El Colegio de la Frontera Sur

Factores determinantes sobre la presencia de murciélagos en bosques secundarios bajo manejo tradicional en Lacanhá, Selva Lacandona, Chiapas, México

TESIS

Presentada como requisito parcial para optar al grado de Doctor en Ciencias en Ecología y Desarrollo Sustentable

por

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2013

El Colegio de la Frontera Sur

San Cristobal de las Casas, 19 de abril de 2013.

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Factores determinantes de la presencia de murciélagos en bosques secundarios bajo manejo tradicional en Lacanhá, Selva Lacandona, Chiapas, México

para obtener el grado de:

Doctor en Ciencias en Ecología y Desarrollo Sustentable

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Agradecimientos

Quiero agradecer a mi tutor, el Dr. Samuel I. Levy Tacher por su apoyo y la oportunidad de trabajar con murciélagos en la Selva Lacandona durante los últimos cuatro años.

A Cristina Peñaloza Guerrero quiero agradecer por su amor y apoyo incondicional durante todos los años.

A los técnicos que ayudaron con el trabajo de campo en la selva, Manuel Castellanos Chan’kin, José Chan’kin, Adolfo Chan’kin, Matias Chan’kin, Eduardo Chan’kin, Moniek Wulms, Rianne van Toor, Vita Hommersen, Antonio Sánchez González y Merle Rodríguez. Gracias a Eva Chan’kin y Manuel Castellanos por prestar sus acahuales.

Un agradecimiento especial al Dr. Jorge Galindo González, Dr. Neptali Ramírez Marcial, Dr. Luis Bernardo Vázquez y Dr. Fred de Boer por su asesoría durante la investigación.

Al Consejo Nacional de Ciencia y Tecnologia – CONACyT México, por la beca otorgada para la realización de mis estudios.

Al Idea Wild y Fondo Institucional de Fomento Regional para el Desarrollo Científico, Tecnológico y de Innovación (FORDECYT) por proveer redes de niebla para la captura de murciélagos.

A toda mi familia, y en especial mi mama, papa, mis dos hermanas y mi hermano por su apoyo en todos mis viajes hacia el extranjero.

Resumen general

El paisaje en la comunidad de Lacanhá-Chansayab en Chiapas, México es excepcional dentro del contexto regional, al presentar una matriz de selva interrumpida por pequeñas áreas de milpas o vegetación secundaria. Este paisaje heterogéneo, determina la estructura de la comunidad de los murciélagos, en términos de la disponibilidad de alimento y refugios.

La presente tesis se enfocó en evaluar y analizar el efecto de la matriz de selva sobre la comunidad de murciélagos y la dispersión de semillas en parches de bosque secundario bajo manejo tradicional lacandón. El primer objetivo de la tesis fue evaluar la diversidad, abundancia, riqueza y la contribución a la diversidad total de los murciélagos en bosques secundarios, dominados por *O. pyramidale* y rodeados parcial (<35%) y mayormente (>85%) por selva. También, se evaluó la estructura y composición de la vegetación secundaria y de las áreas con selva en relación con la presencia de los murciélagos. El segundo objetivo fue evaluar la diversidad y abundancia de semillas dispersadas por murciélagos en la selva y parches de bosque secundario con diferente proporción de selva circundante, y se relacionó la disponibilidad de alimento con la dispersión de semillas.

La diversidad y riqueza de los murciélagos fueron mayores en la selva, y la diversidad de murciélagos entre la selva y los parches de bosque secundario mayormente rodeados de selva fue similar. El bosque secundario parcialmente rodeado de selva presentó una menor diversidad en relación con las otras

condiciones. La diversidad y riqueza de murciélagos y la contribución total a la diversidad estuvieron correlacionadas positivamente con la proporción de selva que rodea a los bosques secundarios, mientras que la abundancia de murciélagos fue positivamente correlacionada con la cobertura de dosel.

La diversidad y riqueza de semillas dispersadas por los murciélagos en la selva fue similar a la encontrada en parches rodeados mayormente por selva. Además, en estas condiciones se encontró una mayor abundancia de murciélagos dispersando semillas de especies sucesionales tardías en comparación con la registrada en los parches parcialmente rodeados por selva, donde los murciélagos dispersaron principalmente semillas de arbustos y árboles de etapas sucesionales tempranas. Dos murciélagos frugívoros grandes (*Artibeus lituratus* y *A. jamaicensis*) fueron más abundantes en la selva y parches mayormente rodeados por selva. Estas especies dispersaron semillas de árboles de diferentes etapas sucesionales como *Cecropia* spp, *Ficus* spp y *Brosimum alicastrum*. En cambio la dispersión de semillas por los murciélagos pequeños (*Carollia sowelli* y *C. perspicillata*) en bosques secundarios con menor proporción de selva, fue dominada por especies de etapas sucesionales tempranas (*Piper auritum* y *Piper aduncum*). Para ambos procesos es probable que los murciélagos contribuyan con la dispersión de semillas que favorece la regeneración de la selva.

Capítulo I

Introducción general

Introducción

México es uno de los cinco países más ricos en biodiversidad en el mundo (Myers et al. 2000), e incluye el área megadiversa en la Selva Lacandona, Chiapas (Mendoza y Dirzo 1999). En esta región la mayoría de los mamíferos son murciélagos (57%), con una riqueza que abarca aproximadamente 60 especies (Medellín 1994). El impacto de las actividades humanas sobre las selvas mexicanas ha sido intenso desde tiempos prehispánicos (Amram 1937), y se ha acentuado sobre todo en años recientes. En particular, en la Selva Lacandona en el estado de Chiapas, el 23% de su área total se ha convertido en potreros, milpas y bosque secundario en menos de 20 años (Mendoza y Dirzo 1999), como consecuencia de un fuerte proceso de colonización con el establecimiento de numerosos centros de población humana, la expansión de las vías de comunicación, la tala inmoderada de las masas forestales y la apertura de nuevas áreas de selva para su aprovechamiento agropecuario (Miranda 1952, Muench 1978, Nations y Night 1980).

Los murciélagos desempeñan un papel importante dentro de los ecosistemas tropicales al formar parte en los procesos de polinización, dispersión de semillas, y como depredadores (Fleming 1988, Thies y Kalko 2004) en la regulación de algunas poblaciones de invertebrados (Kalka et al. 2008), con lo cual coadyuvan de manera singular en la salud de estos ecosistemas (Kunz et al. 2011). La pérdida del hábitat y otros fenómenos asociados a la fragmentación del paisaje, tienen efectos ecológicos importantes sobre la estructura y composición de la flora y la fauna. Estos cambios pueden afectar no sólo a los murciélagos, sino también a los procesos ecológicos en los que estos mamíferos participan. La capacidad adaptativa de los murciélagos les ha permitido habitar y prosperar en una gran variedad de ecosistemas tanto en la región tropical como en las zonas templadas (Nowak 1991). Sin embargo, la diversidad de murciélagos se ha visto afectada por la fragmentación de los ecosistemas tropicales (Silver et al. 2002), al limitar la disponibilidad de refugios y sitios de forrajeo para estos mamíferos (Kunz y Lumsden 2003, Rodriguez-Herrera et al. 2007). No obstante, algunas especies se han adaptado y proliferan en paisajes fragmentados en donde han sido capaces de encontrar alimento y refugio (Burkey 1989). De esta manera, la presencia del disturbio viene a jugar un papel determinante en la modificación de este tipo de paisajes y en los procesos de adaptación de las especies a su medio. Este proceso constituye la parte fundamental de la hipótesis de disturbio intermedio (HDI), en donde la diversidad puede variar según la intensidad, frecuencia y el tiempo transcurrido desde el último disturbio (Connell 1978). Así, un disturbio de baja intensidad libera pocos recursos que permiten la llegada y establecimiento de especies oportunistas. En el otro extremo, un disturbio de alta intensidad, si bien libera una gran cantidad luz y otros de recursos, generando condiciones que excluyen a las especies típicas del ecosistema original (Sheil y Burslem 2003) y que implica un aumento de la diversidad de las especies colonizadoras. El disturbio intermedio por un lado permite la liberación de recursos suficientes para que prosperen las especies oportunistas y a su vez permite que se conserven las condiciones favorables para la sobrevivencia de las especies originales del ecosistema. Lo anterior implica un aumento de la diversidad a una escala a nivel paisaje. La mayoría de los murciélagos frugívoros prefieren forrajear cerca de sus refugios con el objeto de reducir el costo energético (Heithaus y Fleming 1978), y por lo tanto, la distancia entre el refugio y el área de forrajeo es un factor importante que afecta la dispersión de semillas en paisajes fragmentados.

Una de las causas principales de la conversión de áreas forestales tropicales es su aprovechamiento agropecuario con el uso de roza-tumba-quema (rtq). Esta práctica permite, de manera rápida y efectiva, la conversión de la selva en áreas agrícolas y eventualmente a bosques secundarios, por lo que es muy probable que en las siguientes décadas los bosques secundarios ocupen un alto porcentaje del área total de los bosques en el mundo (Castelletta et al. 2000). El aprovechamiento de las selvas mediante la rtq tiene como consecuencia la fragmentación del paisaje, que inicialmente consiste en la perforación de la cubierta vegetal y posteriormente en la formación de remanentes de selva inmersos en una matriz de bosque secundario; estos fragmentos de selva son además el último refugio para muchas especies de fauna y flora, entre ellos los murciélagos (Schulze et al. 2000). La gran mayoría de bosques secundarios están rodeados por áreas agrícolas o potreros (Gorchov 1993). Por lo que la mayoría de estudios con murciélagos (Bernard y Fenton 2003, Galindo-González y Sosa 2003, Gorressen y Willig 2004) se han realizado en paisajes constituidos, principalmente, por una matriz de áreas agropecuarias o bosque secundario en fases sucesionales incipientes y con parches, remanentes o fragmentos de selva.

La etnia maya-lacandona de la comunidad de Lacanhá Chansayab en Chiapas, México, utiliza un manejo tradicional de sus recursos mediante el sistema de producción agrícola de rtq. El manejo del paisaje incluye la conservación de la selva, aprovechando pequeñas áreas adentro de la matriz de selva para la producción milpera (cultivo de maíz, frijol, calabaza). El sistema de rtq lacandón se sustenta en una serie de técnicas que los agricultores han desarrollado a partir de su conocimiento ecológico tradicional sobre las especies vegetales y animales de la región (Amram 1937, Gadgil et al 1993). Los terrenos comunales en Lacanhá presentan una alta heterogeneidad espacial, formada por una matriz de selva interrumpida por pequeños parches de 0.5 a 1.0 ha de áreas agrícolas (milpas) y bosque secundario que permiten una mayor diversidad de flora y fauna, en comparación con lo que se podría encontrar en un área homogénea compuesta sólo por selva (eg., Gascon et al. 1999). Cabe destacar que esta condición, matriz de selva interrumpida por pequeñas áreas de milpas o vegetación secundaria, es excepcional dentro del contexto del paisaje regional, donde predomina una situación inversa. Es decir, una matriz de áreas agropecuarias y bosque secundario interrumpida con pequeños relictos de selva. A escala de paisaje, la variedad de parches de bosques de diferentes etapas sucesionales puede promover la diversidad de murciélagos, en congruencia con la HDI, al contener una mayor variedad de nichos en relación a un área homogénea (selva) poco perturbada. El bosque secundario que se encuentra como parte del paisaje de Lacanhá puede variar en cuanto a la composición de sus árboles dominantes. Sin embargo, se puede reconocer la preferencia de algunos agricultores tradicionales para procurar la rápida recuperación de sus bosques secundarios, después del aprovechamiento agrícola, mediante la siembra, al final del periodo de cultivo, de un árbol que en maya lacandón nombran Chujum y que comúnmente es conocido como Balsa (*Ochroma pyramidale* - Malvaceae) (Anónimo 1999). Esta especie es nativa, de rápido crecimiento y se comercializa en Sur América; *Ochroma pyramidale* es capaz de enriquecer los suelos agotados por la agricultura y la ganadería, así como de rehabilitar áreas degradadas a consecuencia de un historial de uso con quemas frecuentes (Levy-Tacher 2000, Levy-Tacher y Golicher 2004, Diemont et al. 2006, Douterlungne et al. 2010).

Por la sensibilidad de los murciélagos a los cambios en el hábitat (Fenton et al. 1992, Medellín et al. 2000, Schulze et al. 2000), es probable que las condiciones en los bosques secundarios dominados por *O. pyramidale* afecten su llegada y comportamiento en comparación con las áreas de selva. Los bosques secundarios dominados por ésta especie podrían presentar diferencias en cuanto a estructura, diversidad y abundancia de ciertas especies vegetales, con respecto a bosques secundarios (mixtos), sin dominancia de *O. pyramidale* con el mismo periodo de descanso o vegetación madura. Diferencias en estructura y composición como la diversidad de plantas, densidad de árboles y apertura del dosel han sido encontrados como factores que afectan la comunidad de murciélagos (Crome y Richards 1988, Medellín et al. 2000, Kalko y Handley 2001, Gorresen y Willig 2004, Ford et al. 2005, Castro-Luna et al. 2007a). Es posible que en los bosques secundarios dominados por *O. pyramidale* que se distinguen por generar un dosel más abierto en comparación con los bosques secundarios mixtos, la entrada y tránsito de ciertas especies o grupos de murciélagos pueda ser favorecida u obstaculizada. A su vez, la presencia de murciélagos puede verse afectada por la menor disponibilidad de refugios en áreas de bosque secundario en comparación con la selva, sin embargo, el bosque secundario puede proveer recursos importantes para los murciélagos, en particular para el grupo de los frugívoros (Castro-Luna et al. 2007b, Soriano y Ochoa 2001). Bajo estas condiciones los murciélagos facilitan la sucesión secundaria al dispersar semillas de especies de las etapas sucesionales tempranas (Gorchov et al. 1993) y tardías, contribuyendo así a la recuperación de áreas perturbadas en la región tropical (Galindo-González et al. 2000). Dentro de este contexto, la matriz de selva funciona como fuente potencial de semillas que contribuye al proceso de regeneración (McClanahan 1986).

El presente estudio tiene como finalidad describir y evaluar la comunidad de murciélagos en un paisaje manejado por los lacandones con predominio la selva alta perennifolia. La selva madura de los alrededores de la comunidad Lacanhá ha sido intervenida por los lacandones actuales y sus ancestros, y es más similar a la vegetación original o primaria que los bosques secundarios por la duración sucesional. Los bosques secundarios en la comunidad de Lacanhá han sido desarrollados en terrenos anteriormente usados con fines agrícolas por un tiempo menor a 50 años. Así, el paisaje conservado de los terrenos comunales de Lacanhá donde abunda la selva y la presencia de bosque secundario dominados por *O. pyramidale*, nos dieron la oportunidad de realizar una serie de investigaciones que nos permitieron reconocer la abundancia y diversidad de murciélagos en bosques secundarios manejados por humanos , en contraste con la selva. Otro de los intereses de esta investigación es avanzar en el entendimiento de la participación de los murciélagos durante el proceso de regeneración de la selva que sirva para el desarrollo de acciones futuras de restauración.

