.66 (0.123)	0.78 (0.101)	0.70 (0.132)	0.79 (0.089)	0.45 (0.352)	0.78 (0.099)	0.73 (0.148)	0.82 (0.220)

Table 4.4. Mean number of ovules; viable and aborted seeds, aborted/ovules and seed set (± SE) obtained during 2010 for *Tillandsia makoyana* in Tropical Dry Forest continuous and fragmented sites western Mexico.

	CONDITION		**SITES**					
			Continuous			*Fragmented*		
Variable	*Continuous*	*Fragmented*	*Ardilla trail*	*Station*	*Tejón trail*	*Arroyo Seco*	*Ranchitos*	*Santa Cruz*
Ovules	173 (6.0)	181 (7.6)	179 (9.6)	190 (12.7)	150 (8.7)	182 (9.3)	182 (16.0)	178 (13.6)
Viable Seeds	149 (6.8)	138 (8.6)	155 (10.7)	166 (14.2)	127 (9.7)	155 (10.4)	135 (17.9)	123 (15.2)
Aborted Seeds	24 (3.0)	43 (6.6)	25 (4.8)	24 (6.1)	24 (4.2)	29 (5.7)	48 (15.4)	56 (15.2)
Seed set	0.84 (0.062)	0.76 (0.090)	0.86 (0.094)	0.85 (0.125)	0.82 (0.094)	0.84 (0.094)	0.73 (0.198)	0.68 (0.176)

Figure legends

Figure 4.1. Plants and flowers of polycarpic *Tillandsia intermedia* and monocarpic *T. makoyana* from Chamela Cuixmala Biosphere Reserve, Mexico. Ramets of a single genet of *T. intermedia* dispersing seeds (A) and inflorescence showing one open flower (B); *Tillandsia makoyana* single ramet plant (C) and flower (D).

Figure 4.2. Mean number of flowers, number of fruits, fruit set, and visitation rates (visits inflorescence^{-1} hour $^{-1}$) for polycarpic *T. intermedia* obtained during 2008-2010 in Tropical Dry Forest sites (continuous: A= Ardilla, E= Station, C= Estero Careyes, T= Tejon; fragmented: AS= Arroyo Seco, R= Ranchitos, SC= Santa Cruz) in western Mexico.

Figure 4.3. Mean number of flowers, number of fruits, fruit set values, and visitation rates (visits inflorescence^{-1} hour $^{-1}$) for monocarpic plant *T. makoyana*) obtained during 2008-2010 in Tropical Dry Forest sites (continuous: A= Ardilla, E= Station, T= Tejon; fragmented: AS= Arroyo Seco, R= Ranchitos, SC= Santa Cruz) in western Mexico.

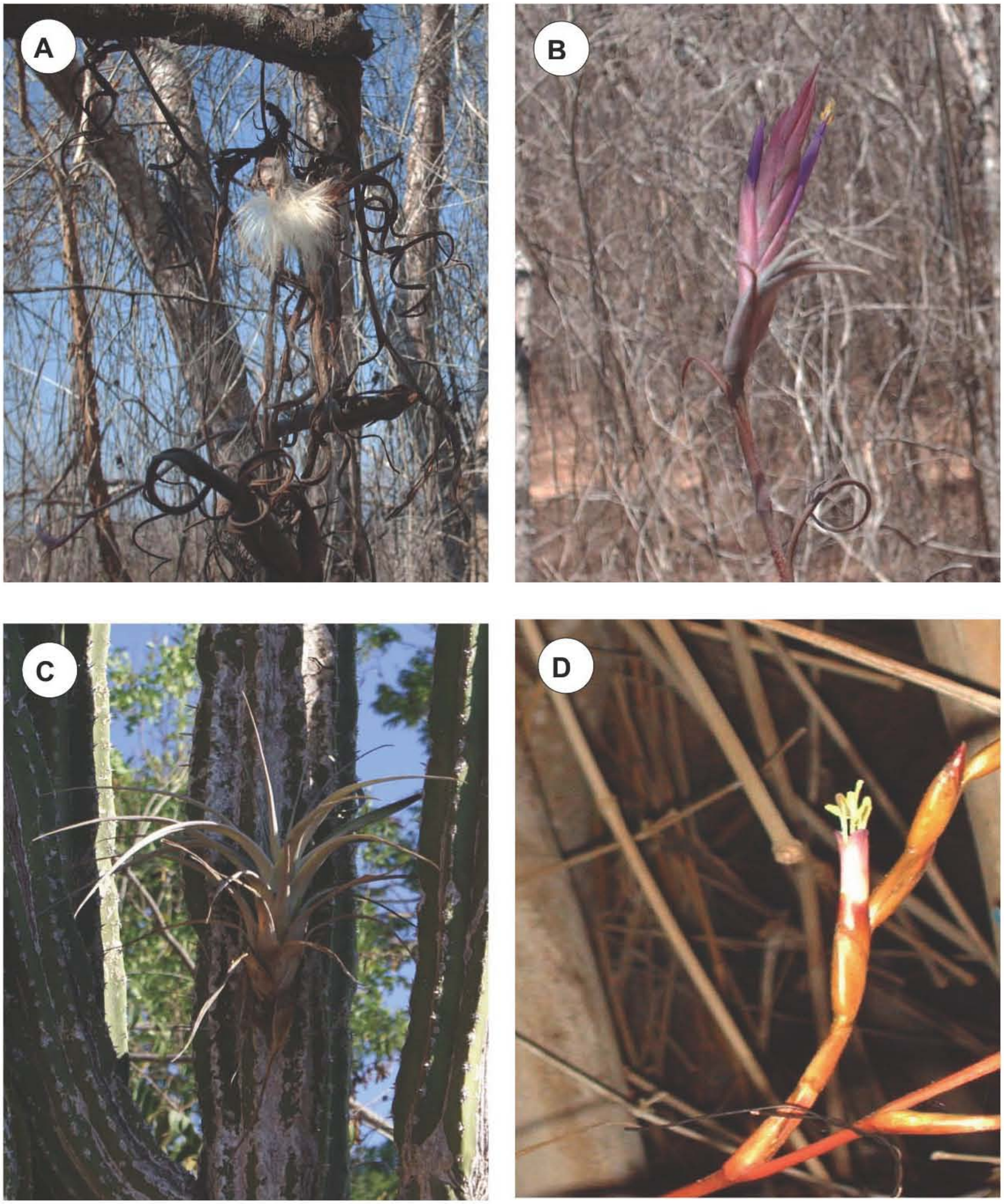


Figure 4.1.

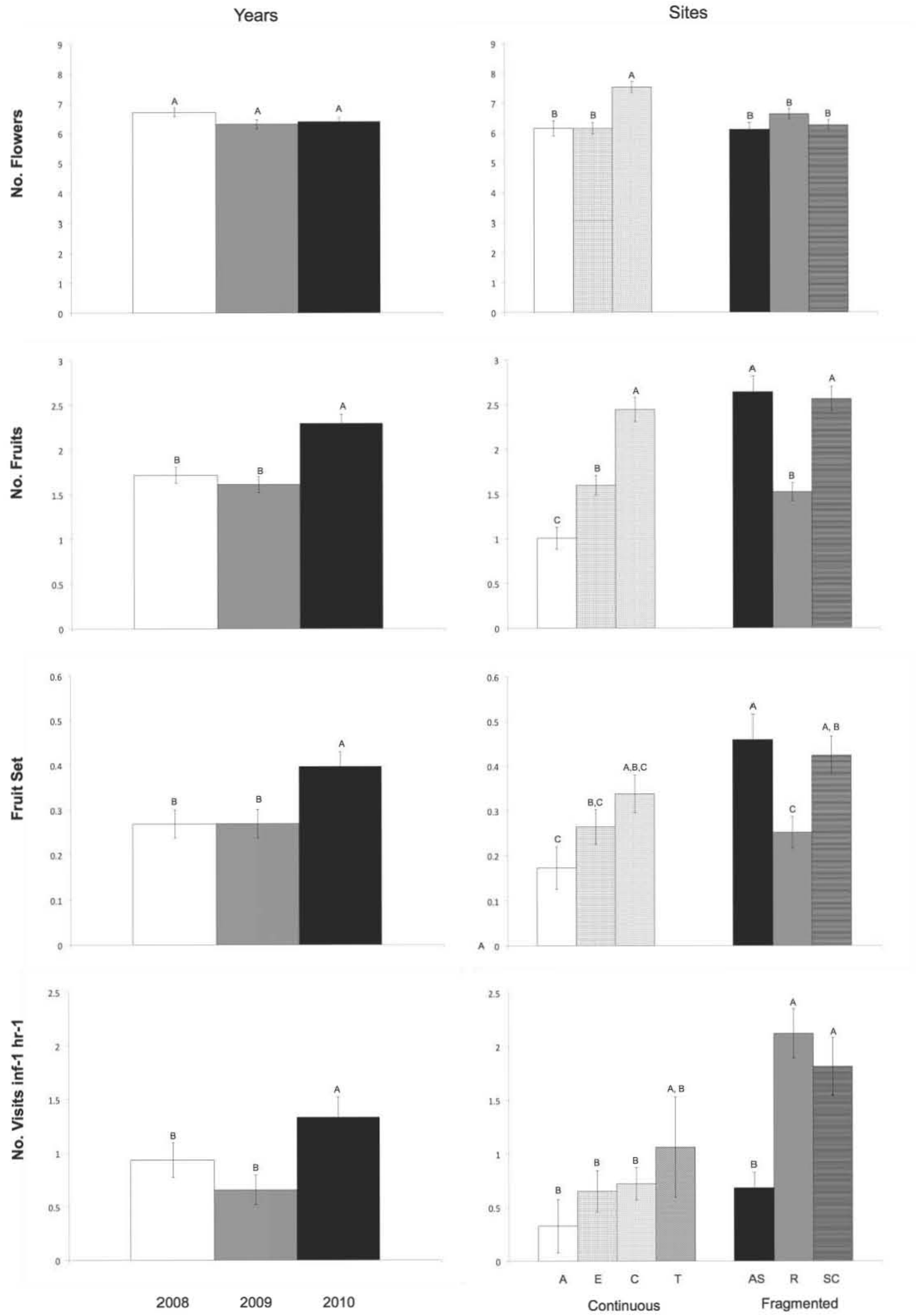
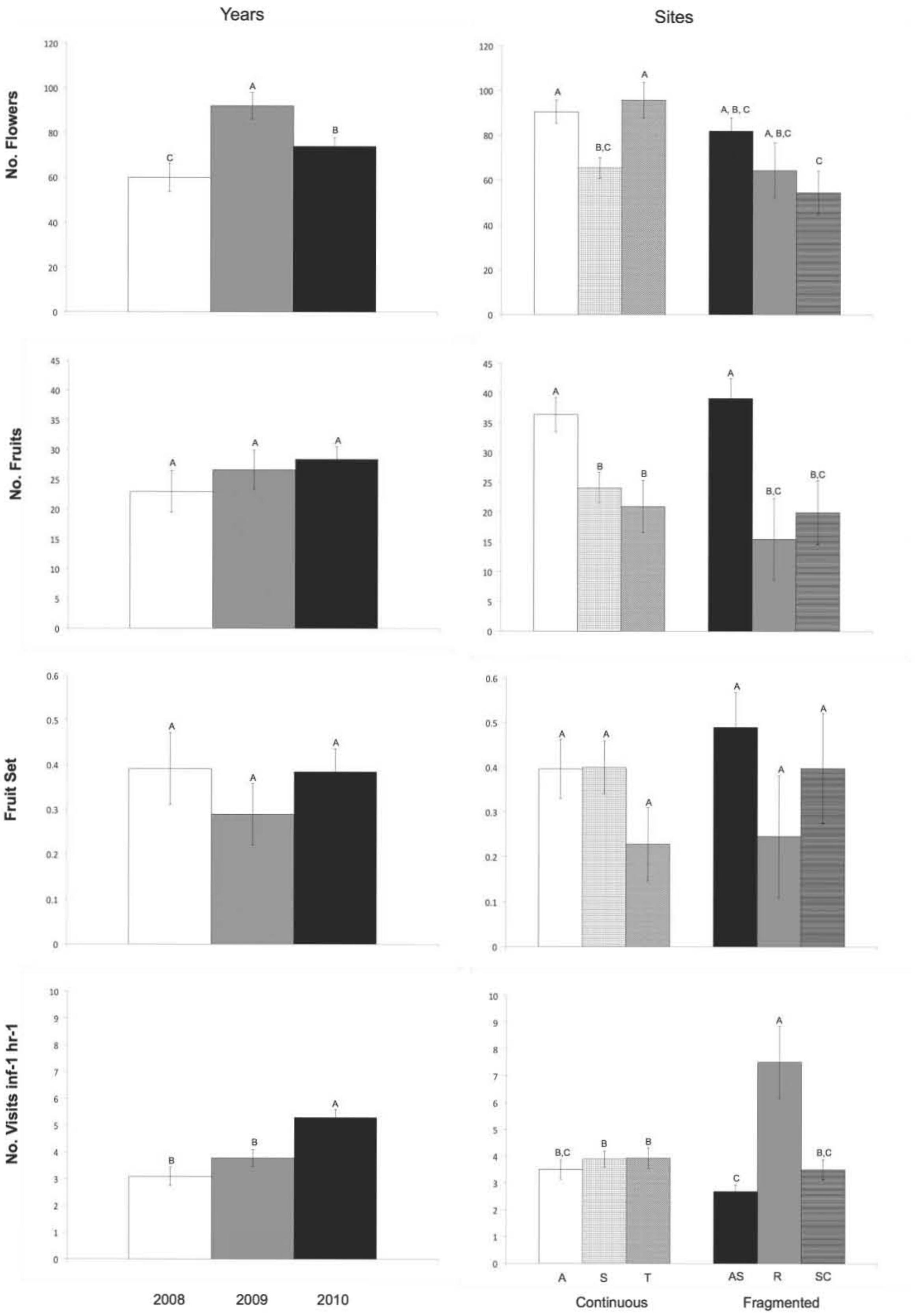

Years
Sites
No. Flowers
No. Fruits
Fruit Set
No. Visits inf-1 hr-1
0
1
2
3
4
5
6
7
8
9
0
0.5
1
1.5
2
2.5
3
0
0.1
0.2
0.3
0.4
0.5
0.6
0
0.5
1
1.5
2
2.5
A
A
A
B
B
A
B
B
A
B
B
B
A
B
B
B
B
C
B
A
A
B
A
B
B
A
C
B,C
A,B,C
A
C
A, B
B
B
A
B
B
B
A, B
B
A
A
A
2008
2009
2010
A
E
C
T
AS
R
SC
Continuous
Fragmented

Figure 4.2.


Years
Sites
No. Flowers
No. Fruits
Fruit Set
No. Visits inf-1 hr-1
0
20
40
60
80
100
120
C
A
B
A
B,C
A
A, B, C
A, B,C
C
0
5
10
15
20
25
30
35
40
45
A
A
A
A
B
B
A
B,C
B,C
0
0.1
0.2
0.3
0.4
0.5
0.6
A
A
A
A
A
A
A
A
A
0
1
2
3
4
5
6
7
8
9
10
B
B
A
B,C
B
B
C
A
B,C
2008
2009
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Continuous
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Figure 4.3.

CAPITULO CINCO

Discusion General

Capítulo Cinco

DISCUSION GENERAL

En este trabajo estudié los factores que influyen en el establecimiento de una red de interacción epífita-forofito en un bosque tropical seco del oeste de México, además estudié la fragilidad de las redes de interacción epífita-forofito en un gradiente sucesional del bosque tropical seco y simulé cómo afecta la frecuencia e intensidad de los disturbios antropogénicos a la red de interacción comensalista epífita-forofito y finalmente estudié aspectos reproductivos de dos especies epífitas selectas del género *Tillandsia* con estrategias reproductivas contrastantes (monocarpismo y policarpismo).

En el segundo capítulo de la tesis evalué los factores que estructuran la red de interacción epífita -forofito en un bosque tropical seco, y encontré que la abundancia de las especies del género *Tillandsia* y de la flora leñosa, el sobrelapamiento espacial, el tamaño del forofito, la densidad de la madera y la rugosidad de la corteza de las especies leñosas son factores que explican parcialmente la estructura de la red de interacción epífita-forofito, además fui capaz de predecir varios valores de índices que describen la topografía de la red de interacción epífita-forofito y encontré que no existe señal filogenética en la red comensalista epífita-forofito.

En el tercer capítulo de la tesis evalué la fragilidad de las redes de interacción epífita-forofito en un gradiente sucesional en un bosque tropical seco y encontré que la densidad de especies de epífitas y especies leñosas no presenta diferencias significativas en el gradiente sucesional. Sin embargo, la densidad de individuos de flora leñosa y epífitas fue menor en el estadio temprano que en los estadios sucesionales intermedio y tardío. Los estadios tempranos e intermedios tenían densidad similar de forofitos e individuos (número de individuos en los cuadrantes), y diferían significativamente del estado sucesional tardío. Esto resultó en un menor número de especies de forofitos y la intensidad de las interacciones en los estadios sucesionales tempranos e intermedios no eran tan fuertes comparados con el estadio sucesional tardío. Sin embargo, el total de especies de epífitas y el tamaño de la red no presentó diferencias significativas en el gradiente sucesional. La simulación de la frecuencia y la intensidad de los disturbios antropogénicos afecta la red de interacción epífita-forofito y se encontró que la red de interacción epífita-forofito es frágil cuando se pierden las especies de flora leñosa más comunes y también cuando se pierden los individuos con mayor diámetro a la altura del pecho, además de que en los estadios sucesionales temprano e intermedio la red epífita-forofito es más frágil que en el bosque maduro debido a que la comunidad de epífitas se pierde más rápidamente al perderse las especies de flora leñosa más abundantes y cuando se pierden los individuos de flora leñosa con mayor diámetro a la altura del pecho.

Finalmente en el cuarto capítulo evalué durante tres años de muestreo (2008-2010) el potencial de producción de propágulos que tienen dos especies de *Tillandsia* con estrategias reproductivas contrastantes (monocarpismo y policarpismo), en condiciones de bosque tropical seco continuo y fragmentado. Encontré similitudes y diferencias en la fenología reproductiva entre ambas especies; las similitudes consisten en florecer entre mayo y julio, tener antesis nocturna, con flores de longevidad de un día, en promedio tienen la misma cantidad de óvulos por ovario y semillas por fruto, los principales visitantes florales para las dos especies de *Tillandsia* estudiadas son *Amazilia rutila* y *Cynanthus latirostris* (Trochillidae) y abejas meliponas (Meliponidae), los frutos tardan un año en madurar y las semillas se dispersan por el viento. Las diferencias consisten en que la especie monocarpica tiene mayor número de flores y frutos por inflorescencia, mayor cantidad de néctar, y es auto-compatible, mientras que la especie policarpica tiene menor número de flores y frutos, prácticamente carece de néctar y es auto-incompatible. Encontré que la fragmentación del hábitat tiene efectos directos en algunos aspectos estudiados:

Existe menor cantidad de individuos reproductivos de las dos especies de *Tillandsia* estudiadas en los fragmentos; el número de flores por inflorescencia es menor significativamente en condiciones de fragmentación para la especie monocarpica (*T. makoyana*) pero no para la especie policarpica (*T. intermedia*) y la tasa de visitas a las flores aumenta en condiciones de fragmentación para *T. intermedia* mientras que para *T. makoyana* no existe diferencias significativas entre ambas condiciones. Además encontré que los individuos remanentes de *Tillandsia* en bosque tropical seco fragmentado potencialmente son fuente de propágulos debido a que no encontré diferencias significativas entre el bosque continuo y fragmentado en el número de óvulos, el número de frutos por inflorescencia, el fruit set, el número de semillas producidas por fruto y el seed set.

Redes de interacción

Los trabajos de redes básicamente se han enfocado en describir las redes de interacciones ecológicas existentes (Bascompte et al. 2003, Berlow et al. 2004, Burns 2007, Blinck y Burns 2009, Burns y Zotz 2010, Silva et al. 2010). Un aspecto fundamental en esta tesis es que en el Capítulo II emplee un método novedoso (Vázquez et al. 2009) para analizar los factores que estructuran la red de interacción *Tillandsia*-forofito, por primera vez en la literatura se realizó este tipo de análisis en una red comensalista. La flora leñosa del bosque tropical seco presenta una distribución agregada en donde ciertas especies de árboles son abundantes (*e.g. Apoplanesia paniculata*) y otras especies menos comunes (*e.g. Caesalpinia sclerocarpa*) (Hubbell 1979), aspectos que crean naturalmente un escenario ideal para evaluar el establecimiento de interacciones biológicas entre plantas epífitas vasculares y la flora leñosa (Benzing 1990).

Comprender los factores que influyen la estructura de las redes observadas de plantas epífitas vasculares permite entender las interacciones ecológicas para el manejo a largo plazo de especies susceptibles a disturbios antropogénicos (Memmott et al. 2004, Strauss y Irwin 2004). Las plantas epífitas vasculares han sido un grupo reconocido como muy suceptible a los disturbios antropogénicos, pero también dentro de esta forma de crecimiento se reconocen familias más frágiles, por ejemplo la familia Orchidaceae (Turner et al. 1994, Flores-Palacios y García-Franco 2004, Martin *et al*. 2004), mientras que otras familias son más resistentes a los disturbios antropogénicos, por ejemplo la familia Bromeliaceae (Barthlott *et al.* 2001, Flores-Palacios y García-Franco 2004). Básicamente esta conclusión se ha hecho con base en que muchas especies de la familia Bromeliaceae son heliofilas, lo que contribuye a que los individuos remanentes no necesariamente mueran a causa de los cambios microclimáticos causados después de la fragmentación del hábitat. Pero el supuesto de que la familia Bromeliaceae no es afectada, en particular el género *Tillandsia*, se ha hecho sin evaluar cómo afecta la frecuencia de los disturbios antropogénicos a las plantas epífitas vasculares, aspecto crucial de entender en sucesión ecológica y que prácticamente no ha sido evaluado para las comunidades vegetales de plantas epífitas vasculares, ni para otras formas de crecimiento.

Sucesión ecológica

Evaluar la frecuencia de los disturbios antropogénicos es crucial para las especies del genero *Tillandsia* y demostrar que también es un grupo muy vulnerable ante escenarios de disturbios antropogénicos por que tienen tasas bajas de crecimiento, ciclos de vida largo como resultado de que presentan gran eficiencia en el uso de agua y de los minerales; metabolismo del ácido crasuláceo (CAM); y una baja relación superficie volumen. A pesar de tener características que les permite vivir en ambientes extremos, como es el dosel del bosque tropical seco por tener poca disponibilidad de agua, gran intensidad de luz y falta de nutrientes. Además existe dependencia de las especies de *Tillandsia* con los árboles de gran talla (DAP) para su desarrollo, no presentan bancos de semillas, generalmente las especies presentan dispersión limitada y el establecimiento de nuevos individuos depende de una producción alta de semillas para que se puedan establecer en ramas y micrositios adecuados (Benzing 1973, Turner *et al.* 1994, Nadkarni *et al.* 2001, Martin *et al.* 2004, Reyes-García *et al.* 2008, Cascante-Marin *et al.* 2009, Sayago *et al.* 2013).