En primera instancia, se realizaron recorridos de campo identificando dos condiciones dominantes del paisaje de Lacanjá Chansayab: la selva y los bosques secundarios, donde se pretendía estudiar el comportamiento de los murciélagos. Fue a partir de esta experiencia que se reconoció lo diverso y complejo que era el contexto biológico donde vivían los lacandones, así como las múltiples posibilidades para el desarrollo de la tesis doctoral. Mi interés por considerar a la selva, además de su estado de conservación y su amplia representación en el paisaje de Lacanhá, fue por su importancia como refugio para un gran número de murciélagos. En estas dos condiciones, selva y bosques secundarios, se comenzó la búsqueda de áreas de muestreo propicias para la investigación. Uno de los primeros hallazgos importantes fueron los parches de bosque secundario dominados por *O. pyramidale*, aislados o conectados con otros bosques secundarios o colindantes con milpas. Así, la primer parte de esta investigación se enfocó a reconocer la influencia que podría tener la proporción de selva alrededor de estos bosques dominados por *O. pyramidale* para la comunidad de murciélagos. A partir de este acercamiento se llevó a cabo la segunda parte de este proyecto, la cual consistió en evaluar el efecto de la mayor o menor proporción de la selva sobre la dispersión de semillas por los murciélagos frugívoros en parches de bosque secundario dominado por *O. pyramidale*.

Objetivo general

Determinar el efecto del tipo de matriz circundante presente en bosque secundario manejado con *Ochroma pyramidale*, sobre la composición y estructura de la comunidad de murciélagos y evaluar su papel en la regeneración de la selva a través de sus habilidades de dispersión de semillas, en la comunidad Lacanhá, Chiapas, México.

Hipótesis generales

1. La proporción de selva alrededor de los bosques secundarios dominados por *O. pyramidale* en la comunidad Lacanhá, Chiapas, México, afecta positivamente la diversidad y riqueza de murciélagos y la dispersión de semillas de la etapa sucesional tardía, debido a la disponibilidad de frutos de esta etapa sucesional.

2. La mayor apertura del dosel en los bosques secundarios afecta negativamente la abundancia de murciélagos en la comunidad Lacanhá, Chiapas, México.

Objetivos particulares

Capitulo II

Objetivo

- Evaluar el efecto de los bosques secundarios dominados por *O. pyramidale* rodeados parcial o mayormente por selva sobre la comunidad de murciélagos.

Capítulo III

Objetivo:

- Evaluar la diversidad y abundancia de semillas dispersadas por murciélagos frugívoros en selva y bosques secundarios dominados por *O. pyramidale* rodeados parcial o mayormente por selva.

Descripción general del área de estudio

Este estudio fue ejecutado en los terrenos de la subcomunidad de Lacanhá-Chansayab en el margen occidental de la Reserva de la Biosfera Montes Azules, Chiapas, México (16º 45’ 00” N, 91º 08’ 00” O) con un elevación de 350 m.s.n.m. (Anónimo 1974). Los suelos predominantes, de acuerdo con la clasificación FAO/UNESCO son aerisoles húmicos, asociados con rendzina en las áreas calizas, o con regozol éutrico en las áreas de areniscas; son suelos constituidos por series paralelas de conglomerados formadas por calizas y areniscas (Anónimo, 1974).

El clima es cálido húmedo (Am) con lluvias abundantes en verano y parte del otoño, y una temporada seca corta (marzo-mayo). La temperatura media anual es de 25ºC y la precipitación media anual es de 2300 a 2500 mm (García 1973, Anónimo 1974, Muench 1978).

La actividad principal de la etnia maya-lacandona de la comunidad Lacanhá ha sido el manejo sustentable de sus recursos mediante el sistema de producción agrícola de rtq (Nations y Nigh 1980). Sin embargo, la participación de los agricultores en el ecoturismo o en empleos fuera de la comunidad ha cambiado las actividades principales, resultando en un impacto antropogénico relativamente bajo sobre la selva. Por lo tanto, ha sido posible mantener una mayor área continua de selva alta perennifolia, bosque tropical perennifolio (Pennington y Sarukhán 1968, Miranda y Hernández 1963, Rzedowski 1978), o bosque lluvioso de montaña baja (Breedlove 1973). Según la clasificación lacandona de la vegetación, en la comunidad Lacanhá-Chansayab existen dos tipos de vegetación madura, monte alto y chaparral, y el resto de la cobertura vegetal lo conforman los bosque secundario y las milpas que se derivan de ellos. El monte alto corresponde a la selva alta perennifolia donde destacan las especies *Brosimum alicastrum, Aspidosperma megalocarpon*, *Dialium guianense, Ficus* spp.*, Erblichia xylocarpa, Guatteria anomala, Poulsenia armata, Terminalia amazonia* y *Swietenia macrophylla*. El chaparral es un tipo de vegetación con árboles de menor talla (de 20 a 30 m de altura) en relación a la selva alta perennifolia, en donde abundan las lianas y bejucos. Se presenta en rodales de hasta cinco ha dentro del monte alto, en lugares con inundaciones estacionales, cerca de los ríos y en suelo con alto contenido de materia orgánica (Levy 2000). El paisaje está constituido por parches de bosque secundario y milpas embebidos en una matriz de vegetación madura (Fig 1).

En los parches de bosque secundario se reconoce una técnica desarrollada por los agricultores tradicionales que permite una acelerada recuperación de la selva después de su aprovechamiento agrícola (Levy-Tacher y Golicher 2004, Levy-Tacher et al. 2000), la cual se sustenta en la utilización del árbol *Ochroma pyramidale*, una especie nativa de interés comercial y de rápido crecimiento, capaz de enriquecer los suelos agotados por la agricultura y la ganadería, así como de rehabilitar áreas degradadas a consecuencia de un historial de uso con quemas frecuentes (Levy-Tacher 2000, Levy-Tacher y Golicher 2004, Douterlungne et al. 2010). En 2004, se comprobó que el *O. pyramidale* acelera notablemente el funcionamiento del ecosistema selvático, al identificarse un aumento de 5% de la materia orgánica del suelo, bajo la copa de densas poblaciones de este árbol, en comparación con áreas compuestas por otras especies arbóreas (Levy y Golicher, 2004).

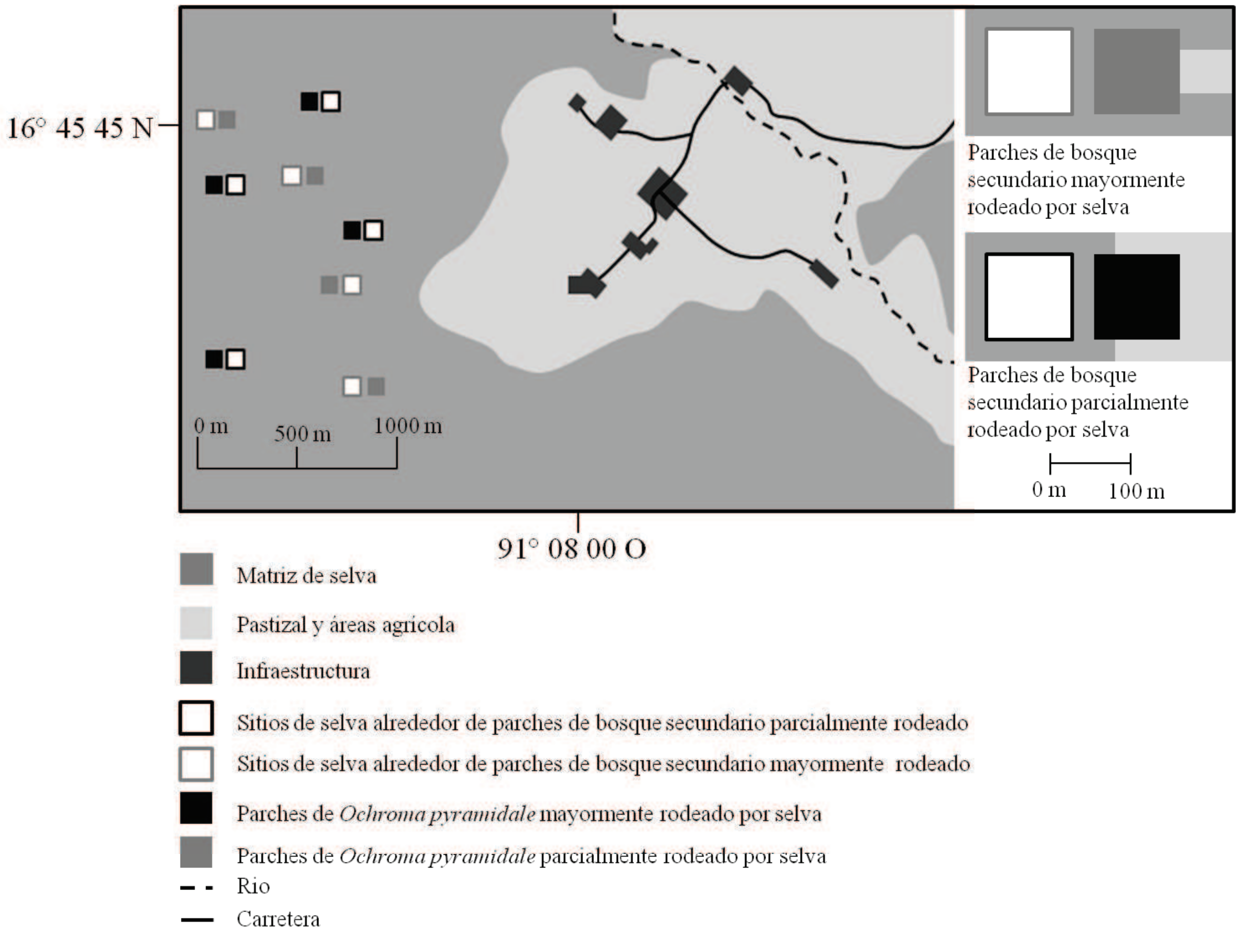

Fig. 1. Área del estudio y las posiciones geográficas de los sitios en la comunidad de Lacanhá, Chansayab en el estado de Chiapas, México.

Capítulo II

Efecto de la calidad de la matriz de la selva en la estructura del ensamble de murciélagos en parches de bosque secundario

Tropical rainforest matrix quality affects bat assemblage structure in secondary forest patches

Artículo publicado en línea en octubre 2, 2012, Journal of Mammalogy.

doi: http://dx.doi.org/10.1644/12-MAMM-A-005.1

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RH: BATS IN SECONDARY FOREST PATCHES

Tropical rainforest matrix quality affects bat assemblage structure in secondary forest patches

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We studied the Phyllostomidae bat assemblage structure in patches of secondary forest dominated by *Ochroma pyramidale* pioneer trees, largely (>85%) or partially (<35%) surrounded by a matrix of tropical rainforest, to test 3 hypotheses: 1). highest bat diversity and richness is observed in the matrix rainforest in comparison to secondary forest patches; 2). the proportion of rainforest surrounding secondary forest positively affects bat diversity and richness; and 3). canopy openness is an important structural variable negatively affecting bat abundance. Rainforest control sites had the highest bat species diversity and richness, and contributed more to total diversity. Bat diversity was similar between secondary forest patches largely enclosed by rainforest and their controls, but higher diversity, richness, and contribution to total diversity were recorded in largely enclosed patches compared to partially enclosed patches. Partially enclosed patches were dominated by 2 small frugivorous understory bat species (*Carollia sowelli* and *Carollia perspicillata*), whereas largely enclosed patches were dominated by 2 large-bodied, canopy-dwelling, frugivorous bats (*Artibeus lituratus* and *Artibeus jamaicensis*), which primarily feed on figs, a tree species that is abundant in rainforest. Bat diversity, richness, and contribution to total diversity were positively correlated with the proportion of area with rainforest, and bat abundance was negatively correlated with canopy openness.

Key words: Chiroptera, matrix habitat, *Ochroma pyramidale*, Phyllostomidae, slash and burn, spatial configuration, vegetation structure

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The importance of maintaining fragments of tropical rainforest in an unfavorable matrix of degraded areas for the conservation of intact fauna assemblages has been confirmed in several studies (Faria et al. 2006, Galindo-González and Sosa 2003, Harvey and González Villalobos 2007). However, the continuing destruction and isolation of rainforest will favor generalist species, increase colonization by invasive species (Umetsu and Pardini 2007), and reduce immigration rates and species richness (Doak and Mills 1994, Simberloff 1988), as matrices of agricultural fields or secondary forest restrict movement to suitable habitat patches. A dominating and extensive matrix of rainforest can, however, increase animal diversity (MacArthur and Wilson 1967). We define matrix as a connected area of dominating surface in a landscape; the response to the matrix depends on the species of interest. Mobile species, such as bats, are generally able to cross open areas, but the reduction in traveling and foraging activity in matrices of agricultural lands suggests the importance of forest cover in determining the matrix as either favorable or non-favorable (Medina et al. 2007, Schulze et al. 2000,).

Bats play an important role in the regulation of insect herbivory (Kalka et al. 2008, Van Bael et al. 2003) and in seed dispersion and pollination (Fleming and Sosa 1994, Galindo-González et al. 2000, Kelm et al. 2008, Kunz et al. 2011), and thereby modify plant community composition (Brown and Hutchings 1997, Laurance 1994, Tocher et al. 1997). Hence, the destruction of a matrix of rainforest can trigger important cascading effects (Fahrig 2001, Vandermeer and Carvajal 2001). Slash and burn agriculture has frequently perforated original rainforest matrices, creating singular isolated or multiple connected patches of secondary forest and agricultural fields. Clearing rainforest or felling trees by logging or natural causes influence rainforest dynamics, changing the community composition and vegetation structure. According to the intermediate disturbance hypothesis these impacts can favor local species richness and diversity of floral and faunal species (Collins 1987, Connell 1978, Wilkinson 1999). However, in the case of bats, highest bat species richness (Estrada and Coates-Estrada 2002) and diversity (Castro-Luna et al. 2007) have been recorded in areas of low disturbance continuous forest or forest fragments of remaining rainforest. Continuous areas of late successional rainforest are important refuges for Phyllostominae bats (Kunz and Lumsden 2003, Rodríguez-Herrera et al. 2007), and hold important forage areas for most habitat-dependent, large-bodied bat species (Faria et al. 2006, Galindo-Gonzalez 2004, Schulze et al. 2000), which are usually absent in areas of higher disturbance. Areas of higher disturbance such as secondary forest can attract bat species tolerant to landscape modification, usually smaller bodied species, which are indicators of forest disturbance (Schulze et al. 2000).

The configuration and composition of disturbed areas and the remaining rainforest influence landscape heterogeneity, and therefore the bat community structure through species-specific reactions to changes in availability of foraging habitat and refuges. Their response to landscape characteristics depends on the scale and the sensitivity of the bat species, such as their home-range size and day-to-day movement patterns (Gorresen et al. 2005). The species' sensitivity to disturbance, such as small patches of secondary forest immersed in a matrix of rainforest, is expected to differ among bat species, depending on their home range size, which is related to the species' body mass (Kelt and van Vuren 1999) and their capacity to tolerate different degrees of disturbances (Galindo-Gonzalez 2004).

The spatial layout of disturbed areas and the importance of a favorable matrix have often been confounded in previous studies (Castro-Luna et al. 2007, Vargas-Contreras et al. 2009). Moreover, structural and compositional differences such as plant diversity and woody cover can affect bat assemblage (Kalko and Handley 2001, Medellín et al. 2000), but mostly the influence of canopy openness is an important factor negatively affecting bat abundance (Castro-Luna et al. 2007, Crome and Richards 1988, Ford et al. 2005, Gorresen and Willig 2004). In this paper we quantify the impact of changes in the matrix layout, the spatial settings of secondary forest patches in a matrix of rainforest, and variation in forest composition and vegetation structure on bat assemblages. We tested whether: 1). highest bat diversity and richness is observed in the matrix rainforest in comparison to secondary forest patches, which is in contrast to the predictions derived from the intermediate disturbance hypothesis; 2). the proportion of continuous rainforest surrounding secondary forest patches favors bat diversity, richness, and abundance of disturbance-sensitive (large-bodied) bat species; and 3). increasing canopy cover favors bat abundance. To test these hypotheses, we studied the diversity, richness, and abundance of bat species in patches of secondary forest largely enclosed by rainforest, patches of secondary forest only partially enclosed, and control sites within the rainforest matrix, and related bat community structure to changes in vegetation structure and composition.

Materials and Methods

The study was carried out in the Maya Lacandon community of Lacanhá Chansayab on the margin of Montes Azules Biosphere reserve, Chiapas, Mexico (16°46’08”N, 91°08’12”W) with an elevation of 350 m asl. The climate is humid and warm with a mean annual temperature of 24.7 °C and a mean annual precipitation of >2,000 mm (Pennington and Sarukhán 2005). The farmers of this community sustainably manage natural resources using a traditional slash and burn system (Nations and Nigh 1980). The involvement of farmers in ecotourism (Hernandez Cruz et al. 2005), employment outside the community (Diemont et al. 2006), and its relatively small population size (ca. 500 inhabitants) results in a low anthropogenic impact on the rainforest, maintaining a continuous area of rainforest. The predominant vegetation consists of evergreen rainforest with dominant species such as *Dialium guianense, Brosimum alicastrum, Swietenia macrophylla, Ficus* spp., and *Spondias mombin* (Miranda and Hernández 1963). Secondary forests in Lacanhá can vary in composition, depending on the preference of the landowner. *Ochroma pyramidale* (Malvaceae) is often preferred by farmers in Lacanhá, as it is known for its fast growth and capacity to enrich degraded soils (Douterlungne et al. 2010, Levy-Tacher 2000, Levy-Tacher and Golicher 2004).

Study sites

The study included a total of 16 sites in the Maya Lacandon community; 8 sites were secondary forest patches with areas of 0.5-1.0 ha and 8 were control sites of rainforest. The secondary forest patches had been part of slash-and-burn agriculture and had been abandoned for a period of 10-15 years. Replicates (4) of secondary forest patches were classified as partially enclosed patch, with less than 35% enclosed by rainforest. The other 4 sites of secondary forest patches were classified as largely enclosed patch, with more than 85% enclosed by rainforest (Table 1). The secondary forest patches were dominated by *O. pyramidale*. The control sites in the matrix of continuous rainforest were located in close proximity to the secondary forest patches (Fig. 1). Each control site of rainforest was chosen in the immediate vicinity of a secondary forest patch, in order to exclude distance as a possible factor affecting bat arrival in secondary forest patches.

Bat sampling

Bats were sampled each month using 3 (12 x 2.4 m, 36 mm mesh) mist nets per site, set at ground level, starting 0.5 h before sunset until 4 h after, 1 night per site, from April 2010-March 2011. The total sampling effort was 74,649.6 m^2 h (Straube and Bianconi 2002). Trails, roads, and rivers were avoided while capturing bats, for their potential bias towards bat species using pathways (Palmeirim and Etheridge 1985), and mist nets were placed at least 25 m from the border of sites to avoid edge effect. Bats were identified using field guides (Álvarez et al. 1994, Medellín et al. 2008, Reid 1997). The forearm of each individual was marked upon release with a colored marker, to avoid recounting during the same night.

Species were grouped into ecological guilds: frugivorous, omnivorous, insectivorous, hematophagous, and carnivorous-insectivorous (Estrada and Coates-Estrada 2001, Estrada et al. 2006, Medellín and Gaona 1999). Procedures followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the postgraduate office of El Colegio de la Frontera Sur (ECOSUR).

Vegetation structure variables

Vegetation structure variables were measured in 6 quadrants of 10 x 10 m (600 m^2) per site, measuring tree diameter at breast height (DBH) and height, and identifying all trees >5 cm DBH. Percentage of canopy openness was measured at 15 random points for each site using a hemispheric crown densiometer (Forestry Suppliers inc. Jackson, Mississippi). Trees were divided into 3 height categories; 5-10 m, 10-20 m, and >20 m. Local diversity (Shannon-Wiener *H´*), average height, and basal area of trees were calculated per site.

Data analysis

Bat species richness and diversity (Krebs 1989) were calculated per site. Species richness was calculated using EstimateS (Colwell 2005) and the JACKKNIFE 2 estimator. Species diversity was calculated with the Shannon-Wiener *H*' index. Each site had a different contribution towards total local diversity. To evaluate the contribution of local diversity of each site to the total diversity we calculated the species diversity (Simpsons index) and distinctiveness of sites to the total diversity (Lu et al. 2007). The analysis was executed in the R program (R Development Core Team 2008), using the “contribdiv” function from the vegan package (Oksanen et al. 2011). The number of rare bat species was calculated by classifying a species as rare if <10 bats were recorded in each treatment. Rank abundance curves were made following Krebs (1989).

All response and explanatory variables were tested for normality using either Kolmogorov-Smirnov or Shapiro-Wilk normality tests, depending on the number of observations per variable. Non-normal data were normalized using logarithm transformations. Data was analyzed for differences among treatments with an ANOVA, followed by Tukey post-hoc tests for normally distributed data, and a Kruskal-Wallis test, followed by Bonferroni corrected Mann-Whitney *U* post hoc tests for non parametric data. Analyses were conducted in SPSS 17 (SPSS, Inc. 2007).

A forward multiple regression was performed in SPSS 17, using bat diversity, richness, contribution to total diversity, and bat abundance as response variables, and canopy openness, number of trees, mean tree height, number of trees per height class (<10 m, 10-20 m , >20 m), vegetation diversity (H'), and (arcsin transformed) percentage of surrounding rainforest as predictor variables.

Results

Bat species composition

A total of 2,588 bats, from 30 species belonging to 4 families were captured, 1,074 individuals in the 8 secondary forest sites and 1,514 in the 8 control sites (Appendix I). The Phyllostomidae family, with 27 species, contributed most to species richness and accounted for 98% of all bats.

Estimated species richness ($\chi^2_{3,172} = 85.682$, $P < 0.001$) and bat diversity ($\chi^2_{3,172} = 84.793$, $P < 0.001$) were both different among treatments (Figs. 2a and 2b), both presenting the lowest values in partially enclosed patches in comparison with largely enclosed patches and control sites. The contribution to the local diversity of each treatment was different among treatments ($F_{3,\ 12} = 43.250$, $P < 0.001$; Fig.2c), with lowest values for the partially enclosed patches, followed by largely enclosed patches and the controls respectively. Bat abundance seemed slightly higher for both control treatments, but was statistically non-significant, due to high variability within controls ($\chi^2_{3,44} = 4.7656$, $P = 0.199$; Fig. 2d). The relative rank-abundance curves (Fig. 3) showed a short tail and a steeper decrease for partially enclosed patches, because of the lower number and the larger relative differences between bat species' abundances in comparison with the respective control sites. However, 3 bat species had a higher relative abundance in both treatment plots, illustrating a lower evenness of the treatments compared to their controls. The rank abundance curves of largely enclosed patches and their respective controls (Fig. 3) presented a similar steepness; with the same 3 most abundant bat species and the control rainforest having more species at lower abundances than the largely enclosed patches.

Frugivorous bat abundance was similar among all treatments, with a slightly higher (non-significant) abundance in controls ($\chi^2_{3,44} = 2.116$, $P = 0.549$; Table 2). We found that 4 frugivorous bat species represented 66% of the total abundance, *A. lituratus*, *A. jamaicensis*, *C. sowelli*, and *C. perspicillata* (Fig. 4). The abundances of *A. lituratus* ($\chi^2_{3,188} = 43.396$, $P < 0.001$) and *A. jamaicensis* ($\chi^2_{3,188} = 37.764$, $P < 0.001$), both large frugivorous canopy bats, were different among treatments with higher abundances in control treatments, followed by patches largely enclosed, and lowest abundance in partially enclosed patches. The abundance of both *C. sowelli* ($\chi^2_{3,188} = 27.415$, $P < 0.001$) and *C. perspicillata* ($\chi^2_{3,188} = 13.710$, $P = 0.003$), both small frugivorous species, was highest in partially enclosed patches.

Abundance of omnivorous ($\chi^2_{3,44} = 4.777$, $P = 0.029$) and carnivorous/insectivorous bats ($\chi^2_{3,44} = 4.600$, $P = 0.032$) were both different among treatments, with higher abundances in control treatments than in forest patch treatments. Omnivorous bat abundance ($Z_{1,\,22} = -2.908$, $P = 0.003$) as well as carnivorous/insectivorous bat abundance ($Z_{1,22} = -3.310$, $P = 0.005$) was lower in partially enclosed patches compared to the surrounding rainforest. Hematophagous abundance was higher in both control treatments compared to partially enclosed patches and largely enclosed patches, but this was not significantly different ($\chi^2_{3,44} = 3.259$, $P = 0.353$).

A total of 18 bat species were classified as rare, 16 of which belonged to the family Phyllostomidae (Appendix I). Most rare species, 17, were found in control treatments. In forest patches 11 rare species were captured in largely enclosed patches, while only 4 in partially enclosed patches.

Vegetation census

Control treatments had a significantly higher average tree height ($\chi^2_{3,1115} = 38.488$, $P < 0.001$), basal area ($\chi^2_{3,1116} = 23.911$, $P < 0.001$), and lower canopy openness ($\chi^2_{3,236} = 171.262$, $P < 0.001$; Table 2) in comparison with both forest patch treatments. The maximum height for both secondary forest treatments was 25 m, while control treatments reached a maximum height of 35 m. The total number of trees in both forest patch treatments was higher than in control treatments ($F_{3,12} =$

9.695, $P = 0.002$). The number of trees below 10 m was similar among treatments ($F_{3,12} = 1.072$, $P = 0.398$), but the number of trees between 10 and 20 m ($F_{3,12} = 7.048$, $P = 0.005$) and number of trees above 20 m ($F_{3,12} = 5.405$, $P = 0.014$) were higher in partially enclosed patches and largely enclosed patches. The tree species diversity (Shannon-Wiener *H'*) was slightly higher for both control treatments, but not significantly so ($F_{3,12} = 1.341$, $P = 0.307$).

Relationship between landscape/vegetation variables and bat composition/abundance

The forward multiple regression showed a positive effect of the proportion of surrounding rainforest on 3 response variables: bat species richness ($R^2 = 0.794$, $F_{1,14} = 54.018$, $P < 0.001$), species diversity ($R^2 = 0.551$, $F_{1,14} = 17.158$, $P = 0.001$), and contribution to total diversity ($R^2 = 0.790$, $F_{1,14} = 52.625$, $P = 0.002$). Bat abundance was negatively related to canopy openness ($R^2 = 0.430$, $F_{1,14} = 10.542$, $P = 0.006$). The model did not include significant predictors after the inclusion of the first predictor.

Discussion

The JACKKNIFE 2 richness estimator predicted a total of 34 bat species for the whole area, equal to 34 species registered in a similar area by Medellín et al. (2000). The 30 species encountered represent 88% of the expected total number of species. Due to the absence of both acoustic sampling or canopy mist nets during this study, our estimates of bat diversity and abundance may be low, as the probability of recording aerial insectivorous (MacSwiney et al. 2008) and canopy bats (e.g., Emballonurids—Kalko and Handley 2001) is greatly reduced without the use of these methods (Bernard 2001, Kalko and Handley 2001, MacSwiney et al. 2008). However, the techniques we used are widely well accepted as effective sampling methods for phyllostomid bats (Kunz and Kurta 1988, Moreno and Halffter 1999, Fenton et al. 1992), facilitating comparisons among studies (Castro-Luna et al. 2007, Medellin et al. 2000, Schulze et al. 2000), and we expect that the use of other, more time-consuming, sampling methods would not have changed our results.

The highest bat species diversity, richness, and contribution to total diversity were found in areas of continuous rainforest, probably because of a combination of several factors: 1). higher diversity of food resources, 2). higher abundance of food resources, 3). more roosting opportunities such as tree cavities in older and larger trees (Kunz and Lumsden 2003), and 4). greater availability of plant species to build refuges as temporary tent making sites (Rodriguez-Herrera et al. 2007). The rainforest in this study is a relatively large area, perforated by slash-and-burn patches, agricultural fields, and secondary forest patches in different successional stages, where several Piperaceae and Solanaceae species are very common. The close proximity of areas with agricultural fields or secondary forest in different successional stages can increase the attractiveness for certain bat species, such as small understory frugivorous bat species (e.g., *Carollia*) which are known to have a small home range and roost close to multiple feeding areas (Bonaccorso et al. 2006, Heithaus and Fleming 1978). Lower availability of and higher competition for adequate roosting sites in secondary forest areas is also likely to restrict small understory frugivorous bats towards areas of continuous rainforest where more shelter opportunities are available (Fleming 1991). Moreover, Gorresen & Willig (2004) showed that continuous rainforest provides greater food diversity for bat species during periods of food scarcity.