En el Capítulo III de mi tesis mostré cómo al considerar la frecuencia de los disturbios antropogénicos el panorama para el género *Tillandsia* cambia drásticamente, por lo que debe de ser considerado como un grupo vulnerable ante disturbios antropogénicos, y más si consideramos que el género *Tillandsia* es el género más diverso de la familia Bromeliaceae (16.4%), y que la mayor riqueza de especies del género *Tillandsia* se encuentra en México (48%) con un alto porcentaje de endemismos (69%) y que los bosques tropicales secos de México son cruciales para este género en México, por la riqueza de especies que alberga, alrededor del 30% de especies de *Tillandsia* se distribuyen en bosques tropicales secos de México y 29% son especies endémicas (Hammel et al. 2003, Espejo-Serna et al. 2004).

Otra aportación importante del Capítulo III es que mostré que no podemos seguir considerando al bosque tropical seco como un tipo de vegetación resiliente ante los disturbios antropogénicos, debido a que estos supuestos han valorado únicamente a la flora leñosa sin incluir a otras formas de crecimiento importantes como las epífitas (Murphy y Lugo 1986, Ewel 1997, Segura et al. 2003). Si consideramos que la comunidad de *Tillandsia* no se recupera después de 15 años de que han ocurrido disturbios antropogénicos, y que estos datos han sido generados en parcelas permanentes que presentan un escenerario en donde los disturbios antropogénicos (ganaderia y agricultura) han sido excluidos, este estudio sugiere que se pueden necesitar décadas para que la abundancia, la diversidad de epífitas y la proporción de forofitos se recupere en sitios de bosque tropical seco alterados, asi como sucede en otros tipos de vegetación como por ejemplo el bosque tropical lluvioso (Benzing 1990 y 2000). Además es necesario considerar el papel que tienen los disturbios naturales.

Los disturbios naturales como los huracanes ocurridos en el área de estudio recientemente, Huracán Jova categoría II ocurrido en octubre de 2011 y el huracán Patricia categoría V ocurrido en octubre de 2015, pudieran promover la caida de los forofitos o de los individuos de *Tillandsia* lo que provoca la mortalidad de los individuos de *Tillandsia,* pudiendo eventualmente causar extinciones locales, esto pudiera ocurrir principalmente en los sitios con disturbios antropogénicos (Benzing 1990), debido a que los disturbios antropogénicos promueven la disminución poblacional de las especies del genero *Tillandsia,* podríamos suponer que las poblaciones que se encuentran en sitios con disturbios antropogénicos sean más vulnerables ante los disturbios. Pero también existen especies de epífitas que tienen dispersión secundaria y cuando ocurren huracanes tienen la capacidad de dispersarse y colonizar nuevos forofitos *e.g. T. usneoides* (Benzing 2000).

Las especies de *Tillandsia* son un componente importante de la diversidad biológica de los bosques tropicales secos debido a que establecen interacciones biológicas con distintos taxa sirviendo como recursos para la construcción de nidos de aves (*e.g. T. usneoides*), como microhabitats para mosquitos y anfibios, y como recursos alimenticios para polinizadores como los colibríes (Benzing 1990 y 2000). Por lo que es necesario entender el papel potencial de reproducción que pueden tener los individuos remanentes una vez que han ocurrido disturbios antropogénicos que promuevan la fragmentación del hábitat debido a que la contribución que estos individuos tengan como fuentes de propagulos puede ser crucial para el mantenimiento a largo plazo de las poblaciones, más aún si consideramos que se han reportado especies de *Tillandsia* que tienen dispersión de semillas limitada (Cascante-Marin *et al.* 2009).

Fragmentación del hábitat y reproducción de plantas epífitas

Los trabajos que estudian el efecto de la fragmentación del hábitat sobre la polinización en especies de plantas que requieren de vectores bióticos para transferir el polen a otros individuos de su misma especie, han documentado que la fragmentación en términos generales tiene consecuencias negativas en el movimiento del polen en poblaciones que han quedado aisladas y que se pudiera estar promoviendo la endogamia y la deriva génica (*e.g.* Quesada *et al.* 2003, Ashworth *et al.* 2004, Johnson *et al.* 2004, Quesada *et al.* 2004, Aguilar *et al.* 2006). Es importante señalar que la gran mayoría de los trabajos se han realizado principalmente con especies arbóreas policarpicas, mientras que las epífitas vasculares han sido uno de los grupos menos estudiados en este sentido (Aguilar et al. 2006) y el monocarpismo nunca habia sido evaluado con el enfoque de fragmentación del hábitat en plantas con ciclo de vida largo ni en la forma de crecimiento epifita.

Las especies monocárpicas deben tener una mayor fecundidad para poder mantener poblaciones viables (Zeineddine y Jansen 2000) aspecto que puede verse favorecido por el hecho de que los individuos monocárpicos no tendrán que invertir recursos después de su único evento reproductivo en aspectos relacionados con el mantenimiento del soma como son el crecimiento, el mantenimiento y la defensa (Begon et al. 1995). Estos aspectos se relacionan con lo que encontré en la especie monocarpica (*T. makoyana*) debido a que tiene mayor número de frutos por inflorescencia, mayor fruit set y seed set, por lo que es necesario entender la dependencia que tienen estas plantas con sus polinizadores y entender cómo afecta la fragmentación del hábitat a los polinizadores. Las especies de colibríes (*A. rutila*, *C. latiirostris* y *Heliomaster constantii*) registradas visitando a *T. makoyana* y *T. intermedia* representan el 43% de las especies registradas para la región (Arizmendi y Ornelas 1990, Arizmendi *et al.* 2002). Las visitas se documentaron en ambas condiciones de bosque tropical seco, el grupo de los colibríes se ha documentado que responde de forma diferencial a la perturbación del hábitat, encontrándose especies que pueden verse beneficiadas por los disturbios antropogénicos mientras que otras pueden ser perjudicadas ante la presencia de estos, pero aún no existen datos suficientes que muestren la tendencia que este grupo de polinizadores tiene ante escenarios de disturbios antropogénicos (Stoufer y Bierregaard Jr.1995, Borgella Jr. *et al.* 200, Winfree et al. 2011). En este trabajo documenté que la tasa de visitas de las flores aumenta en condiciones de fragmentación para la especie policarpica (*T. intermedia*) y que para la especie monocarpica (*T. makoyana*) no cambia entre condiciones, además existen mayor diversidad de visitantes florales para la especie policarpica (*T.* intermedia) en condiciones de fragmentación, aspecto que podría reflejar escases de recursos florales en condiciones de fragmentación del bosque tropical seco (Wolf 1970, Stiles 1975, Neill 1987, Arizmendi y Ornelas 1990). Estos aspectos podrían estar promoviendo la geitonogamia para la especie monocarpica que es auto-compatible (*T. makoyana*), lo que podría promover la deriva génica en la población. Estos aspectos no ocurren en la especie policárpica (*T. intermedia*) debido a que es auto-incompatible (Levin y Anderson 1970, Bawa 1990, Quesada *et al. 2003,* Ashworth *et al.* 2004, González-Astorga *et al.* 2004, Johnson *et al.* 2004, Quesada *et al. 2004,* Aguilar *et al.* 2006).

Encontramos que no existen diferencias significativas en la producción de frutos, el fruit set y el número de semillas en condiciones de bosque tropical seco continuo y fragmentado en la especie monocarpica (*T. makoyana*) y la especie policarpica (*T.*

intermedia) lo que nos suguiere que los individuos remanentes potencialmente son fuentes de propagulos que potencialmente servirán para mantener poblaciones a largo plazo. Sin embargo, el reclutamiento en plantas epífitas vasculares es la etapa más crítica por lo que se requiere gran cantidad de semillas para que ocurra, debido a lo difícil que es por un lado que una semilla llegue a una rama adecuada y que pueda establecerse debido a que existe gran mortalidad de los individuos juveniles a causa de las sequias y/o por la caída de los juveniles antes de fijarse en las ramas, o por la pérdida de ramas (Benzing 1990 y 2000). Ante este escenario tenemos que cuando existen disturbios antropogénicos la estructura del bosque tropical caducifolio es modificada principalmente por la pérdida de dosel (Quesada et al. 2009), por lo que el reclutamiento de individuos pudiera verse afectado si no existieran ramas que sirvan como un sustrato adecuado. Esto potencialmente tendría mayor repercusión a mediano plazo en la especie monocarpica (*T. makoyana*) al tener solo un evento reproductivo debido a que si las semillas producidas no alcanzan las ramas adecuadas no podrá haber reclutamiento, mientras que para la especie policarpica (*T. intermedia*) al tener más de un evento reproductivo tendrá mayor probabilidad de que la estructura de la vegetación se restablezca en los sitios fragmentados siempre y cuando los disturbios lo permitan.

Para conservar a la comunidad de *Tillandsia* en el bosque tropical seco será necesario establecer estrategias que promuevan la conservación de este grupo biológico. Por un lado se deben de establecer áreas naturales protegidas de gran extensión en donde el manejo sea enfocado exclusivamente a la conservación biológica. Cuando necesariamente tengan que realizase prácticas que promuevan el disturbio antropogénico como agricultura y ganadería, en estos sitios se debe de considerar el tiempo que potencialmente los disturbios pudieran persistir: Cuando el disturbio antropogénico sea constante en el sitio *e.g.* pastizales, será necesario permitir la existencia de árboles remanentes que simulen una cerca viva y si el disturbio se prevea que durará pocos años en los sitios *e.g.* cultivo de maíz será necesario permitir la existencia de forofitos remanentes en la parcela lo que potencialmente permitirá que cuando el bosque se regenere la comunidad de *Tillandsia* tenga oportunidad de colonizar nuevos árboles. La existencia de forofitos remanentes además podría tener diversos usos como sería la extracción de madera a largo plazo, y/o para la obtención de frutos y/o sombra para el ganado. Un aspecto fundamental que permitirá la conservación de la comunidad de *Tillandsia* a largo plazo es que se tiene que incrementar el lapso de tiempo entre las actividades de roza tumba y quema en los sitios.

Recomendaciones para la conservación de epifitas

Los resultados obtenidos en este estudio muestran evidencia de que la conservación a largo plazo de epífitas dependerá de las áreas naturales protegidas que tengan zonas núcleo exclusivamente para la conservación. En los sitios en donde ocurrirá disturbios antropogénicos será necesario implementar estrategias que permitan que la comunidad de *Tillandsia* no desaparezca de estos sitios. Las estrategias a seguir son: 1. Que los árboles que se seleccionan para proveer de sombra al ganado o para hacer cercas vivas sean forofitos saludables que alberguen la mayor diversidad y abundancia de epífitas del sitio y 2. Incrementar el tiempo de los ciclos del uso y abandono de la tierra hasta por tres décadas.

Investigaciones futuras

Es necesario realizar estudios a largo plazo de la comunidad de *Tillandsia* en la mayor cantidad de tipos de vegetación posibles en el territorio mexicano debido a que México es un centro de diversificación de este género ya que cuenta con 192 especies de las cuales 133 son endémicas. En específico en la Reserva de la Biosfera Chamela Cuixmala se debe de establecer un estudio a largo plazo, para comprender los requerimientos que tiene cada especie de *Tillandsia* para mantener poblaciones viables en la región. Será indispensable realizar trabajos demográficos de las distintas especies de *Tillandsia* y así conocer el tiempo que requiere cada especie en tener su primer evento reproductivo, el intervalo de tiempo entre los distintos eventos reproductivos y la cantidad de eventos reproductivos posibles de un individuo, será indispensable evaluar la dispersión de semillas y realizar experimentos de germinación de semillas en condiciones naturales.

Es necesario conocer la respuesta de la comunidad de *Tillandsia* ante escenarios de calentamiento global debido a que se considera que la comunidad de epífitas es muy vulnerable al calentamiento global, en parte esto se debe a que es una comunidad muy vulnerable a la presencia de huracanes que de acuerdo con los modelos del cambio climático se incrementará la incidencia de huracanes de categoría 4 y 5 en la escala de Saffir-Simpson. En la región de Chamela han ocurrido dos huracanes intensos en los últimos años: el 10 de octubre de 2010 el huracán Jova categoría III en la escala de Saffir-Simpson toco tierra y 23 de octubre de 2015 el huracán Patricia categoría V, ambos huracanes impactaron a la comunidad de *Tillandsia* debido a que en algunos sitios se perdió hasta el 90% de los individuos de *Tillandsia*. Es necesario realizar estudios en la zona para evaluar la capacidad de recuperación de la comunidad e investigar como responderá a largo plazo la comunidad debido a que es posible que existan especies más susceptibles dentro de la comunidad de *Tillandsia*.

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APENDICES

SUPPLEMENTARY MATERIAL

This file contains the following supplementary material:

Supplementary Tables and Figures

This section contains the following tables and figures:

Table S1. *Performance of models in predicting interaction frequencies among epiphyte and woody species*

Table S2. *Phylogenetic signal in species degree, strength, ecological similarity, abundance and wood density*

Figure S1. *Observed and model yielded values of generality, interaction evenness, nestedness (N), number of phorophyte species, phorophyte interaction strength asymmetry and vulnerability*

Figure S2. *Bromeliad-phorophyte observed and example networks yielded by models of network determinants*

Figure S3. *Predicted mean frequencies of models of network determinants against observed frequencies*

Figure S4. *Phylogenetic hypothesis for phorophyte species and* Tillandsia *spp.*

Table S1. Performance of models in predicting interaction frequencies among epiphyte and woody species. The number (%) of links whose observed frequencies fall outside of the 95%CI of the frequencies predicted by the models are indicated, as well as the number (%) of woody species (WS) and of epiphyte species (ES) involved in those interactions. The models shown incorporate data on: A- species abundance, B- bark texture of woody species, D- plant size (DBH), S- spatial overlap, W- wood density, as indicated by the letters composing the name of the model. In the Null model all interactions have the same probability to occur.

Model	Outside CI	Below lower CI			Above upper CI		
	Links	Links	WS	ES	Links	WS	ES
Null	46 (7.6)	0 (0)	0 (0)	0 (0)	46 (7.6)	20 (40)	10 (83.3)
A	87 (14.5)	39 (6.5)	17 (34)	5 (41.6)	48 (8)	20 (40)	11 (91.6)
AS	79 (13.1)	41 (6.8)	25 (50)	6 (50)	38 (6.3)	15 (30)	11 (91.6)
ADS	46 (7.6)	13 (2.1)	11 (22)	4 (33.3)	33 (5.5)	15 (30)	11 (91.6)
ABDS	45 (7.5)	11 (1.8)	9 (18)	4 (33.3)	34 (5.6)	16 (32)	11 (91.6)
ADSW	48 (8)	18 (3)	13 (26)	5 (41.6)	30 (5)	15 (30)	10 (83.3)
ABDSW	43 (7.2)	11 (1.8)	9 (18)	4 (33.3)	32 (5.3)	15 (30)	11 (91.6)

Table S2. Phylogenetic signal for phorophytes and for epiphytes on species degree, species strength, similarity in assemblage of partners and abundance, and for phorophytes on wood density. For degree, strength, abundance and wood density the *K*-statistic (number of topologies with significant phylogenetic signal or P-value) is reported. For ecological similarity, *Z*-statistic (P-value) is reported. Phylogenetic signal in pooled data and Sites 2 and 3 was calculated over 100 fully resolved topologies and averaged. For Site 1 it was calculated over one fully resolved tree.

	Degree	Strength	Ecological similarity	Abundance	Wood density
Phorophytes					
Pooled data	0.42 (45/100)	0.38 (0/100)	593.46 (0/100)	0.32 (0/100)	0.36 (100/100)*
Site 1	0.61 (P = 0.35)	0.49 (P = 0.55)	14.73 (P = 0.37)	0.45 (P = 0.71)	0.53 (P = 0.68)
Site 2	0.32 (0/100)	0.37 (0/100)	211.45 (0/100)	0.45 (11/100)	0.34 (0/100)
Site 3	0.57 (0/100)	0.65 (0/100)	154.44 (0/100)	0.29 (0/100)	0.38 (100/100)**
Epiphytes					
Pooled data	0.86 (30/100)	0.79 (30/100)	94.6 (0/100)	0.57 (0/100)	
Site 1	0.39 (P = 0.88)	0.52 (P = 0.59)	8.61 (P = 0.14)	0.65 (P = 0.72)	
Site 2	0.79 (25/100)	0.66 (25/100)	68.62 (0/100)	0.82 (0/100)	
Site 3	0.68 (0/100)	0.64 (0/100)	29.34 (0/100)	0.67 (33/100)	

* P ≈ 0.09, ** P = 0.06

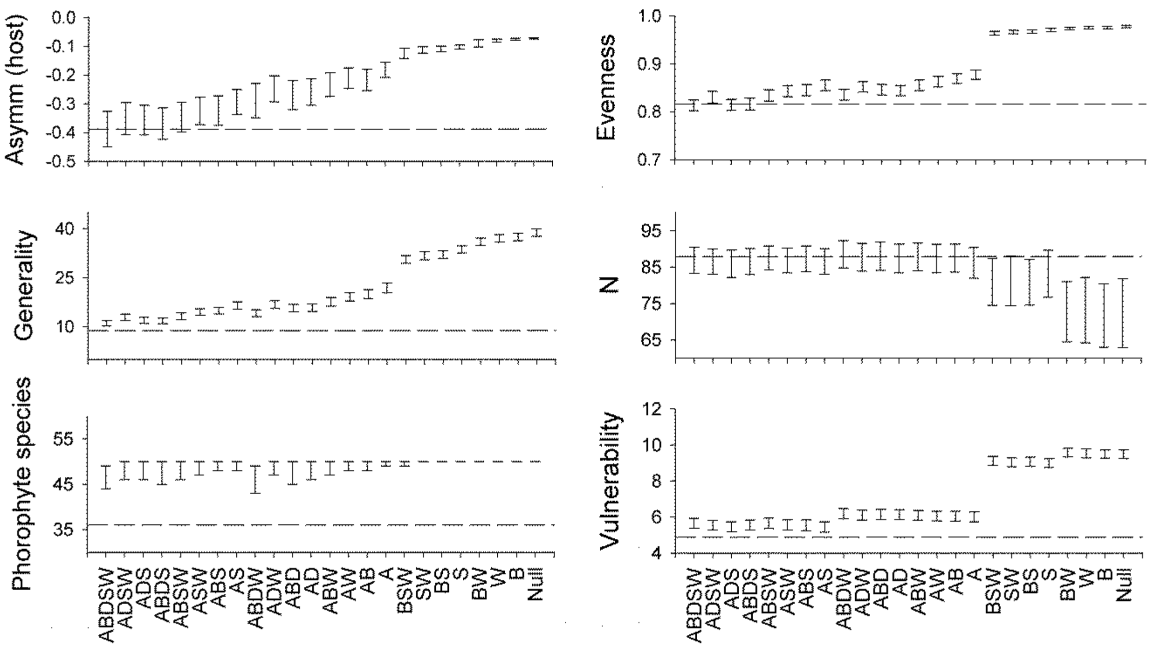

Figure S1. Comparison between observed values of network statistics and the predicted values of networks yielded by models of determinants of network structure incorporating information on: A- species abundance data; B- bark texture of woody species, D- plant size (DBH), S- spatial overlap of epiphyte and woody species; W-wood density of woody species, and their combinations. Null- null model assigning the same probability of occurrence to all interactions. The dashed line indicates the observed value. Phorophyte interaction strength asymmetry, interaction evenness, generality, nestedness (N), number of phorophyte species and vulnerability are shown.

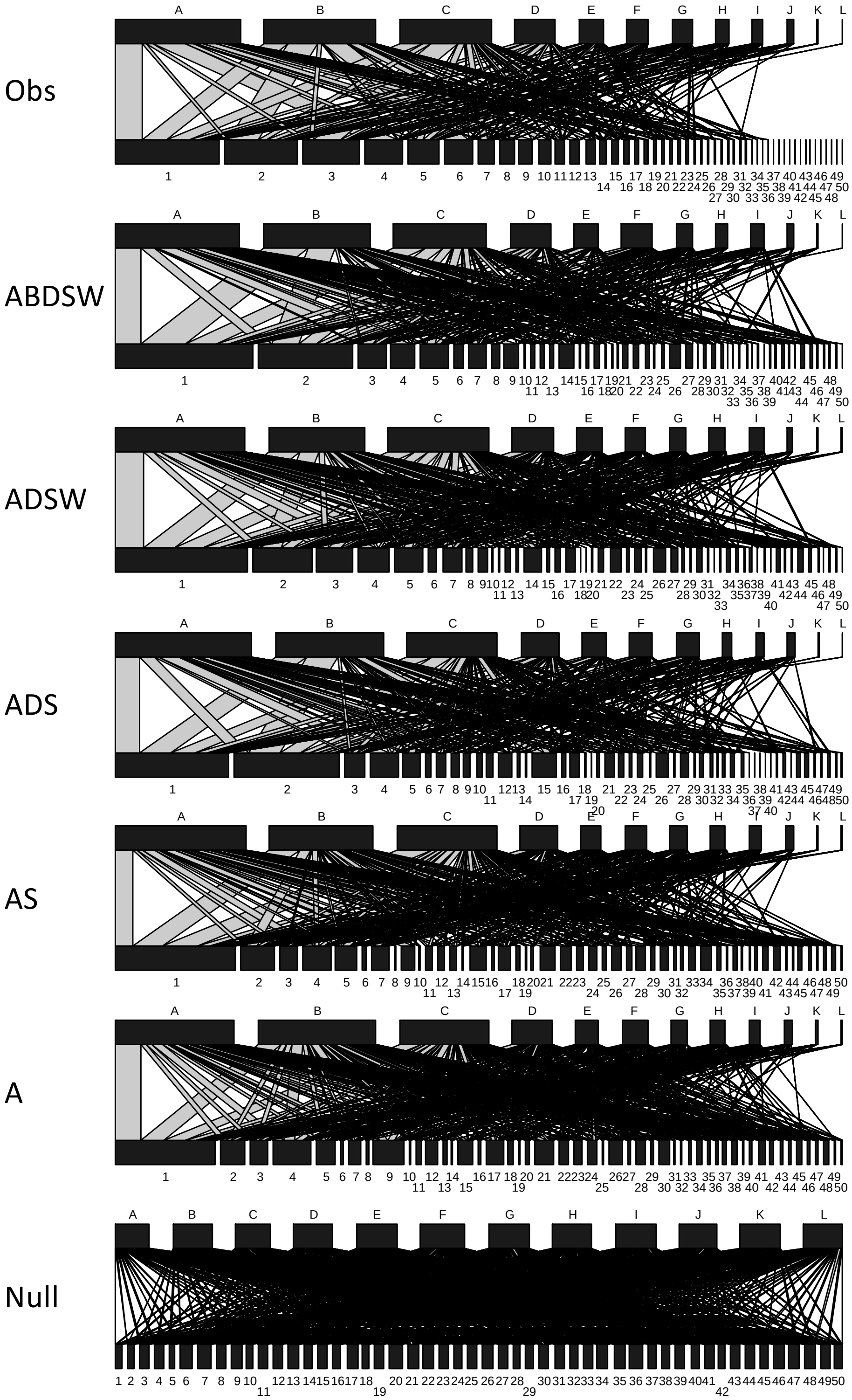

Figure S2. The bromeliad-phorophyte network observed in a tropical dry forest of western Mexico (top) and the interaction networks yielded by one run of the randomization algorithm that assigns interactions according to probability matrices of the models of network determinants that consider: A-abundance of epiphytes and woody species, B-bark texture, D- size of woody individuals (diameter at breast height), S- spatial overlap of epiphyte and woody species and W- wood density, as indicated by the name of the model. On each network, the widths of the rectangles represent the relative interaction frequencies of bromeliad species (top) and phorophyte species (bottom). Links among species and their relative frequency are represented by the lines connecting rectangles and their width, respectively. Networks are drawn to the same scale, and thus interaction frequencies are comparable. Species order and code is the same at all networks. Species identity is shown in Appendix S1.