The rainforest matrix represents an area of low disturbance where species such as *Vampyrum spectrum*, *Chrotopterus auritus*, and several other carnivorous-insectivorous bat species were captured. These species are usually found in continuous forest and mosaic habitats (Estrada & Coates-Estrada 2002, Schulze et al. 2000), but are probably positively affected by the variety and abundance of favourable food resources found in continuous rainforest (Gorresen and Willig 2004) in contrast to secondary forest areas. Food resources for carnivorous-insectivorous bats, such as small non-flying mammals and arthropods are usually more abundant and diverse in intermediately disturbed areas (Connell 1978, Schuldt et al. 2010) than in disturbed areas (Estrada et al. 1994, Schuldt et al. 2010). On the other hand, continuous rainforest represents a low disturbance habitat, but holds the highest diversity of bats, in contrast to the intermediate disturbance hypothesis which predicts that species diversity should be greatest at intermediate levels of disturbance. Our results agree with those of Castro-Luna et al. (2007) and Medellín et al. (2000), with highest bat species diversity in areas of low disturbance. Highest bat diversity in rainforest sites of low disturbance is likely to be related to the refuge opportunities provided by continuous rainforest. Although areas of intermediate disturbance can promote high species diversity in comparison with lower or higher disturbance areas (Sheil and Burslem 2003), increased refuge resources in areas of low disturbance are likely to remain of considerable importance for bat species (Kunz and Lumsden 2003, Rodriguez-Herrera et al. 2007), positively affecting diversity of bat captures. Therefore, we believe that the intermediate disturbance hypothesis may not apply for bats because of the importance of low disturbed areas providing important refuge opportunities.

Our 2nd evaluation (whether bat community composition is positively affected by the proportion of surrounding rainforest in secondary forest patches) showed that similar values of bat diversity and abundance were encountered in largely enclosed patches of secondary forest when compared to control treatments in continuous forest. However, richness and the contribution to total diversity were lower in largely enclosed patches than in the control sites. Several habitat dependent species, mainly carnivorous-insectivorous bats, prefer rainforest areas without passing through areas of secondary forest (Galindo-González 2004), even if largely enclosed by rainforest. Although these species are dependent on continuous areas of rainforest, they can sporadically be found foraging in areas of secondary forest of more than 10 years. Several of these species, *Mimon bennettii*, *Trachops cirrhosus*, and *Tonatia saurophila* were indeed recorded in secondary forest patches, largely enclosed by rainforest, and were absent in partially enclosed patches.

Artibeus lituratus and *A. jamaicensis* were the most abundant species in control treatments, reached relatively high numbers in largely enclosed patches, with similar abundance of *A. jamaicensis* as in its controls, but low abundance of both large frugivorous were recorded in partially enclosed patches. These large frugivorous bat species are known to feed on fruits from canopy tree species, such as *Ficus maxima, Ficus americana*, *Brosimum alicastrum* (Moraceae), and other mature forest fruits (Gaona 1997, Guevara et al. 1997) and these bat species are therefore expected to be found in continuous rainforest, where trees of the above mentioned tree species are of sufficient age to carry fruits. Evidently, areas of secondary forest do not form a barrier to the movement of these bat species, where structural similarities could play an important role in facilitating bat movement (Gascon et al. 1999).

Overall bat species diversity, richness, and contribution to total diversity were lower in partially enclosed patches than in their control treatments. Total bat abundance was similar; however, no carnivorous-insectivorous bats, and fewer omnivorous bats were captured in partially enclosed patches in comparison to control treatments. Frugivorous bats were the most abundant guild in each site, with large differences between species. In partially enclosed patches the small frugivorous *C. perspicillata*, *C. sowelli*, and *S. lilium* were frequently captured and are known for their preference for Piperaceae and Solanaceae fruits, mostly encountered in regenerating areas or areas of high disturbance (Williams-Guillén and Perfecto 2010). A possible explanation for the high abundance of small frugivorous bat species in partially enclosed patches is its connectivity to other disturbed areas, secondary forest, or agricultural fields. Small frugivorous bat species feed on resources of high abundance (Heithaus et al. 1975), resources which are likely to be more abundant in connected areas of secondary forest and agricultural fields.

Differences in vegetation structure between secondary forest patches and control sites included canopy cover, basal area, species diversity, density, and average height. However, only the relation between canopy cover and abundance of bats was confirmed, which is consistent with our third hypothesis that the percentage of canopy cover positively affects bat abundance, following the results of earlier studies (Castro-Luna et al. 2007, Ford et al. 2005, Gorresen and Willig 2004), where overlapping crowns of mature trees can improve shelter from predators and provide adequate roosting sites (Evelyn et al. 2003). The secondary forest patches of our study differed only slightly in vegetation structure in comparison with rainforest sites.

Secondary forest patches were dominated by mature *O. pyramidale*, a tree with specific structural characteristics, including a narrow, thin crown (Selaya et al. 2008) and sparse branching below the crown. Therefore, bats may perceive areas dominated by *O. pyramidale* as a relatively open, which, on one hand, might facilitate their movement, while on the other hand could also impede movement of bat species due to higher predation risk (Russo et al. 2007) compared to secondary forest patches without *O. pyramidale*. Further study is needed to test for the effects of tree architecture on bat movement, predation risk, and bat abundance.

Overall, we found highest bat diversity and richness in continuous rainforest. Secondary forest patches largely enclosed by rainforest had higher bat diversity and richness than partially enclosed patches. The proportion of surrounding rainforest was an important factor in determining the diversity and richness of bat species, while canopy openness was negatively related to bat abundance. The importance of nearby rainforest areas to secondary forest for the persistence of bat species has also been reported by Castro-Luna et al. (2007), but our study emphasizes the importance of the proportion of surrounding rainforest as a mechanism affecting bat assemblage structure in secondary forest areas. This study describes how continuous rainforest surrounding disturbed areas increases bat species diversity, and we therefore hypothesize that the larger diversity of bat species in areas of secondary forest patches enclosed by rainforest results in an increase in the provision of ecological services, such as dispersal of seeds, pollination of flowers, and contribution to successional development, as well as predation of herbivores, triggering important cascading effects.

Acknowledgements

This research was funded by Etnobiología para la Conservación A.C. and by a doctoral scholarship awarded to the first author by CONACyT-Mexico (Reg. 239503). Idea Wild and FORDECyY (116306) provided mist nets. We are grateful to M. Castellanos and E. Chankin for allowing us to work on their lands. Furthermore, we would like to thank J. Chankin, A. Chankin, C. Peñaloza Guerrero, R. van Toor, V. Hommersen, M. Wulms, and A. Sanchez for their help in the fieldwork.

Resumen

Estudiamos el ensamble de murciélagos de la familia Phyllostomidae en parches de vegetación secundaria dominada por árboles pioneros de *Ochroma pyramidale* (Malvaceae) en dos condiciones de vegetación circundante, aquellos mayormente

rodeados por una matriz de bosque tropical (>85%), y los rodeados parcialmente (<35%). Se probaron tres hipótesis: 1) la matriz de bosque tropical que rodea parches de vegetación secundaria presenta una mayor diversidad y riqueza de murciélagos en comparación con la vegetación secundaria; 2) la proporción de bosque tropical que rodea a la vegetación secundaria favorece la diversidad, riqueza y abundancia de murciélagos sensibles al disturbio; y 3) el incremento en la apertura del dosel disminuye la abundancia de murciélagos. Los sitios de control de bosque tropical, presentaron la mayor diversidad y riqueza de murciélagos y contribuyeron mayormente a la diversidad total. En los parches de vegetación secundaria mayormente rodeados de bosque tropical se encontró que la diversidad de murciélagos fue similar a las áreas de control de bosque tropical. Sin embargo, los parches de vegetación secundaria mayormente rodeados por bosque tropical presentaron mayor diversidad y riqueza de murciélagos y contribuyeron a la diversidad total en comparación con parches de vegetación secundaria parcialmente rodeados por bosque tropical. En parches de vegetación secundaria parcialmente rodeados dominaron dos especies murciélagos frugívoros pequeños, característicos de vegetación secundaria (*Carollia sowelli* y *Carollia perspicillata*). Mientras que en los parches mayormente rodeados las capturas mostraron la dominancia de dos especies de murciélagos frugívoros grandes (*Artibeus lituratus* y *Artibeus jamaicensis*), típicos de vegetación madura que se alimentan principalmente de higos (*Ficus* spp.), un árbol abundante del bosque tropical. La diversidad, riqueza y la contribución total a la diversidad estuvieron correlacionadas positivamente con la proporción de bosque tropical, mientras que la abundancia de murciélagos fue negativamente correlacionada con la apertura de dosel.

Literature cited

Álvarez T, Álvarez-Castañeda ST, López-Vidal JC. 1994. Clave para murciélagos mexicanos. Centro de Investigaciones Biológicas del Noreste, S.C. y Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. México.

Bernard E. 2001. Vertical stratification of bat communities in primary forest of Central Amazon, Brazil. Journal of Tropical Ecology 17:115-126.

Bernard E, Fenton MB. 2003. Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. Biotropica, 35: 262–277.

Bonaccorso FJ. et al. 2006. Evidence for exploitative competition: Comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). Biotropica, 39:249–256.

Brown KS, Hutchings RW. 1997. Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterfies. Pp. 91-110 in Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities (W.F., Laurance, and R. O. Jr. Bierregaard, eds.). University of Chicago Press, Chicago, Illinois.

Castro-Luna AA, Sosa, VJ, Castillos-Campos G. 2007. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. Animal conservation, 10:219-228.

Collins SL. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology, 68:1243-1250.

Colwell RK. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.0.0. http://purl.oclc.org/estimates. 01-10-2011.

Connell JH. 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science, 199:1302-1310.

Crome FHJ, Richards GC. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology, 69:1960-1969.

Diemont SAW, Martin JF, Levy-Tacher SI, Nigh RB, Ramirez Lopez P, Golicher JD. 2006. Lacandon Maya forest management: Restoration of soil fertility using native tree species. Ecological Engineering, 28:205-212

Doak DF, Mills LS. 1994. A useful role for theory in conservation. Ecology, 75:615-626.

Douterlungne D, Levy-Tacher SI, Golicher JD, Román Dañobeytia F. 2010. Applying indigenous knowledge to the restoration of degraded tropical rain forest dominated by bracken. Restoration Ecology, 18:322-329.

Estrada A, Coates-Estrada R, Meritt D JR. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography, 17:229–241.

Estrada A, Coates-Estrada, R. 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography, 24: 94-102.

Estrada A. Coates-Estrada R. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation, 103:237–245.

Estrada CG, Damon A, Sánchez Hernández C, Soto Pinto L, Ibarra Núñez G. 2006. Bat diversity in montane rainforest and shaded coffee under different management regimes in southeastern Chiapas, Mexico. Biological Conservation, 132:351-361.

Evelyn MJ, Stiles DA, Young RA. 2003. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. Biological Conservation, 115:463–473.

Fahrig L. 2001. How much habitat is enough? Biological Conservation 100:65-74.

Faria DR, Laps R, Baumgarten J, Cetra M. 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodiversity and Conservation, 15: 587-612.

Fenton MB, et al. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica, 24:440–446.

Fleming TH. 1991. The Relationship between Body Size, Diet, and Habitat Use in Frugivorous Bats, Genus Carollia (Phyllostomidae). Journal of Mammalogy, 72: 493-501.

Fleming TH, Sosa VJ. 1994. Effects of Nectarivorous and Frugivorous Mammals on Reproductive Success of Plants. Journal of Mammalogy, 75:845-851.

Ford WM, Menzel MA, Rodrigue JL, Menzel JM, Johnson JB. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. Biological Conservation, 126:528–539.

Galindo-González J. 2004. Clasificación de los murciélagos de la región de Los Tuxtlas,Veracruz, respecto a su respuesta a la fragmentación del hábitat. Acta Zoológica Mexicana (nueva serie), 20: 239-243.

Galindo-González J, Sosa VJ. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. The Southwestern Naturalist, 48: 579-589.

Galindo-González J, Guevara S, Sosa VJ. 2000. Bat-and bird-generated seed rains at isolated trees in pastures in tropical rain forest. Conservation Biology, 14:1693-1703.

Gaona O. 1997. Dispersión de semillas y hábitos alimenticios de murciélagos frugívoros en la Selva Lacandona, Chiapas. Undergraduate thesis. Universidad Nacional Autonoma de Mexico, Mexico, D.F.

Gascon C. et al. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation, 91: 223-229.

Gorresen PM, Willig MR. 2004. Landscape-scale responses of bats to habitat fragmentation in Atlantic Rainforest of Paraguay. Journal of Mammalogy, 85: 688–697.

Gorresen PM, Willig MR, Strauss RE. 2005. Multivariate analysis of scale-dependent associations between bats and landscape structure. Ecological Applications, 15: 2126–2136.

Guevara S, Laborde J, Liesenfeld D, Barrera O. 1997. Potreros y ganadería. Pp. 43-58. En: Gonzalez-Soriano E, Dirzo R, Vogt R (o Eds). Historia Natural de Los Tuxtlas. Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, D.F.

Harvey CA, González Villalobos JA. 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity Conservation, 16: 2257-2292.

Heithaus ER, Fleming TH, Opler PA. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology, 56: 841–854.

Heithaus ER, Fleming TH. 1978. Foraging Movements of a Frugivorous Bat, *Carollia perspicillata* (Phyllostomatidae). Ecological monographs, 48: 127-143.

Hernandez Cruz RE, Bello Baltazar E, Montoya Gomez G, Estrada Lugo EIJ. 2005. Social adaptation: Ecotourism in the Lacandon forest. Annals of Tourism Research, 32: 610-627.

Kalka MB, Smith AR, Kalko EKV. 2008. Bats limit arthropods and herbivory in a tropical forest. Science, 320: 71.

Kalko EKV, Handley CO Jr. 2001. Neotropical bats in the canopy: diversity, community structure and implications for conservation strategies. Plant Ecology, 153: 319-333.

Kelm DH, Wiesner K, Helversen O. 2008. Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. Conservation Biology, 22: 733–741.

Kelt DA, van Vuren D. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80:337-340.

Krebs CJ. 1989. Ecological methodology. Harper and Row, New York.

Kunz TH, Kurta A. 1988. Capture methods and holding devices. Pp. 1-29 in Ecological and behavioral methods for the study of bats. (T. H. Kunz, eds.). Smithsonian Institution Press, Washington, DC.

Kunz TH, Lumsden LF. 2003. Ecology of cavity and foliage roosting bats. Pp. 3- 69 in Ecology of bats (TH Kunz and MB Fenton, eds.). The University of Chicago Press, Chicago and London.

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. 2011. Ecosystem services provided by bats. Annual New York Academy of Sciences. 1223: 1–38. doi: 10.1111/j.1749-6632.2011.06004.x.

Laurance WF. 1994. Rainforest fragmentation and the structure ofsmall mammal communities in tropical Queensland. Biological Conservation, 69: 23-32.