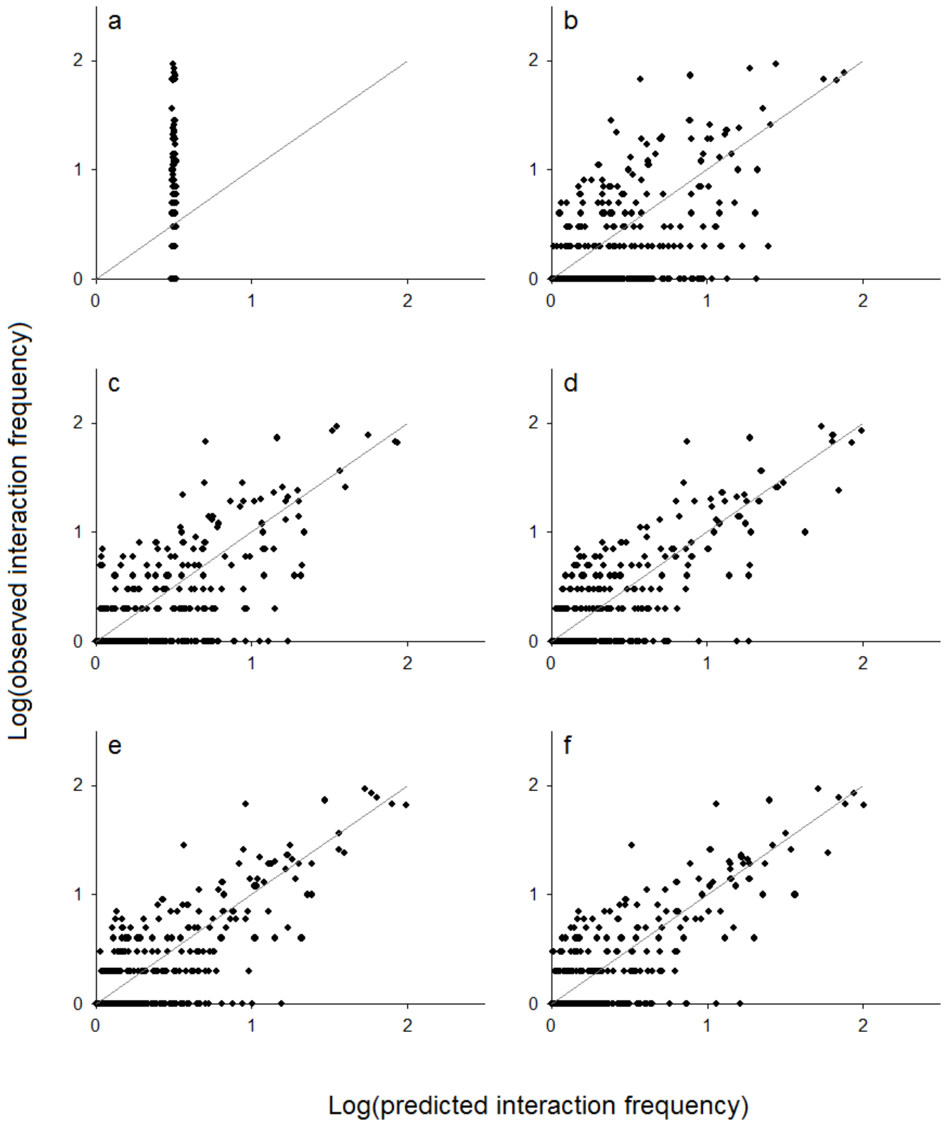

Figure S3. Predicted mean frequencies of models of network determinants against observed frequencies of the 600 possible pairwise interactions between 12 *Tillandsia spp*. and 50 woody species of a tropical dry forest of western Mexico. The best performing models of one, two, three, four and five factors are shown. -a- Null model, b- A model, c- AS model, d- ADS model, e- ADSW model, f- ABDSW model. The line of perfect fit between predicted and observed values is indicated in grey. Model names as in figure 2.

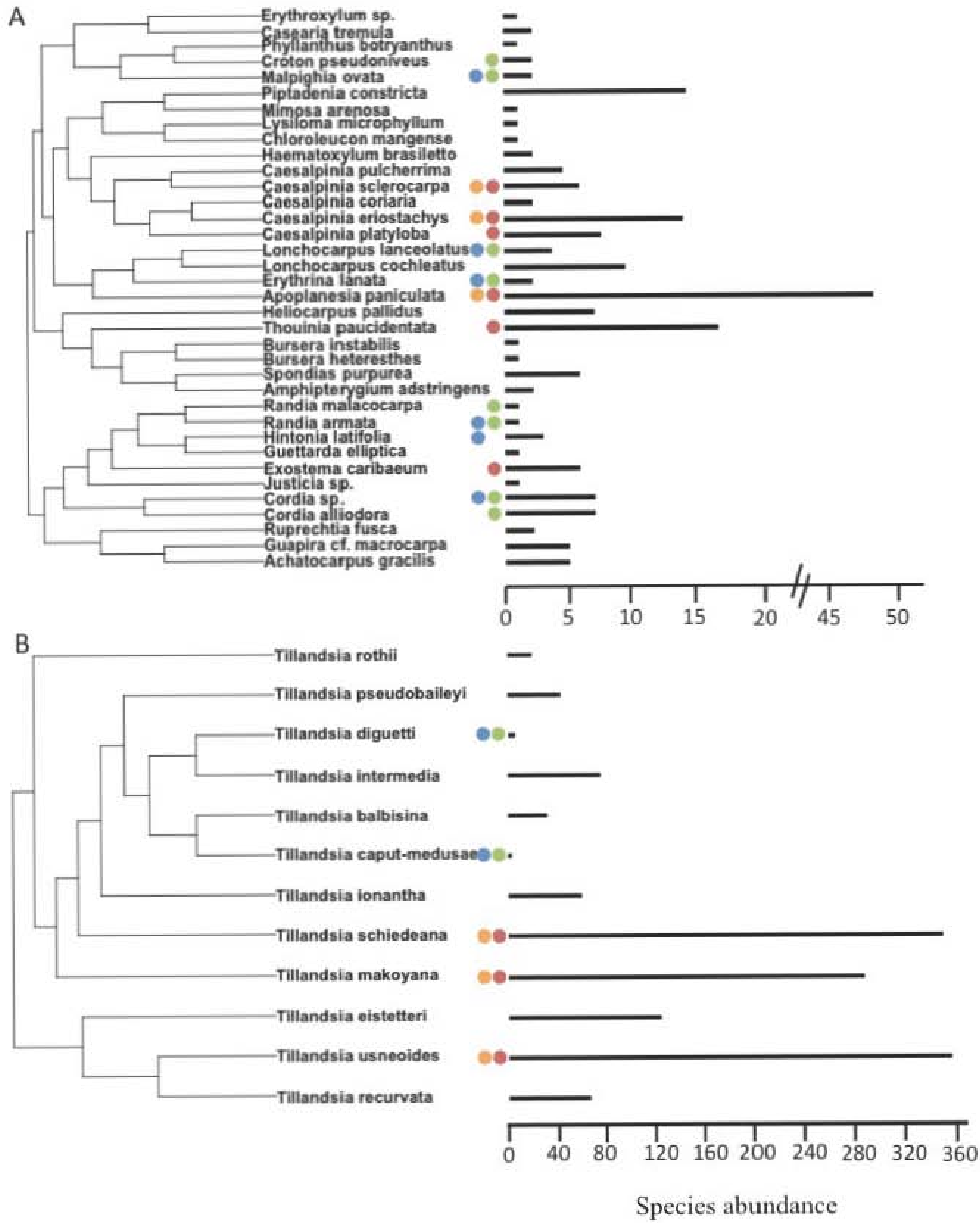

Figure S4. Phylogenetic hypothesis for the pooled dataset of phorophyte species (A) and of

Tillandsia species (B) (a random fully-resolved tree), and its total species abundance. Circles indicate the species with highest (red) and lowest (green) species degree, and highest (orange) and lowest (blue) species strength.

Appendix S1 *Woody and epiphyte species recorded and their trait values*

List of woody species at the study plots. The number (ID) used in figures 1 and S2, bark category and wood density value for each species are shown. In the cases when data on wood density was not available for a given species, the mean value for other species of the genus was used.

FAMILY	**SCIENTIFIC NAME**	**ID**	**BARK**	**WOOD DENSITY**	**WOOD DENSITY REFERENCE**
Acanthaceae	*Justicia sp.*[a]	31	2	0.77	mean value
Achatocarpaceae	*Achatocarpus gracilis*[a]	24	2	0.80	[1]
Amaranthaceae	*Lagrezia monosperma*	46	2	0.87	[1]
Anacardiaceae	*Spondias purpurea*[a]	12	3	0.31	[2]
Boraginaceae	*Cordia alliodora*[a]	17	3	0.73	[2]
	Cordia sp.[a,b]	28	3	0.73	[2]
Burseraceae	*Bursera arborea*	38	1	0.25	[2]
	B. heteresthes[a]	10	2	0.40	[2]
	B. instabilis[a]	20	1	0.24	[2]
Erythroxylaceae	*Erythroxylum sp.*[a,b]	16	2	0.99	[2]
Euphorbiaceae	*Croton alamosanus*	39	2	0.92	[1]
	C. niveus[b]	40	3	0.77	[2]
	C. pseudoniveus[a]	18	3	0.82	[1]
	C. roxanae[b]	41	2	0.77	[2]
	C. suberosus	42	3	0.50	[2]
	Phyllanthus botryanthus[a]	32	2	0.73	[1]
Flacourtiaceae	*Casearia tremula*[a]	23	3	0.74	[2]
	Xylosma velutinum[b]	50	3	0.75	[2]
Julianiaceae	*Amphipterygium adstringens*[a]	11	4	0.39	[2]
Leguminosae	*Apoplanesia paniculata*[a]	1	3	0.94	[2]
	Caesalpinia coriaria[a]	6	4	1.14	[3]
	C. eriostachys[a]	2	4	0.74	[2]
	C. platyloba[a]	5	3	1.03	[2]
	C. pulcherrima[a]	26	3	0.84	[4]
	C. sclerocarpa[a]	3	2	1.39	[2]
	Chloroleucon mangense[a]	25	2	0.99	[5]
	Erythrina lanata[a]	33	3	0.32	[2]
	Haematoxylum brasiletto[a]	13	3	0.95	[2]
	Lonchocarpus cochleatus[a]	21	2	0.79	[2]
	L. lanceolatus[a,b]	34	2	0.80	[2]
	Lysiloma microphyllum[a]	14	2	0.92	[2]
	Mimosa arenosa[a]	8	2	1.01	[2]
	Piptadenia constricta[a]	9	3	1.11	[2]