Levy-Tacher SI. 2000. Sucesión causada por roza-tumba-quema en las selvas de Lacanhá, Chiapas. Ph.D. dissertation, Colegio de Posgraduados. Montecillo, Texcoco, Estado de México, México.

Levy-Tacher SI, Golicher JD. 2004. How predictive is traditional ecological knowledge? The case of the Lacandon Maya Fallow Enrichment System. Interciencia, 29: 496-503.

Lu H-P, Wagner HH, Chen X-Y. 2007. A contribution diversity approach to evaluate species diversity. Basic and Applied Ecology, 8: 1-12.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton.

MacSwiney G, Clarke FM, Racey PA. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. Journal of applied ecology, 45: 1364-1371.

Medellín RA, Gaona O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats in Chiapas, Mexico. Biotropica, 31: 432-441.

Medellín RA, Equihua M, Amin MA. 2000. Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests. Conservation Biology, 14:1666-1675.

Medellín RA, Arita HT, Sánchez O. 2008. Identificación de los murciélagos de México: Clave de campo. Segunda Edición. Instituto de Ecológica, UNAM. México.

Medina A, Harvey CA, Sanchéz Merlo D, Vílchez S, Hernández B. 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. Biotropica, 39: 120-128.

Miranda F, Hernández XE. 1963. Los tipos de vegetación de México y su clasificación. Boletin de la Sociedad Botánica de México, 28: 29-179.

Moreno CE, Halffter G. 1999. Assessing the completeness of bat biodiversity inventories using species accumulation curves. Journal of Applied Ecology, 37: 149-158.

Nations J, Nigh R. 1980. The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. Journal of Anthropological Research, 36:1-30.

Oksanen J, Simpson G, Solymos P. 2011. Community ecology package, http://vegan.r-forge.r-project.org/. 05-08-2011.

Palmeirim JM, Etheridge K. 1985. The influence of man-made trails on foraging by tropical frugivorous bats. Biotropica, 17: 82–83.

Pennington TD, Sarukhán J. 2005. Árboles tropicales de México. Tercera edición. Universidad Nacional Autónoma de México y Fondo de Cultura Económica, México, D.F.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org. Accessed 15 July 2010.

Reid FA. 1997. A field guide to the mammals of Central America and southeast Mexico. Oxford University Press, New York.

Rodríguez-Herrera B, Medellín RA, Timm RM. 2007. Murciélagos Neotropicales que acampan en hojas. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Russo D, Cistrone L, Jones G. 2007. Emergence time in forest bats: the influence of canopy closure. Acta Oecologica, 31: 119-126.

Selaya NG, Oomen RJ, Netten JJC, Werger MJA, Anten NPR. 2008. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. Journal of Ecology, 96: 1211-1221.

Schuldt A., et al. 2010. Tree Diversification Promotes Insect Herbivory in Subtropical Forests of South-east China. Journal of Ecology, 98: 917-926.

Schulze MD, Seavy NE, Whitacre DF. 2000. A Comparison of the

Phyllostomid Bat Assemblages in Undisturbed Neotropical Forest and in Forest Fragments of a Slash-and-Burn Farming Mosaic in Petén, Guatemala. Biotropica, 32:174-184.

Sheil D, Burslem DFRP. 2003. Disturbing hypotheses in tropical forests. Trends in Ecology and Evolution, 18: 18-26.

Simberloff DS. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology, Evolution and Systematics, 19: 473-511.

Sikes RS, Gannon WL and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy, 92: 235-253.

SPSS, Inc. 2007. SPSS. Version 17.0. SPSS, Chicago, Illinois.

Straube FC, Bianconi GV. 2002. Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de redes-deneblina. Chiroptera Neotropical, 8: 150–152.

Tocher M, Gascon C, Zimmerman B. 1997. Fragmentation effects on a central Amazonian frog community: a ten-year study. Pp. 91-110 in Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities (W. F. Laurance, Jr., and R. O. Bierregaard, eds.). University of Chicago Press, Chicago, Illinois.

Van Bael SA, Brawn JD, Robinson K. 2003. Birds defend trees from herbivores in a Neotropical forest canopy. Proceedings of the National Academy of Sciences, 100: 8304-8307.

Vandermeer J, Carvajal R. 2001. Metapopulation dynamics and the quality of the matrix. The American Naturalist, 158: 211-220.

Umetsu F, Pardini R. 2007. Small mammals in a mosaic of forest remnants and anthropogenic habitats: evaluating matrix quality in an Atlantic forest landscape. Landscape Ecology, 22: 517–53

Vargas-Contreras JA, Medellín RA, Escalona-Segura G, Interián-Sosa L. 2009. Vegetation complexity and bat-plant dispersal in Calakmul, Mexico. Journal of Natural History, 43: 219-243

Wilkinson DM. 1999. The disturbing history of intermediate disturbance. Oikos, 84: 145-147.

Williams-Guillén K, Perfecto I. 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. Biotropica, 42: 506-613.

Submitted 6 January 2012. Accepted 17 May 2012.

Associate Editor was Ricardo A. Ojeda.

Table 1. Characteristics of each site per treatment; partially enclosed forest patches with control rainforest, and largely enclosed forest patch with their respective rainforest control sites.

	Partially enclosed								Largely enclosed							
	Forest patch				Control rainforest				Forest patch				Control rainforest			
Site	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Age	11	10	13	13	>40	>40	>40	>40	15	15	12	13	>40	>40	>40	>40
Size	0.75	0.94	0.94	0.57	1.0	1.0	1.0	1.0	0.76	0.72	0.94	0.67	1.0	1.0	1.0	1.0
% of surrounding rainforest	20	25	35	35	100	100	100	100	85	85	100	100	100	100	100	100

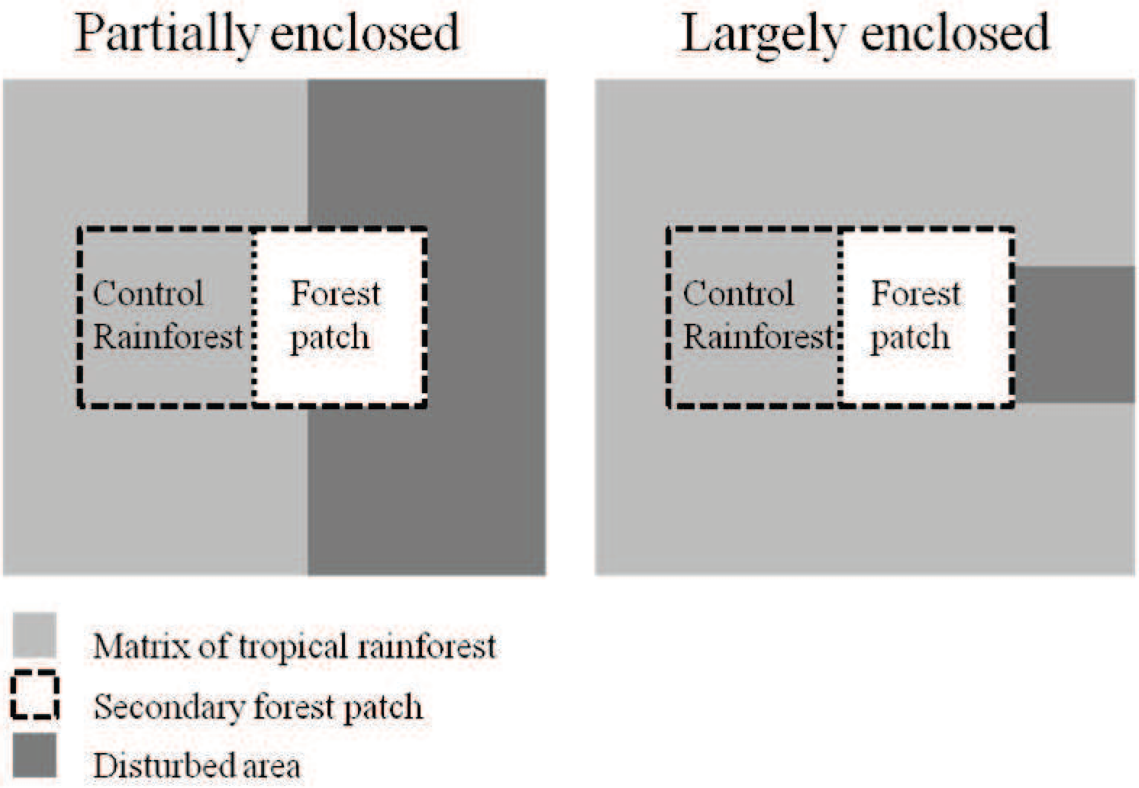

Fig. 1. Schematic layout of the experimental design used in this study. Secondary forest partially enclosed by control area of tropical rainforest and areas of secondary forest largely enclosed by control area of tropical rainforest.

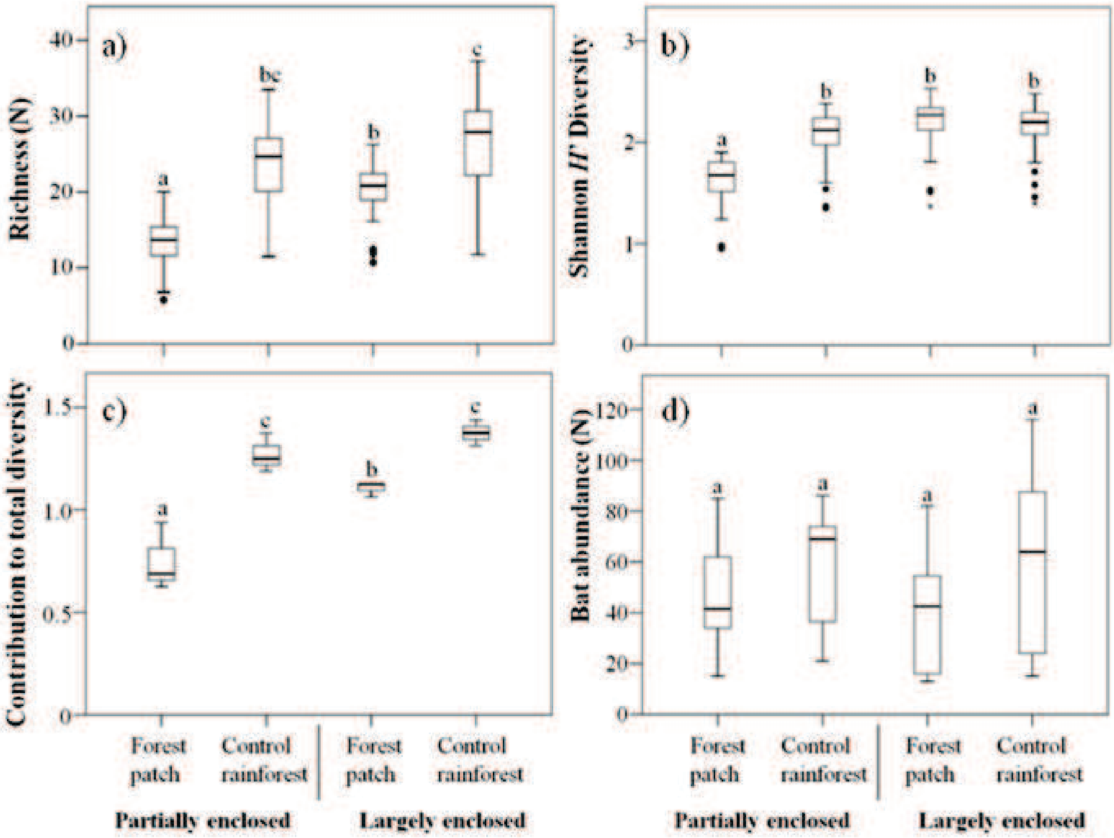

Fig. 2. Box plots representing the mean value of a) JACK2 richness, b) Shannon-Wiener H' diversity index of bats, c) contribution to total diversity and d) bat abundance for each treatment. Box plots with the same letters are not significantly different, based on a Kruskal-Wallis and post hoc Mann-Whitney U test with Bonferroni correction.

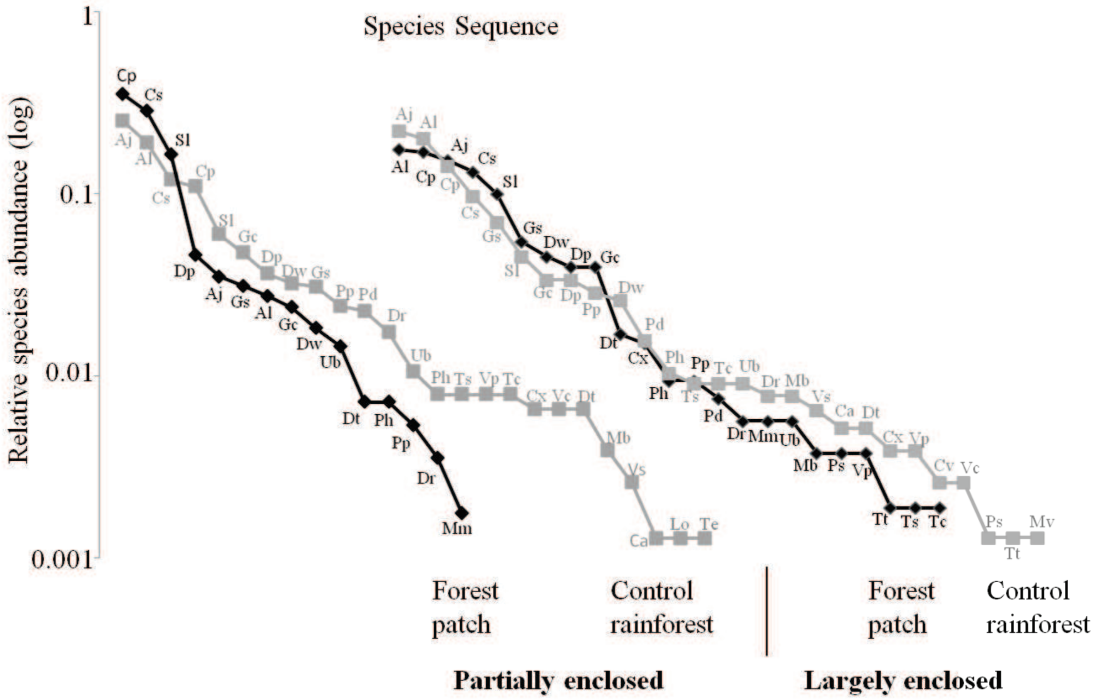

Fig. 3. Rank abundance curves of relative abundance of bat captures for each treatment of secondary forest (black) and control (gray). Letters represent species names, with 1st letter for genus and 2nd letter for species (Cx, however, represents Centurio senex).