	Pterocarpus orbiculatus[b]	47	3	0.45	[4]
Malpighiaceae	*Bunchosia palmeri*	37	2	0.74	[4]
	Malpighia ovata[a]	35	2	0.77	mean value
Myrtaceae	*Eugenia capuli*[b]	43	2	0.82	[3]
Nyctaginaceae	*Guapira cf. macrocarpa*[a]	22	3	0.69	[2]
Polygonaceae	*Ruprechtia fusca*[a]	27	3	0.70	[2]
Rubiaceae	*Exostema caribaeum*[a]	7	4	0.99	[2]
	Guettarda elliptica[a]	19	2	0.97	[2]
	Hintonia latifolia[a]	30	3	0.87	[2]
	Randia armata[a,b]	36	2	0.78	[4]
	R. malacocarpa[a,b]	29	2	0.78	[4]
Sapindaceae	*Serjania brachycarpa*	48	2	0.77	mean value
	Thouinia paucidentata[a]	4	2	0.98	[2]
Sterculiaceae	*Guazuma ulmifolia*	44	3	0.67	[2]
	Waltheria indica	49	2	0.77	mean value
Theophrastaceae	*Jacquinia pungens*	45	2	0.81	[2]
Tiliaceae	*Heliocarpus pallidus*[a]	15	3	0.69	[2]

a Phorophytes

b Mean value for the genus was used

List of vascular epiphyte species of the Bromeliaceae at the study plots. For each species, the letter (ID) used in figures 1 and S2, the abundance by site, the presence of secondary dispersal and whether the species is endemic to Mexico are indicated.

SCIENTIFIC NAME	**ID**	**SITE (ABUNDANCE)**	**SECONDARY DISPERSAL**[a]	**Endemic**[b]
Tillandsia balbisiana	I	1(8), 2(21), 3(2)		
T. caput-medusae	L	1(0), 2(1), 3(0)		
T. diguetii	K	1(0), 2(4), 3(0)		X
T. eistetteri	D	1(0), 2(112), 3(1)		X
T. intermedia	E	1(0), 2(25), 3(43)	X	X
T. ionantha	G	1(2), 2(14), 3(39)		
T. makoyana	C	1(6), 2(197), 3(53)		X
T. pseudobaileyi	H	1(0), 2(36), 3(1)		
T. recurvata	F	1(5), 2(46), 3(10)		
T. rothii	J	1(0), 2(4), 3(15)		X
T. schiedeana	B	1(6), 2(10), 3(295)		
T. usneoides	A	1(193), 2(135), 3(20)	X	

a *T. intermedia*: R. Sayago, personal observation. *T. usneoides*: [6]

b [7]

Abundance by site, summed DBH value by site, and epiphyte partners for the woody species at the study plots.

WOODY SPECIES ID	SITE (ABUNDANCE)	SITE (DBH)	PARTNER ID (frequency)
31	1(0), 2(1), 3(0)	1(0), 2(13), 3(0)	I(1), D(1)
24	1(1), 2(2), 3(1)	1(6), 2(15), 3(13)	E(2), G(2), B(1)
46	1(0), 2(0), 3(1)	1(0), 2(0), 3(6)	
12	1(5), 2(1), 3(0)	1(99), 2(15), 3(0)	I(1), C(1), H(1), A(25)
17	1(4), 2(3), 3(0)	1(40), 2(27), 3(0)	A(12)
28	1(7), 2(0), 3(0)	1(71), 2(0), 3(0)	A(3)
38	1(0), 2(0), 3(1)	1(0), 2(0), 3(6)	
10	1(0), 2(0), 3(1)	1(0), 2(0), 3(18)	E(1), C(3), F(1), B(27)
20	1(0), 2(1), 3(0)	1(0), 2(9), 3(0)	D(1), E(2), C(3), A(2)
16	1(0), 2(1), 3(0)	1(0), 2(14), 3(0)	D(6), E(2), C(4), J(1), B(1)
39	1(0), 2(0), 3(1)	1(0), 2(0), 3(6)	
40	1(2), 2(0), 3(0)	1(18), 2(0), 3(0)	
18	1(2), 2(0), 3(0)	1(17), 2(0), 3(0)	A(10)
41	1(1), 2(1), 3(1)	1(6), 2(0), 3(5)	
42	1(0), 2(1), 3(1)	1(0), 2(6), 3(7)	
32	1(0), 2(0), 3(1)	1(0), 2(0), 3(6)	G(1), B(1)
23	1(0), 2(1), 3(1)	1(0), 2(9), 3(7)	E(2), G(2), B(3)
50	1(1), 2(0), 3(0)	1(14), 2(0), 3(0)	
11	1(0), 2(1), 3(1)	1(0), 2(11), 3(20)	D(4), E(2), G(5), C(8), F(2), B(7)
1	1(1), 2(26), 3(21)	1(76), 2(241), 3(265)	I(5), D(25), E(9), G(20), C(66), H(6), F(13), J(5), B(65), A(76)
6	1(0), 2(1), 3(1)	1(0), 2(10), 3(19)	I(1), D(1), E(7), G(2), C(2), B(67)
2	1(0), 2(5), 3(8)	1(0), 2(173), 3(226)	I(2), K(1), D(27), E(18), G(11), C(23), H(9), F(13), J(6), B(83), A(9)
5	1(0), 2(7), 3(1)	1(0), 2(87), 3(5)	I(3), D(19), E(4), G(3), C(18), H(4), F(12), J(1), B(1), A(22)
26	1(0), 2(0), 3(5)	1(0), 2(0), 3(61)	C(1), B(3)
3	1(0), 2(5), 3(1)	1(0), 2(78), 3(16)	I(7), L(1), K(3), D(16), E(5), G(1), C(72), H(10), F(6), J(5), B(13), A(18)
25	1(0), 2(0), 3(1)	1(0), 2(0), 3(14)	E(1), B(3), A(1)
33	1(0), 2(1), 3(1)	1(0), 2(7), 3(6)	A(1)
13	1(0), 2(0), 3(2)	1(0), 2(0), 3(20)	E(4), C(3), B(18)
21	1(7), 2(1), 3(1)	1(79), 2(8), 3(7)	D(1), C(2), H(1), A(4)
34	1(0), 2(1), 3(3)	1(0), 2(6), 3(20)	C(1)

14	1(0), 2(1), 3(0)	1(0), 2(11), 3(0)	I(3), D(1), G(1), C(7), H(4), F(2), B(1)
8	1(1), 2(0), 3(0)	1(50), 2(0), 3(0)	I(4), C(5), F(4), B(6), A(21)
9	1(14), 2(0), 3(0)	1(125), 2(0), 3(0)	I(2), C(1), F(1), A(35)
47	1(1), 2(0), 3(0)	1(15), 2(0), 3(0)	
37	1(2), 2(0), 3(0)	1(18), 2(0), 3(0)	
35	1(1), 2(1), 3(0)	1(17), 2(8), 3(0)	C(1)
43	1(1), 2(0), 3(0)	1(12), 2(0), 3(0)	
22	1(3), 2(2), 3(0)	1(18), 2(19), 3(0)	C(2), A(6)
27	1(0), 2(0), 3(2)	1(0), 2(0), 3(17)	E(1), B(2)
7	1(0), 2(6), 3(0)	1(0), 2(47), 3(0)	D(5), E(5), G(3), C(18), H(1), F(4), J(1), B(1), A(6)
19	1(0), 2(0), 3(1)	1(0), 2(0), 3(6)	E(2), G(1), B(6)
30	1(0), 2(1), 3(2)	1(0), 2(12), 3(14)	C(1), B(1)
36	1(1), 2(0), 3(0)	1(7), 2(0), 3(0)	A(1)
29	1(0), 2(1), 3(0)	1(0), 2(7), 3(0)	D(3)
48	1(1), 2(1), 3(0)	1(7), 2(6), 3(0)	
4	1(11), 2(3), 3(3)	1(207), 2(26), 3(17)	I(1), D(2), E(1), G(2), C(3), H(1), F(2), B(1), A(92)
44	1(2), 2(0), 3(0)	1(52), 2(0), 3(0)	
49	1(0), 2(1), 3(0)	1(0), 2(7), 3(0)	
45	1(4), 2(0), 3(0)	1(44), 2(0), 3(0)	
15	1(0), 2(3), 3(4)	1(0), 2(40), 3(54)	I(1), D(1), G(1), C(11), F(1), A(4)

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Appendix S2 *Supplementary Methods*

This appendix contains further information of the following sections of the methods:

a) Network statistics utilized

b) Incorporation of DBH and bark texture of woody individuals to models of network determinants

c) Likelihood analysis

d) Randomization algorithm

e) Phylogenetic signal analysis

a) Details on the network statistics utilized

We used network statistics that characterize several aspects of network structure [1]: a) connectance, the proportion of links that occur from the total possible (C= number of links/*IJ*); b) nestedness, the tendency of specialized species to interact with a subset of the interaction partners of more generalized species [2], which takes values of increasing nestedness from 0 to 100; to allow comparison with previous work, we used N=100-T, where T is the matrix temperature proposed by Atmar & Patterson [3], with improvements by Rodríguez-Gironés and Santamaría [4]; we also calculated NODF [5]; c) interaction evenness, the heterogeneity of the interaction frequencies in the network [6]; it takes values of increasing evenness from 0 to 1; d) H_2’, the standardized two dimensional Shannon entropy, a quantitative metric of specialization among two parties in the entire network [7]; it takes values of increasing specialization, from 0 to 1; e) generality and vulnerability, the weighted mean number of phorophyte species per epiphyte species, and epiphyte species per phorophyte species respectively [8]; f) interaction strength asymmetry, the difference between a focal species' effect on its interaction partners and the reciprocal effect of the interaction partner on the focal species [9]; it takes values from 0 (high strength symmetry), to 1 (high asymmetry), with the sign indicating the direction of the asymmetry, negative if a high proportion of the focal species' interactions occur with the interacting partner in question (experiences strong effects of its partner), and positive if the focal species represents a high proportion of the interactions of its partner (exerts a strong effect) . The average for phorophytes and for epiphytes was calculated. a) and b) are based on unweighted links (binary matrices), while the remaining are based on weighted links (considering frequencies of interaction).

To allow for comparison, significance of the observed nestedness was assessed against the equivalent to null model 2 of Bascompte et al. [2] that considers species degree (number of links per species). For N, the matrix temperature was calculated using the software BINMATNEST [4], with the recommended settings and null model 3. For NODF we used ANINHADO 3.0 [10] and null model CE.

b) Incorporating diameter at breast height (DBH) and bark texture of woody species to models of network determinants

To incorporate the effect of plant size (DBH) and bark texture in the models, we considered the probability of presence of epiphytes given a bark and/or DBH category, and the expected abundance given the DBH category (bark category did not significantly influence epiphyte abundance). Model calculation is specified in Table 1 of the main text. We assessed the effect of DBH and bark texture on the likelihood of establishment of bromeliads on woody individuals using a forward stepwise (likelihood ratio) logistic regression, which models the probability of an event with two outcomes. The response variable was the presence or absence of bromeliads on woody individuals, and the predicting variables, considered as continuous, were the DBH category (in increments of 1cm) and bark texture category of woody individuals. The model including both variables was significant (Omnibus test for model coefficients: $X^2 = 37.964$, d.f. = 2, $P < 0.001$, Nagelkerke $r^2 = 0.133$). We used the variables of the logistic regression equation (Table 1 in this Appendix) to calculate the probability of finding epiphytes on woody individuals (see Table 1 of the main text), which increased with rougher and more ornamented barks, and with increasing size of woody individuals.

The relation between phorophyte DBH (only woody individuals with epiphytes) and bromeliad abundance was assessed with a simple linear regression. The logarithm of both variables was used. There was a positive and significant relation between the size of phorophytes (DBH) and the epiphytic bromeliad abundance ($F_{1,165} = 758.508$, $P<0.001$, $R^2 = 0.821$), with the coefficient of the regression equation (intercept through the origin) $B = 0.777 \pm 0.028$ SE.

Table 1. Variables in the logistic regression equation explaining the presence of epiphytes on woody individuals (n =363): coefficients (B) and their standard error (SE), the Wald statistic, degrees of freedom (d.f.), significance (Sig.), and the odds ratio for each variable at steps 1 and 2 of a forward stepwise logistic regression are reported.

Step	Variable	B	SE	Wald	d.f.	Sig.	Odds ratio[a] [Exp(B)]
Step 1	DBH	0.077	0.018	18.708	1	<0.0001	1.080
	Constant	-0.843	0.181	21.631	1	<0.0001	0.430
Step 2	Bark[b]	0.610	0.187	10.645	1	0.001	1.841
	DBH[c]	0.068	0.018	14.301	1	<0.0001	1.070
	Constant	-2.410	0.523	21.219	1	<0.0001	0.090

a Indicates the predicted change in odds for a unit increase in the predictor. An odds ratio >1 results in greater probabilities of bearing epiphytes for hosts at higher categories of the predictor.

b Change in -2 log likelihood if the variable removed from the model is significant at the level of P =0.001

c Change in -2 log likelihood if the variable removed from the model is significant at the level of P <0.0001

c) Likelihood analysis

Assuming a multinomial distribution of the probabilities of interaction between woody species *i* and epiphyte species *j* [11], we evaluated the ability of abundance, bark texture, species spatial overlap and plant size to predict the observed frequencies of pairwise interactions by calculating the likelihood of probability matrix **P** given the observed matrix **Y** as follows:

$$L = \frac{N!}{\prod_{i=1}^{I} \prod_{j=1}^{J} y_{ij}!} \prod_{i=1}^{I} \prod_{j=1}^{J} p_{ij}^{y_{ij}}$$

Where N is the sum of elements of matrix **Y**. We used the function dmultinom of the Stats package of R [12] to calculate the likelihoods for the models. To compare the performance of the different models we used the Akaike's Information Criterion (AIC) [13] AIC = -2 ln(L) + 2k, where k is the number of parameters used to generate a probability matrix. The number of parameters was the number of factors involved in the calculation of each probability matrix, except for when plant size is included in a model, which involved two parameters (probability of presence and expected abundance). The model with the lowest ΔAIC, the difference in AIC between a given model and the AIC of matrix **Y** fitted to itself (**Y** normalized), indicates the model that better fits the data.

d) Randomization algorithm

We used the randomization algorithm of Vazquez et al. [11] that assigns the total number of observed interactions (sum of elements in **Y**) to cells of a matrix of size **Y**; each cell has a probability of receiving an interaction defined by the probability matrix of a model. The only constraint of this algorithm is to assign at least one interaction per species, for which in a first step it selects a column for each row with a probability equal to the summed probability of the columns. In the same way it assigns an interaction to each column. After each row and column receive at least one interaction, all cells are considered when assigning the remaining interactions (here a total of 1304 interactions are assigned), and on each step (each assigned interaction) an interaction is added to the selected cell giving rise to a quantitative matrix. The sampling of cells is with replacement. To simulate the realistic scenario in which all woody individuals and species are potential phorophytes, all woody species are represented in the matrices. Because not all woody species had interactions with epiphytes, we did not constrain the algorithm to assign at least one interaction per woody species, though we left the constraint for epiphyte species. This allows for the possibility that by chance some rows (woody species) remain empty. Network statistics are calculated excluding non-interacting woody species.

We ran the algorithm and calculated the network statistics of the observed and generated matrices using the functions provided by Vázquez et al. [11] for R, with modifications to include the calculation of H_2', generality and vulnerability, using the networklevel function in the Bipartite package [1, 14] and nestedness using the nestedtemp and nestednodf functions in the Vegan package [15].

e) Phylogenetic signal analyses

A phylogenetic hypothesis was constructed for each site and assemblage of epiphyte species and their host trees, and for all sites pooled. Phylogenetic hypotheses for host species were constructed using Phylomatic software [16]. To build our phylogeny, we employed the conservative tree available in Phylomatic, which leaves nodes with less than 80% support as soft polytomies. Phylogenetic hypotheses of epiphyte assemblages were constructed in Mesquite v2.75 [17], based on Barfuss et al. [18] and Chew et al. [19]. Since there are no available calibration points for *Tillandsia*, we set all branch lengths equal to one. Topological uncertainty (polytomies) was resolved by generating 100 fully resolved trees in Mesquite v2.75.

We evaluated the presence of phylogenetic signal on species degree, species strength [20] and on the assemblage of interacting partners of the species (ecological similarity) [21]. The presence of a phylogenetic signal indicates that related species have similar structural features or tend to interact with the same set of species. The amount of phylogenetic signal was evaluated with the K- statistic [22], which compares the signal of the data to the expected signal under a Brownian motion model ($K = 1$) of trait evolution on a phylogeny. K was calculated with the function phylosignal of the Picante package of R [23]. We checked Brownian motion assumptions [24] by computing the correlation between the absolute value of each standardized contrast against its standard deviation (i.e. the square root of the sum of its branch lengths). The absence of significant trends would suggest that contrasts are appropriately standardized. All variables fitted Brownian motion assumptions after log-transformation. To detect phylogenetic signal on the identity of each species' interaction partners (ecological similarity) we used Mantel tests comparing phylogenetic distance matrices with ecological distance matrices using the function mantel of the Vegan package of R [15]. Phylogenetic distance matrices between pairs of bromeliad species and pairs of host species were estimated as the expected covariance of the trait between the two species [22]. Ecological distances for pairs of bromeliad species and pairs of host species were calculated as 1-S, where S is the Jaccard index of similarity of interacting partners [25].

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Supplementary Material (SM)

Appendix SM-1. Epiphyte and phorophyte species registered along a successional gradient in western Mexico, in parenthesis is the code of species (*= epiphytes species. endemic to Mexico).

Epiphytes

Bromeliaceae

- *Tillandsia balbisiana* (TIBA)
- *T. caput-medusae* (TICA)
- *T. diguettii** (TIDI)
- *T. eistetteri** (TIEI)
- *T. intermedia** (TIIN)
- *T. ionantha* (TIIO)
- *T. jaliscomonticola** (TIJA)
- *T. makoyana** (TIMA)
- *T. pseudobaileyi* (TIPS)
- *T. recurvate* (TIRE)
- *T. rothii** (TIRO)
- *T. schiedeana* (TISC)
- *T. usneoides* (TIUS)

Phorophytes

Acanthaceae

- *Justicia sp.* (JUSSP)

Achatocarpaceae

- *Achatocarpus gracilis* (ACHGRA)

Anacardiaceae

- *Spondias purpurea* (SPOPUR)

Boraginaceae

- *Cordia alliodora* (CORALL)

Burseraceae

- *Bursera arborea* (BURARB)
- *B. heteresthes* (BURHET)
- *B. instabilis* (BURINS)

Erythroxylaceae

Erythroxylum havanense (ERYHAV)

Euphorbiaceae

Cnidosculus spinosus (CNISPI)
Croton pseudoniveus (CROPSE)
C. roxanae (CROROX)
C. suberosus (CROSUB)
Phyllanthus botryanthus (PHYBOT)
Piranhea mexicana (PIRMEX)

Flacourtiaceae

Casearia corymbosa (CASCOR)
C. tremula (CASTRE)

Julianiaceae

Amphipterygium adstringens (AMPADS)

Leguminosae

Acacia farnesiana (ACAFAR)
Apoplanesia paniculata (APOPAN)
Bauhinia subrotundifolia (BAUSUB)
Caesalpinia caladenia (CAECAL)
C. coriaria (CAECOR)
C. eriosthachys (CAEERI)
C. platyloba (CAEPLA)
C. pulcherrima (CAEPUL)
C. sclerocarpa (CAESCL)
Chloroleucon mangense (CHLMAN)
Erythrina lanata (ERYLAN)
Haematoxylum brasiletto (HAEBRA)
Lonchocarpus cochleatus (LONCOC)
L. constrictus (LONCON)
L. lanceolatus (LONLAN)
Lysiloma microphyllum (LYSMIC)
Mimosa arenosa (MIMARE)
Piptadenia constricta (PIPCON)

Malpighiaceae

Malpighia ovata (MALOVA)

Nyctaginaceae

Guapira cf. macrocarpa (GUAMAC)

Polygonaceae

Coccoloba liebmannii (COCLIE)
Podopterus mexicanus (PODMEX)
Ruprechtia fusca (RUPFUS)

Rubiaceae
- *Exostema caribaeum* (EXOCAR)
- *Guettarda elliptica* (GUEELL)
- *Hintonia latifolia* (HINLAT)
- *Randia armata* (RANAR)
- *R. malacocarpa* (RANMAL)

Sapindaceae
- *Serjania brachycarpa* (SERBRA)
- *Thouinia paucidentata* (THOPAU)

Theophrastaceae
- *Jacquinia pungens* (JACPUN)

Tiliaceae
- *Heliocarpus pallidus* (HELPAL)