	Partially enclosed				Largely enclosed			
	Forest patch		Control rainforest		Forest patch		Control rainforest	
No. trees*	14.50 ± 1.59	**b**	8.75 ± 0.82	**a**	13.92 ± 1.02	**b**	9.54 ± 3.18	**a**
Average basal area (m^2/ha)*	0.03 ± 0.04	**a**	0.13 ± 0.25	**b**	0.04 ± 0.04	**a**	0.13 ± 0.55	**b**
Average height (m)*	12.25 ± 5.77	**a**	16.03 ± 9.08	**b**	13.91 ± 6.63	**b**	12.19 ± 8.02	**a**
No. trees 5-10m	37.25 ± 13.60	**a**	21.25 ± 7.85	**a**	28.00 ± 9.49	**a**	27.25 ± 17.75	**a**
No. trees 10-20m	38.00 ± 11.58	**b**	17.25 ± 3.69	**a**	32.00 ± 7.79	**ab**	18.75 ± 4.99	**a**
No. trees >20m	11.75 ± 5.56	**a**	13.75 ± 4.57	**ab**	23.25 ± 6.02	**b**	11.25 ± 2.22	**a**
Canopy openness (%)	13.45 ± 2.71	**b**	4.80 ± 1.17	**a**	13.10 ± 4.31	**b**	5.45 ± 1.31	**a**
Shannon *H'* Diversity	1.53 ± 0.30	**a**	1.81 ± 0.37	**a**	1.66 ± 0.23	**a**	1.71 ± 0.36	**a**

Table 2. Results of vegetation structure variables per treatment with the mean number of trees (± SD), basal area m^2/ha, mean height (m ± SD), number of trees between 5-10m in height (m ± SD), between 10-20m in height (m ± SD), larger than 20m in height (m ± SD), mean canopy openness (% ± SD) and the mean vegetation diversity according to Shannon *H'*(± SD). Letters in bold represent significant differences between treatments for each vegetation structure variable based on ANOVA and post hoc Tukey test, or Kruskal-Wallis and post hoc Mann-Whitney *U* test with Bonferroni correction (*).

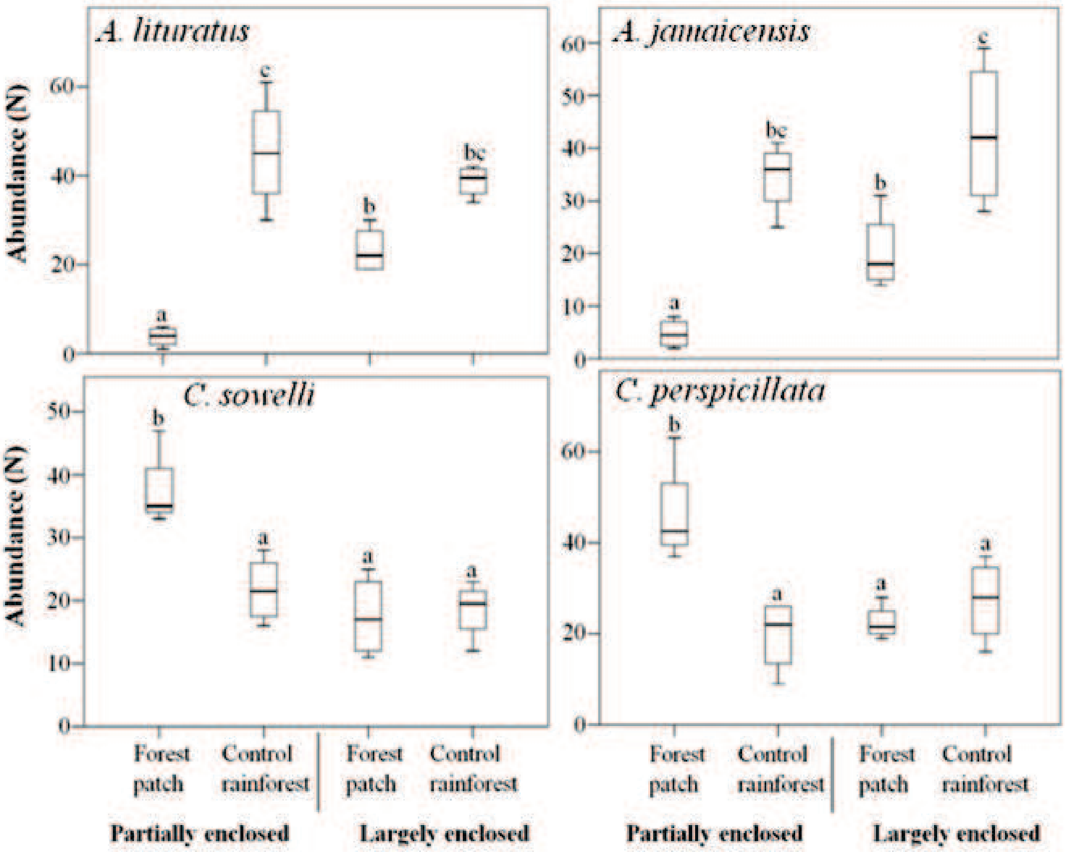

Fig. 4. Box plots of abundance for the 4 most abundant frugivorous bat species per treatment. Box plots with equal letters are not significantly different; based on a Kruskal-Wallis and a post hoc Mann-Whitney U test with Bonferroni correction.

Appendix I. Number of bat captures per bat species per treatment and feeding guild (I = Insectivorous, F = Frugivorous, H = Hematophagous, O = Omnivorous and C-I = Carnivorous-Insectivorous). [a] 4 most common bat species [b] Rare bat species.

				Partially enclosed		Largely enclosed	
Family	Subfamily	Species	Guild	Forest patch	Control rainforest	Forest patch	Control rainforest
Mormoopidae	Mormoopidae	*Pteronotus parnellii*	I	3	18	5	22
Phyllostomidae	Carolliinae	*Carollia perspicillata*[a]	F	185	80	90	109
	Carolliinae	*Carollia sowelli*[a]	F	150	87	70	75
Phyllostomidae	Desmodontinae	*Desmodus rotundus*	H	2	13	3	6
Phyllostomidae	Glossophaginae	*Glossophaga commissarisi*	O	13	35	21	26
	Glossophaginae	*Glossophaga soricina*	O	17	23	29	54
	Glossophaginae	*Lichonycteris obscura*[b]	O		1		
Phyllostomidae	Phyllostominae	*Chrotopterus auritus*[b]	C-I		1		4
	Phyllostominae	*Lophostoma evotis*[b]	I		1		
	Phyllostominae	*Micronycteris microtis*[b]	I	1		3	
	Phyllostominae	*Mimon bennettii*[b]	C-I		3	2	6

	Phyllostominae	*Phyllostomus discolor*	O		17	4	12
	Phyllostominae	*Phyllostomus stenops*[b]	O			2	1
	Phyllostominae	*Tonatia saurophila*[b]	C-I		6	1	7
	Phyllostominae	*Trachops cirrhosus*[b]	C-I		6	1	7
	Phyllostominae	*Vampyrum spectrum*[b]	C-I		2		5
Phyllostomidae	Stenodermatinae	*Artibeus jamaicensis*[a]	F	19	138	81	171
	Stenodermatinae	*Artibeus lituratus*[a]	F	15	181	93	155
	Stenodermatinae	*Artibeus phaeotis*	F	25	27	21	26
	Stenodermatinae	*Artibeus toltecus*[b]	F	4	5	9	4
	Stenodermatinae	*Artibeus watsoni*	F	10	24	24	20
	Stenodermatinae	*Centurio senex*[b]	F		5	8	3
	Stenodermatinae	*Chiroderma villosum*[b]	F				2
	Stenodermatinae	*Platyrrhinus helleri*[b]	F	4	6	5	8
	Stenodermatinae	*Sturnira lilium*	F	87	44	53	35
	Stenodermatinae	*Uroderma bilobatum*[b]	F	8	8	3	7
	Stenodermatinae	*Vampyressa pusilla*[b]	F		6	2	3
	Stenodermatinae	*Vampyrodes caraccioli*[b]	F		5		2
Thyropteridae	Thyropteridae	*Thyroptera tricolor*[b]	I			1	1

Vespertilionidae	Vespertilionidae	*Myotis volans*[b]	I				1
		Total		**543**	**742**	**531**	**772**

Capítulo III

Efecto de la matriz de selva en la dispersión de semillas por murciélagos en parches de bosque secundario

Rainforest matrix affects seed dispersal by bats in secondary forest patches

Rainforest Matrix affects Seed Dispersal by Bats in Secondary forest patches

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Article submitted to Biodiversity and Conservation

Abstract

Studies on frugivorous bats have focused on the effect of disturbance on bat diversity, abundance and their importance as seed dispersers. However, nearby rainforest, with higher food diversity and abundance, and a higher frugivorous bat diversity and abundance, can fulfill an important role in facilitating vegetation development of disturbed areas. To test this assumption we compared the diversity and abundance of seeds dispersed by bats in rainforest and patches with different proportions of enclosing rainforests. Furthermore, we related fruit availability with seed dispersal by frugivorous bats, and analyzed the differences in seed dispersal of two large (*Artibeus lituratus* and *Artibeus jamaicensis*) and two small frugivorous bats (*Carollia perspicillata* and *Carollia sowelli*). Highest diversity of seeds dispersed by bats was found in rainforest and largely enclosed patches, while highest richness of seed dispersed was encountered in partially enclosed patches and rainforest. More bats from rainforest and largely enclosed patches dispersed late-successional stage seeds than in partially enclosed patches, which fed more on early-successional stage shrubs. Patches partially enclosed by rainforest had highest abundances of two small frugivorous bat species that dispersed mainly early-successional *Piper* seeds. Two abundant large frugivorous bats encountered in patches that were largely enclosed by rainforest, dispersed mostly *Cecropia* seeds, as well as seeds from late-successional trees such as *Ficus* spp. A larger amount of surrounding rainforest facilitates dispersion of late-successional stage seeds by bats which will contribute to the development from early-successional secondary forest vegetation towards climax rainforest.

Key words: Chiroptera; frugivorous bats; matrix habitat; *Ochroma pyramidale*; Phyllostomidae; plant succession; spatial configuration.

Introduction

The distribution of frugivorous Phyllostomidae bats, a species-rich family, is highly abundant in the tropics and regarded more abundant than other mammals groups (Bonaccorso 1979, Terborgh 1984). Frugivorous bats feed on a variety of fruits, and can facilitate plant succession by dispersing seeds such as shrubs, vines and trees of different successional stages, and therefore fulfill an important role by influencing vegetation changes and recovery (Gorchov et al. 1993, Galindo-González et al. 2000, Lobova and Mori 2004). The abundance and species richness of these frugivorous bats is positively affected by the presence of undisturbed rainforest and forest cover (Gorressen and Willig 2004), due to the higher diversity and greater abundance of resources, such as food and roosting patches (Fenton et al. 1992, Schulze et al. 2000, Saldaña-Vazquez et al. 2010, Garcia-Estrada et al. 2011). Some frugivorous bat species prefer to forage nearby roosts to minimize energy expenditure and predation risk (Heithaus and Fleming 1978). However, with increasing distance between suitable roosts and suitable foraging habitat, bats are required to forage further away. In areas dominated by pastures, frugivorous bats efficiently disperse early-successional tree and shrub seeds between fragments (Guevara and Laborde 1993, Galindo-González et al. 2000, Henry and Jouard 2007). Hence, the presence of patches of undisturbed rainforest could function as an important seed source for the dispersal of seeds towards areas of higher disturbance, and thereby facilitate vegetation development. In a previous study the proportion of rainforest surrounding patches of secondary forest has been positively related to bat diversity and richness (Vleut et al. in press). Abundant frugivorous bat species were two relatively small species (*Carollia perspicillata* and *Carollia sowelli*; forearm less than 45 mm, body mass less than 20 g; Nowak 1991) and were frequently captured in secondary forest patches partially enclosed by rainforest, and two large frugivorous bats (*Artibeus jamaicensis* and *Artibeus lituratus*; forearm greater than 48 mm, body mass 44—87 g; Nowak 1991) were more abundant in secondary forest patches largely enclosed by rainforest and in rainforest (Vleut et al. in press). Small frugivorous bat species have been recorded frequently in disturbed areas, and their abundance has been related positively with fruit abundance (Saldaña-Vazquez et al. 2010). Large frugivorous bats feed on large fruits of especially mid-to late-successional plant species (Kalko et al. 1996, Galindo-González et al. 2000) and can therefore fulfill an important role in the development of early-to mid-successional forest with the dispersal of fruits of these late-successional plant species.

To analyze the importance of rainforest on seed dispersal by frugivorous bats in secondary forest with different proportion of surrounding rainforest, we investigated the richness, diversity and abundance of seeds dispersed by frugivorous bats and fruit availability in rainforest and in secondary forest patches that are either largely or partially enclosed by rainforest. We expect that; (1) richness and diversity of seeds dispersed by bats is higher in rainforest and in secondary forest patches largely enclosed by rainforest than partially enclosed forest patches and bats ‘diet is dominated by fruits of mid-to late-successional stage plant species. (2) Fruit availability in secondary forest patches positively affects the abundance of bats, and finally (3) the seed dispersal of the previously mentioned two large frugivorous bats in rainforest and largely enclosed secondary forest patches is dominated by fruit of mid-to late-successional plant species, whereas the two small frugivorous bats, abundant in partially enclosed secondary forest patches, disperse mostly early-successional stage fruits.

Material and methods

The study was carried out on the margin of the Biosphere reserve Montes Azules, Chiapas Mexico (16° 46’ 08” N, 91° 08’ 12” W) with an elevation of 350 m above sea level, The climate is warm-humid with a mean annual temperature of 24.7 °C and a mean annual precipitation >2000 mm, with most rains falling between June and October (Pennington and Sarukhán 2005). The local Lacandon farmers have supported themselves for centuries through methods of slash and burn agroforestry, in a matrix of tropical rainforest perforated by patches of secondary forest and agricultural fields (Nations and Nigh 1980, Levy-Tacher and Aguirre 2005, Diemont et al. 2006). The vegetation consists of evergreen rainforest with dominant species such as *Dialium guianense, Brosimum alicastrum, Swietenia macrophylla, Ficus spp.* and *Spondias mombin* (Miranda 1963).