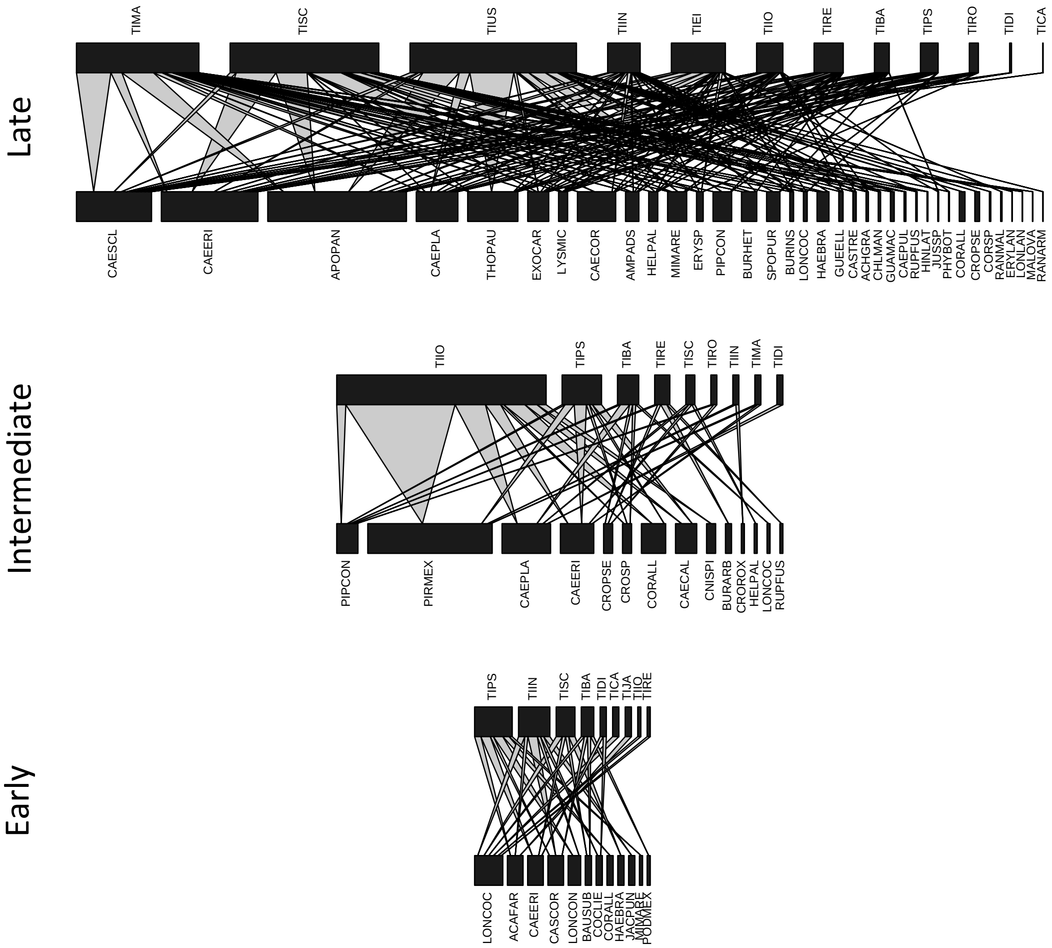

Figure SM-1. The bromeliad-phorophyte networks of the early (bottom), intermediate (middle) and late (top) successional stages of tropical dry forest in western Mexico. Rectangles represent epiphyte (top) and phorophyte (bottom) species. The width of the rectangles represents the relative interaction frequencies of bromeliad and phorophyte species. Links among species and their relative frequency are represented by triangles connecting the rectangles and their width, respectively. For a better display, the bromediad-phorophyte networks of the early and intermediate succesional stages are represented 6.3 times wider than the late successional stage network. Phorophyte species codes are the first three letters of the genus and the first three letters of the species. Epiphyte species codes are the first two letters of the genus and species. Species identity is shown in appendix SM-1.

Table SM-1. Nestedness results for the epiphyte-phorophyte networks from early, intermediate and late successional sites and stages (site datasets for each stage were pooled to construct the networks) of tropical dry forest in western Mexico. *NODF*, *Z-score* of NODF, mean NODF for null networks and *P-values* are given for each network. Two sites from the early stage had only one epiphyte and one phorophyte species and were omitted from the site level analyses.

Successional stage	Site id #	*NODF*	*Z-score*	mean *NODF* (1000 null networks)	*P-value*
Networks by site					
Early	1	43.83	0.90	38.35	0.375
Intermediate	2	85.00	1.98	62.02	0.117
	3	19.44	-0.32	21.26	0.878
	4	17.11	-0.85	21.32	0.455
Late	5	71.24	2.04	55.51	0.037*
	6	75.14	4.36	60.36	0.001***
	7	67.82	2.67	56.33	0.013*
Networks by stage (pooled datasets):					
Early	3 sites	40.28	0.83	35.95	0.375
Intermediate	3 sites	36.75	-0.11	37.31	0.920
Late	3 sites	62.89	2.82	56.35	0.007**

Table SM-2. Pearson correlation coefficients among network indices analysed and network dimensions.

	Strength	Links	Size
Indices:			
Connectance	0.26	0.15	-0.02
Generality	0.92**	0.88**	0.88**
$H_2{}'$	-0.69	-0.62	-0.54
Interaction evenness	-0.28	-0.05	0.09
NODF	0.58	0.47	0.36
Specialization asymmetry	0.44	0.32	0.29
Vulnerability	0.79*	0.92**	0.92**
Web asymmetry	-0.81*	-0.73⍰	-0.73⍰
Z_{NODF}	0.88**	0.83*	0.75⍰
Dimensions:			
Interaction strength		0.96***	0.92**
Number of links	0.96***		0.98***
Network size	0.92**	0.98***	

***$P<0.001$
** $P<0.01$
* $P<0.05$
⍰ $P<0.062$

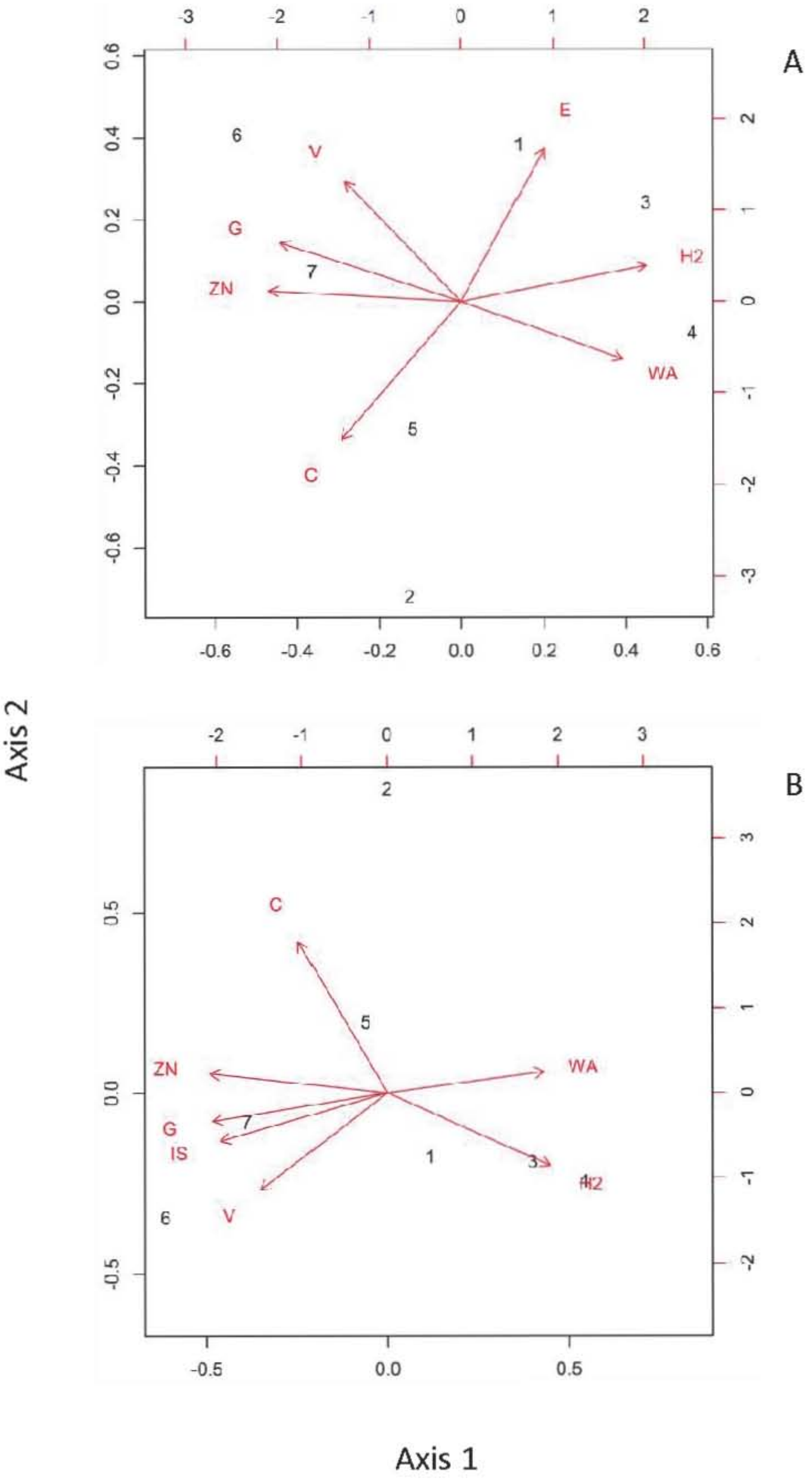

Figure SM-2. Principal component analyses including different indices. A-PCA of network indices of main text except specialization asymetry (proportion of variance explained: 0.62 in first component and 0.25 in second component). B- PCA including interaction strength, the network indices most correlated to it, and the least correlated index (connectance) (proportion of variance explained: 0.72 in first component and 0.18 in second component). C- connectance, E- interaction evenness, G- generality, H2- H_2´specialization, IS- interaction strength, SA- specialization asymmetry, V- vulnerability, WA- web asymmetry, ZN- *Z-score* of *NODF*.

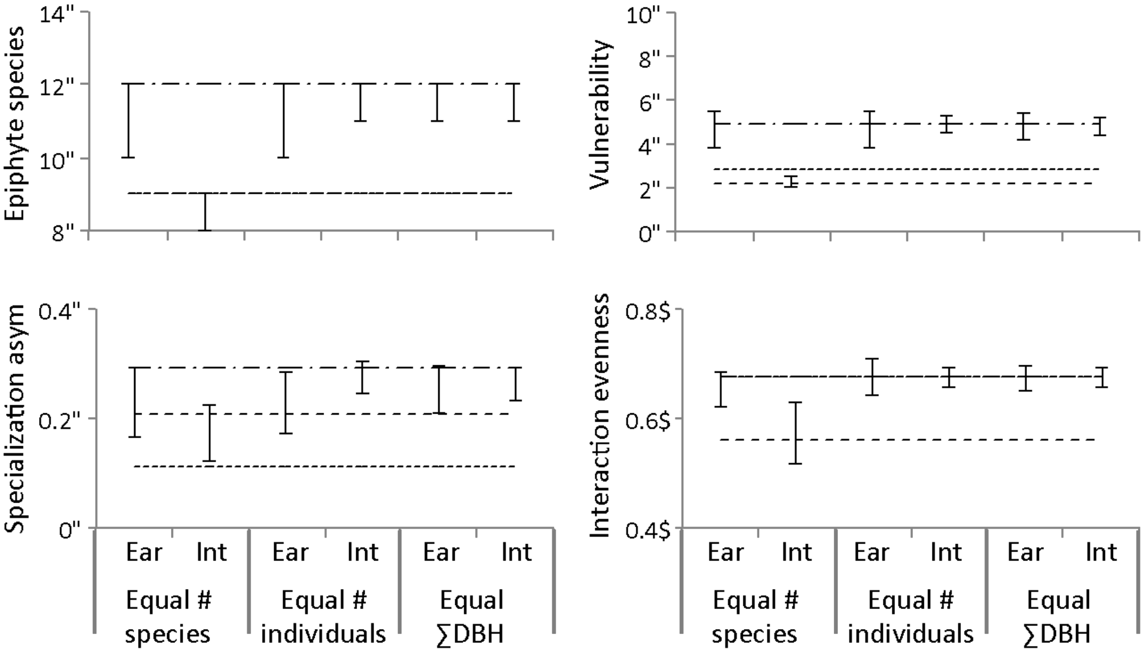

Figure SM-3. Mean index values ± 95% confidence intervals of networks generated by randomly removing tree species or individuals from the late successional stage network (n=100), matching the number of species, individuals and biomass (summed DBH across trees) of the successional stages. Dotted line: observed value for early successional stage, dashed line: observed value for the intermediate successional stage, dotted-dashed line: observed value for the late successional stage. Ear= Early successional stage, Int= Intermediate successional stage. Specialization asym= Specializacion asymmetry.