Study area

The study area comprised of 8 secondary forest patches and 8 tropical rainforest sites. The 8 secondary forest patches were abandoned 10-15 years ago and were between 0.5-1.0 ha, dominated by the fast growing pioneer species *Ochroma* *pyramidale* (Malvaceae). This wind dispersed tree species is often preferred by farmers, and so seeds are spread during the fallow period accompanied with weeding of undesired plants to ensure its dominance (Levy-Tacher 2000, Levy-Tacher and Golicher 2004, Douterlungne et al. 2010). *Ochroma pyramidale* shortens the fallow period by facilitating the conversion of secondary forest for agricultural use (Nations and Nigh 1980, Levy-Tacher 2000), partly because of its low light wood density of 0.16 g cm^3 (Byrne and Nagle 1997). The secondary forest patches dominated by *O. pyramidale* were classified into two groups, depending on the proportion of surrounding rainforest; 4 patches were partially (<35%) enclosed by rainforest, and 4 patches largely enclosed by rainforest (>85%). The proportion of surrounding rainforest was estimated by dividing the length of the border connected with rainforest by the total length. When secondary forest patches were not surrounded by rainforest, they were surrounded by either secondary forest or agricultural fields. The 8 control sites, each of 1.0 ha, were chosen inside the rainforest matrix, located in the close vicinity of their respective secondary forest patches to exclude distance as possible factor affecting bat presence in each treatment site. More detailed information on study design and study areas can be found in Vleut et al. (2012).

Fruit availability

The production of fruits was monitored at monthly intervals, prior to each bat capturing, for all fruit bat food plant species within the study sites, determining and counting individual trees and shrubs that carried ripe fruits. Food plants were encountered using line-transect walks of approximately 80 x 3 m, avoiding edges.

The use of line transects is a practical and efficient method for the estimation of population densities (Anderson et al. 1979). The assessment of fruit ripeness proved difficult for certain tree species, therefore we did not count number of fruits, but counted plants carrying mature fruits for all plant species, which we believe constitutes a reliable estimation of fruit presence. To minimize alarming roosting bats, vegetation was not disturbed during the census. We considered all shrubs, trees and vines with fruits as potential food source for frugivorous bats, according to seeds from the reference database . Fruit availability was corrected for differences in patch size and fruits not found in our collection of seeds dispersed by bats were not considered as part of the diet of frugivorous bats and eliminated from the analysis.

Bat seed dispersal

From the moment bats get entangled in mist nets they usually defecate in the next seconds or eventually in the cloth bag in which they were held (Galindo-González et al. 2009). To be able to retrieve information on the seeds dispersed by individual bats a plastic of 1.4 m wide and 12 m long was placed below each mist net. This is an efficient technique of collecting seeds (Galindo-González et al. 2009), and also allows for the retrieval of fruits transported by bats. Bats were sampled each month using 3 (12 x 2.4 m, 36 mm mesh) mist nets per site, set at ground level, starting 0.5 h before sunset until 4 h after, 1 night per site, from April 2010-March 2011. The time a bat individual needs to defecate can vary between season, habitat or bat species (Thomas 1988). We therefore kept each individual for a maximum of 30 min in a cloth bag to ensure recovery of all fecal samples per bat as possible.

Seeds dispersed by bats remain intact through gut transit, enabling plant species identification (Janzen 1983, Wendeln et al. 2000). The collected fecal samples were gathered and kept in small paper bags to dry and seeds were then separated from fruit pulp, insect and possible other fecal remains. When possible, seeds were identified to species level using a reference database from a previous study in the same area (Wulms 2009).

Data analysis

We evaluated species richness and diversity of dispersed seeds according to Shannon (*H'*) (Krebs 1989) using EstimateS (EstimateS software, Version 7.5, Copyright R. K. Colwell: http//viceroy.eeb.uconn.edu/estimates, Colwell 2005). The ICE estimator (Incidence-based Coverage Estimator) was chosen to estimate species richness, because it has proven to be one of the best richness estimators for our data characteristics and grain size (Hortal et al. 2006). For each plant species encountered in the seeds dispersed by frugivorous bats we determined life form and successional stage in which species is most abundant, based on previous studies (Greig 1993, Guevara 1997, Levy-Tacher and Aguirre-Rivera 2005, Pennington and Sarukhán 2005). Life form was divided into shrub or tree, and for each life form the successional stage was determined as early-successional stage (light demanding plant species) or late-successional species (shade tolerant plant species) based on tolerance to shade and seed size (Swaine and Whitmore 1988, Whitmore 1989).

All data was tested for normality using Shapiro and Wilk normality tests. We attempted a log-transformation if data did not follow a normal distribution. Diversity, richness and abundance of seeds dispersed by bats as well as fruit availability and number of bats dispersing seeds per life form and successional stage were analyzed for difference between treatments with an ANOVA, followed by Tukey *post-hoc* tests for normally distributed data, and a Kruskal-Wallis chi-quadrate test, followed by Bonferroni corrected Mann-Whitney *U post-hoc* tests for non-parametric data. Statistical analyses were conducted in SPSS 17 (SPSS inc 2007). We applied a non-metric multidimensional scaling (NMDS) to ordinate the frequency of bats per dispersed seed species per site, based on Bray–Curtis dissimilarities (e.g. Magurran 2004). We evaluated the ordination using the stress value, scaled between 0-100 (McCune and Grace 2002). The scores of the first and second axes were compared among treatments with a MANOVA and Pillai's test, both NMDS and MANOVA were carried out in the program R (R Development Core Team 2006). The relationship between food availability in each secondary forest and rainforest treatment and the abundance of bats that dispersed these seeds was tested using linear regression.

We calculated the disperser importance index (DII) (Galindo-González et al. 2000) for the two small frugivorous and two large frugivorous bats. For each of these bat species we estimated the relative abundance of captured bats (B) and the percentage of bat individuals with seeds in fecal samples (S). DII was S*B/1000, and ranged from 0 to 10. Fecal samples with at least one seed species were counted as one event, samples with two seeds species were counted as two events and so on.

Results

Bat seed dispersal

From all 2588 bats captures, 2457 were frugivorous (Appendix 1), we collected 1065 fecal samples, with seeds belonging to 28 plant species, nine of which could not be identified, and three only identified to genus level. A total of 28 fruits from eight plant species were also collected, carried by bats.

Bat seed dispersal richness (ICE) was lowest in largely enclosed patches ($\chi^2_{3,188}$=65.084, $P < 0.001$; Fig. 1a), while diversity of the seed dispersed was lowest in partially enclosed patches (Shannon-Wiener H'; $\chi^2_{3,188} = 27.766$, $P < 0.001$; Fig1b). The number of bats that dispersed seeds was similar among conditions ($\chi^2_{3,188} = 6.566$, $P = 0.087$; Fig. 1c).

The NMDS ordination analysis of the sites, based on the frequency of bats per dispersed seed species (Fig. 2), was achieved within 3 runs of the data, and resulted in a low stress value of 8.542. The first axis successfully separated the partially enclosed sites from the largely enclosed sites ($F_{1,6} = 54.141$, $P < 0.001$) and rainforest sites surrounding the partially enclosed patches ($F_{1,6} = 14.549$, $P < 0.001$).

The number of frugivorous bats which dispersed seeds from early-successional trees was not different among treatments ($\chi^2_{3,188} = 2.779$, $P = 0.427$), which was also the case for late-successional shrubs ($\chi^2_{3,188} = 5.697$, $P = 0.127$; Table 1). More early-successional shrubs were dispersed in partially enclosed patches ($\chi^2_{3,188} = 21.738$, $p < 0.001$), and the abundance of bats dispersing late-successional seeds was highest in control, followed by largely enclosed patches and lowest abundance in partially enclosed patches ($\chi^2_{3,188} = 33.982$, $P < 0.001$).

The seeds dispersed by the two large and two small most abundant frugivorous bat species differed per bat species and consisted of a total of 28 plant species (Table 2). *C. sowelli* dispersed seeds from 16 different plant species, mostly *Piper aduncum* and *P. auritum*, rather similar to the diet of *C. perspicillata* with 14 different plant species. *Artibeus lituratus* dispersed seeds from 15 different plant species, dominated by *Cecropia obtusifolia*. *Artibeus jamaicensis*, with 9 different plant species in its diet, fed mostly on *C. obtusifolia* and *Ficus maxima*.

Fruit availability

The fruit availability in the secondary forest patches consisted of only four shrub species: *Piper auritum, P. aduncum, P. hispidum*, *P. aeruginosibaccum*, and one tree *C. obtusifolia*. All of these species were available in partially enclosed patches, while *P. aduncum* and *P. auritum* with available fruits were not found in largely enclosed patches. Food availability of *P. hispidum* ($Z = -1.851$, $P = 0.064$, $N = 96$), *P. aeruginosibaccum* ($Z= -1.611$, $P = 0.107$, $N = 96$), and *C. obtusifolia* ($Z = -0.373$, $p = 0.709$, $N = 96$) were not different between partially and largely enclosed patches.

Ficus maxima, *Brosinum alicastrum* and *Quararibea funebris* were the fruit bearing trees in rainforests surrounding forest patches that were partially enclosed, whereas *Ficus americana*, *Ficus maxima* and *Calophyllum brasiliense var.j.* were more abundant in rainforest surrounding forest patches that were largely enclosed. *Ficus maxima* ($Z = -1.000$, $P = 0.317$, $N = 96$) fruit availability was available and similar between both rainforest, same as late-successional shrub species *Piper aeruginosibaccum* ($Z = -0.251$, $P = 0.802$, $N = 96$) and *Piper aequale* ($Z = -0.319$, $P = 0.750$, $N = 96$).

Relation of fruit availability and bat abundance

In partially enclosed patches, the availability of fruit and the number of bats dispersing their seeds was positively correlated for *P. aduncum* (R^2= 0.153, $t_{1,46}$=2.880, P=0.006) and *P. aeruginosibaccum* (R^2=0.207, $t_{1,46}$=3.464, P=0.001). The availability of *C. obtusifolia* (R^2=0.007, $t_{1,46}$=0.556, P=0.574), *P. auritum* (R^2=0.02, $t_{1,46}$=-0.974, P=0.335) and *P. hispidum* (R^2=0.048, $t_{1,46}$=1.524, P=0.134) was not correlated with the abundance of bats dispersing their seeds in these partially enclosed sites. However, in largely enclosed patches there was a positive correlation between *C. obtusifolia* availability and the number of bats dispersing these fruits (R^2=0.307, $t_{1,46}$=2.189, P=0.034). In largely enclosed patches *P. aeruginosibaccum* fruit availability was positively related with the number of bats dispersing seeds of these fruits (R^2=0.122, $t_{1,46}$=2.524, P=0.015), whereas no such correlation could be found for *P. hispidum* (R^2=0.072, $t_{1,46}$=1.888, P=0.065).

Both *Carollia* species abundances were not related with the fruit availability of *P. auritum* in partially enclosed patches. However, a positive relation between *C. sowelli* and *P. aduncum* fruit was found in partially enclosed patches (R^2=0.083, $t_{1,46}$=2.037, P=0.047), similar to the increasing abundance of *C. perspicillata* (R^2=0.213, $t_{1,46}$=3.527, P=0.001). Increasing *P. hispidum* fruit availability caused an increase in both C*. perspicillata* (R^2=0.245, $t_{1,46}$=3.862, P<0.001) and *C. sowelli* (R^2=0.138, $t_{1,46}$=2.715, P=0.009). *Carollia perspicillata* was also positively correlated with the fruit availability of *P. aeruginosibaccum* (R^2=0.397, $t_{1,46}$=5.507, P<0.001). Both *A. jamaicensis* and *A. lituratus* were not related with the fruit availability of *C. obtusifolia* in partially enclosed patches.

In largely enclosed patches, *P. hispidum* fruit availability was positively related with abundance of *C. sowelli* (R^2 = 0.158, $t_{1,46}$ = 2.964, p = 0.005), whereas *P. aeruginosibaccum* fruit availability was positively correlated with *C. perspicillata* (R^2 = 0.397, $t_{1,46}$ = 5.507, P < 0.001). *A. lituratus* abundance was the only bat species positively correlated with the fruit availability of *C. obtusifolia* (R^2 = 0.139, $t_{1,46}$ = 2.703, P = 0.009) in largely enclosed patches.

The fruit availability of late-successional trees in rainforest surrounding partially enclosed or largely enclosed patches presented insufficient number of observations to be able to compute a linear regression between fruit availability and number of bats dispersing their seeds. However, in both rainforest treatments surrounding partially enclosed and largely enclosed *P. aeruginosibaccum* fruit availability was positively correlated with the number of bats dispersing their seeds (R^2 = 0.105, $t_{1,46}$ = 2.323, P = 0.025 and R^2 = 0.207, $t_{1,46}$ = 3.464, P = 0.001 respectively).

Only the abundance of *C. perspicillata* was positively related with the increase in abundance of *P. aeruginosibaccum* in both rainforest treatments surrounding partially and largely enclosed (R^2 = 0.127, $t_{1,46}$ = 2.581, P = 0.013 and R^2 = 0.308, $t_{1,46}$ = 4.524, P < 0.001 respectively). The increase in abundance in *P. aequale* proved not to be related with either *C. perspicillata* or *Carollia sowelli* in both rainforest treatments.

Carollia perspicillata (DII=2.92) and *C. sowelli* (DII=1.95) were the most important dispersers (Table 3). Highest values of seed disperser importance were registered for partially enclosed forest patches ((DII=5.11), followed by largely enclosed forest patches (DII=3.55).

Discussion

Our results show that the frequency of dispersion by bats per seed species successfully separated partially enclosed patches from largely enclosed patches and rainforest sites in the ordination, suggesting the higher similarity in seed species dispersed in rainforest and largely enclosed forest patches. The highest diversity in seeds dispersed by frugivorous bats in both tropical rainforest and largely enclosed forest patches, however, richness of dispersed seed species was lowest in largely enclosed patches. Bat seed dispersal diversity and richness can potentially affect dynamics and the floristic composition of forests of different successional stages. Seed richness was higher in partially than largely enclosed forest patches, probably due to the high species richness in the seeds dispersed by both *Carollia* bat species, but included mostly seed species which were found dispersed by only a small amount of bats. The diversity of dispersed seeds was higher in largely enclosed patches which suggest that although the number of seed species dispersed is lower, the evenness among the seed species dispersed by bats was higher. Since frugivorous bats have a tendency to feed on fruits from mostly early successional plant species (Medellin & Gaona 1999, Galindo-Gonzalez et al. 2000), it is possible that the mosaic secondary forests and agricultural fields surrounding the partially enclosed forest patches provide a higher richness of available fruit species, in contrast to patches largely surrounded by rainforest, explaining lower species richness of dispersed seeds in these patches. The highest richness and diversity of seed dispersed by bats captured in rainforest sites is probably due to the fact that they provide roosting opportunities for most frugivorous bat species and therefore rainforest is a common route for frugivorous bat movement (Kunz y Lumsden 2003, Rodriguez-Herrera et al. 2007).

In both secondary forest patches as well as control rainforest, the seeds dispersed by frugivorous bats comprised mostly of early-successional shrub and tree species. Bat species that disperse early-successional shrub and tree seeds can contribute to a rapid development of early secondary forests (Medellín and Gaona 1999). Longevity is usually short in early-successional stage trees and shrubs, and over time these species will be replaced by shade-tolerant late-successional tree species (Guariguata and Ostertag 2001), which can be dispersed by larger frugivorous bats.

The number of bats that dispersed late-successional stage tree seeds was significantly higher in largely enclosed patches than in partially enclosed patches. Hence, the amount of surrounding rainforest positively affected the number of frugivorous bats dispersing seeds from late-successional trees in secondary forest, even though fruits from these trees were not recorded in either largely enclosed or partially enclosed patches.

The secondary forest patches of this study were dominated by *O. pyramidale*, a fast growing species with an average life span of >20 yr, highly preferred by indigenous farmers for the rapid conversion of agricultural land, without being used for timber or non-timber products (Douterlungne et al. 2010). Their fruits are not eaten by bats, but their flowers are pollinated by nectarivorous bats (Heithaus et al. 1975, Tschapka 2004). After 12 yrs *O. pyramidale* will slowly disappear from the canopy and other species start dominating the secondary forest. Without the colonization of late-successional tree species, early-successional light demanding tree species can benefit from the increased light exposure with disappearing *O. pyramidale*.

In both rainforest and largely enclosed forest patches two large frugivorous bats, *A. lituratus* and *A. jamaicensis*, were highly abundant, both species were encountered dispersing seeds of mid-to late-successional plant species, important for the successional development of secondary forest areas. Their importance as dispersers varied between treatments, but was higher for both species in control rainforest and largely enclosed patches than in partially enclosed patches (Table 3). Both species were thought to be *Ficus* spp. specialists (Fleming 1986), but have since been found to be more generalist frugivorous bats, with their diet consisting of mainly *Cecropia* (Passos and Passamani 2003, Da Silva et al. 2008). In our study *A. lituratus* seemed to specialize in *Cecropia* fruits, representing more than 50% of its diet. The fruit species important in the diet of *A. jamaicensis* were more diverse, including both *Cecropia* species and several *Ficus* species. Both large frugivorous bat species were frequently captured in largely enclosed patches, where *Artibeus lituratus* captures increased with increasing fruit availability of *C. obtusifolia*. These secondary forest patches surrounded by rainforest probably functioned as an alternative for both large frugivorous bat species in periods of low *Ficus* fruit abundance, due to the large proportion of surrounding rainforest with almost year round availability of *C. obtusifolia* fruits (Estrada and Coates-Estrada 1985). *Artibeus jamaicensis* and *A. lituratus* have a diverse diet consisting of species from different successional stages and their contribution to mid-to late-successional development can therefore be considered high in comparison with bat species such as *Carollia spp*. Moreover, the dispersal of seeds and the diet range by both bat species from late-successional stage plants is probably underestimated (Lobova et al. 2009), since many late-successional stage tree fruits include large seeds, which frugivorous bats are unable to swallow, and therefore can only be recorded from bats carrying the fruits when captured.

The two small frugivorous species, *C. sowelli* and *C. persicillata*, were the most important dispersers especially in partially enclosed patches. Their diet consisted of mainly *Piper* fruits (Fleming 1991, Thies and Kalko 2004, Voight et al. 2012), a species that is found abundantly in open areas in dense clusters, typical for the early- to medium successional stages of secondary forests (Álvarez-Buylla Roces 1997). Although there are several *Piper* species that are shade tolerant (*P. hispidum* and *P. aeruginosibaccum*; Greig 1993) in the diet of *Carollia*, the most abundant plant species dispersed by *Carollia* were early-successional shrub species *P. aduncum* and *P. auritum* (Greig 1993).

The fruit availability from two of the four *Piper* species was positively correlated with number of bats dispersing these seeds in partially enclosed patches, in contrast to only one *Piper* species in largely enclosed patches. Partially enclosed patches were mostly surrounded by early-to mid-successional stage forest patches, where *Piper* fruits are abundant (Greig 1993) and therefore increasing fruit availability. *Carollia* bat species face a cost/benefit trade-off between food abundance, foraging energy and sufficient canopy cover to avoid predators (Heithaus and Fleming 1978, Russo et al. 2007). A mosaic of different successional stage forest patches can amplify the foraging area, and increase refuge opportunities. Rainforest probably not only provides refuge opportunities, it also supplies fruit availability, such as *P. aeruginosibaccum* which abundance was not only related with overall frugivorous bats dispersing their seeds in general, but also related with *C. perspicillata* abundance. *Piper* late-successional shrub fruit availability could serve as an alternative for preferred earlier-successional fruit plants *P. aduncum* and *P. auritum.*

Frugivorous bat abundance was not related with the availability of fruit presence of trees in the rainforest sites. This can be partially explained by the method of fruit presence estimation; we counted the number of individual trees with fruit presence, instead of counting mature fruits per plant individual. This might function as an appropriate method for shrubs and trees of small-seeded fruits, with a clumped distribution pattern and a “steady state”, low but constant fruit production of *Piper* and *Cecropia* plant species, but in the case of tree species such as *Ficus* or other late-successional tree species with a “big bang” fruit production several times a year, a patchy distribution (Gentry 1974, Fleming and Heithaus 1981, Fleming et al. 1987, Dumont 2003), this method might not appropriately quantify fruit availability.

In conclusion, the proportion of surrounding tropical rainforest positively affects diversity of seed dispersal and seed dispersal of mid-to late-successional stage fruits. Seeds of these plant species can facilitate the development of secondary forest patches towards older successional stages. Secondary forest patches with a relative small proportion of surrounding tropical rainforest attract bat species with a diet that holds a higher richness of dispersed seeds, but these seeds represented plant species of early-successional stage succession.

Acknowledgments

This research was funded by Etnobiología para la Conservación A.C. and by a doctoral scholarship awarded to the first author by El Consejo Nacional de Ciencia y Technologia (CONACyT) Mexico (Reg. 239503). Idea Wild and Fondo Institucional de Fomento Regional para el Desarrollo Científico, Tecnológico y de Innovación (FORDECYT) (Agreement 116306) provided mist nets. We are grateful to M. Castellano and E.Chankin for allowing us to work on their lands. Furthermore, we would like to thank J. Chankin, A. Chankin, C. Peñaloza Guerrero, R. van Toor, V. Hommersen, M. Wulms and A. Sanchez for their help in the fieldwork. We also like to thank N. Ramírez-Marcial and L.B. Vázquez for useful comments during the writing of the manuscript.

Reference list

Álvarez-Buylla Roces E. 1997. *Cecropia obtusifolia* (chancarro) In: González Soriano E, Dirzo R, Vogt RC (Eds) Historia Natural de Los Tuxtlas. Universidad Nacional de México, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, Mexico, pp 109–114.

Anderson DR, Laake JL, Crain BR, Burnham KP. 1979. Guidelines for line transect sampling of biological populations. Journal of Wildlife Management, 43: 70-78.

Bonaccorso FJ.1979. Foraging and reproductive ecology in a Panamian bat community. Bull Fla State Mus Biol Sci 24: 359-408.

Byrne CE, Nagle DC. 1997. Carbonization of Wood for Advanced Materials Applications. Carbon, 35: 259-266.

Colwell RK. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User’s guide and application. http://purl.oclc.org/estimates. Accessed 10 Dec 2010

CONAFOR. 2012. Lineamientos de operación para proyectos especiales de conservación y restauración forestal.

Da Silva AG, Gaona O, Medellín RA. 2008. Diet and trophic structure in a community of fruit-eating bats in Lacandon forest, Mexico. Journal of Mammalogy, 89:43–49.

Diemont SAW, Martin JF, Levy-Tacher SI, Nigh RB, Ramirez Lopez P, Golicher JD. 2006. Lacandon Maya forest management: Restoration of soil fertility using native tree species. Ecological Engineering, 28: 205-212.

Douterlungne D, Levy-Tacher SI, Golicher JD, Román Dañobeytia F. 2010. Applying indigenous knowledge to the restoration of degraded tropical rain forest dominated by bracken. Restoration Ecology, 18:322-329.

Dumont ER. 2003. Bats and fruit: an ecomophological approach. In: Kunz, TH, Fenton MB (Eds), Bat Ecology. University of Chicago Press, Chicago, IL, pp 398–429

Estrada A, Coates-Estrada R .1985. A preliminary study of resource overlap between howling monkeys (Alouatta palliata) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology, 9: 27–37.

Fenton MB, Acharya LD, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM, Adkins B. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica, 24: 440-446.

Fleming TH. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats, in: Estrada, A., Fleming, T.H. (Eds.), Frugivores and seed dispersal. Dordrecht, pp. 105-118

Fleming TH.1991. The relationship between body size, diet and habitat use in frugivorous bats, Genus *Carollia* (Phyllostomidae). Journal of Mammalogy, 72: 493-501.

Fleming TH, Heithaus ER. 1981. Frugivorous Bats, Seed Shadows, and the Structure of Tropical Forests. Biotropica, 13 :45-53

Fleming TH, Breitwisch R, Whitesides GH. 1987. Patterns of tropical vertebrate frugivore diversity. Annual Review Ecology, Evolution and Systematics, 18: 91-109.

Galindo-González J, Guevara S, Sosa VJ. 2000. Bat-and bird-generated seed rains at isolated trees in pastures in tropical rain forest. Conservation Biology, 14: 1693-1703.

Galindo-González J, Vázquez-Domínguez G, Saldaña-Vázquez RO, Hernández-Montero JR. 2009. A more efficient technique to collect seeds dispersed by bats. Journal of Tropical Ecology, 25: 205-209.

García-Estrada C, Damon A, Sánchez-Hernández C, Soto-Pinto L, Ibarra-Núñez L. 2011. Diets of frugivorous bats in Montane Rain Forest and Coffee Plantations in Southeastern Chiapas, Mexico. Biotropica 44: 394-401

Gentry AH. 1974. Coevolutionary patterns in Central American Bignoniaceae. Annals of the Missouri Botanical Garden, 69: 728-759.

Gorchov DL, Cornejo F, Ascorra C, Jaramillo M. 1993. The role of seed dispersal in the natural regeneration of rainforest after strip-cutting in the Peruvian Amazon. Vegetatio, 107/108: 339–349.

Gorresen PM, Willig MR. 2004. Landscape responses of bats to habitat fragmentation in atlantic forest of Paraguay. Journal of Mammology, 85: 688–697.

Greig N. 1993. Regeneration Mode in Neotropical Piper: Habitat and Species Comparisons. Ecology, 74: 2125-2135

Guariguata MR, Ostertag R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management, 148: 185-206.

Guevara S, Laborde J. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio, 108: 319–338.

Guevara S, Laborde J, Liesenfeld D, Barrera O. 1997. Potreros y ganadería. Pp. 43-58. En: Gonzalez-Soriano E, Dirzo R, Vogt R (o Eds). Historia Natural de Los Tuxtlas. Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, D.F.

Heithaus ER, Fleming TH. 1978. Foraging Movements of a Frugivorous Bat, Carollia perspicillata (Phyllostomatidae). Ecological Monographs, 48:127-143

Heithaus ER, Fleming TH, Opler PA. 1975. Foraging Patterns and Resource Utilization in Seven Species of Bats in a Seasonal Tropical Forest. Ecology, 56: 841-854.

Henry M, Jouard S. 2007. Effect of bat exclusion on patterns of seed rain in tropical rainforest in French Guiana. Biotropica, 39: 510–518.

Hortal, J, Borges PAV, Gaspar C. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. Journal of Animal Ecology, 75: 274–287.

Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist, 104: 501-528.

Kalko, EKV, Herre EA, Handley CO Jr. 1996. Relation of fig fruit characteristics to fruiteating bats in the New and Old World tropics. Journal of Biogeography, 23: 565–576.

Krebs CJ. 1989. Ecological methodology. Harper and Row, New York.

Levy-Tacher SI. 2000. Sucesión causada por roza-tumba-quema en las selvas de Lacanhá, Chiapas. Dissertation, Colegio de Postgraduados.

Levy-Tacher SI, Golicher JD. 2004. How predictive is traditional ecological knowledge? the case of the Lacandon Maya Fallow Enrichment System. Interciencia, 29: 496-503.

Levy-Tacher SI, Aguirre-Rivera JR. 2005. Successional pathways derived from different vegetation use patterns by Lacandon Mayan Indians. Journal of Sustainable Agriculture, 26: 49-82.

Lobova TA, Mori SA. 2004. Epizoochorous dispersal by bats in French Guiana. Journal of Tropical Ecology, 20: 581–582.

Lobova TA, Geiselman CK, Mori SA. 2009. Seed dispersal by bats in the Neotropics. Memoirs of the New York Botanical Garden. New York Botanical Garden Press. The Bronx, New York.

Magurran AE. 2004. Measuring Biological Diversity. Blackwells, Oxford, UK

McCune B, Grace JB. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach.

Medellín RA, Gaona O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica, 31: 478-485.

Miranda F, Hernández XE. 1963. Los tipos de vegetación de México y su clasificación. Boletín de la Sociedad Botánica de México, 28: 29-179.

Nations J, Nigh R. 1980. The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. Journal of Anthropological Research, 36: 1-30.

Nowak RM. 1991. Walker's Bats of the World. London: Johns Hopkins University Press.

Passos JG, Passamani DM. 2003. *Artibeus lituratus* (Chiroptera, Phyllostomidae): biologia e dispersao de sementes no Parque do Museu de Biologia Prof. Mello Leitao, Santa Teresa (ES). Natureza, 1: 1–6.

Pennington TD, Sarukhán J. 2005. Árboles tropicales de México. Tercera edición. Universidad Nacional Autónoma de México y Fondo de Cultura Económica, México, D.F.

R Development Core Team (2006) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org. Accessed 10 Apr 2012.

Russo D, Cistrone L, Jones G. 2007. Emergence time in forest bats: the influence of canopy closure. Acta Oecologica, 31: 119-126.

Rzedowski J. 1978. Vegetación de Mexico. Editorial Limusa, Mexico, DF

Saldaña-Vázquez RA, Sosa VJ, Hernández-Montero JR, López Barrera F. 2010. Abundance responses of frugivorous bats (Stenodermatinae) to coffee cultivation and selective logging practices in mountainous central Veracruz, Mexico. Biodiversity and Conservation, 19: 2111–2124.

Schulze MD, Seavy NE, Whitacre DF. 2000. A Comparison of the Phyllostomid Bat Assemblages in Undisturbed Neotropical Forest and in Forest Fragments of a Slash-and-Burn Farming Mosaic in Petén, Guatemala. Biotropica, 32: 174-184.

SPSS INC. 2007. SPSS. Version 17.0. SPSS Inc., Chicago, Illinois.

Swaine MD, Whitmore TC. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio, 75: 81-86.

Terborgh J. 1984. Five new primate. A study in comparative ecology. Princeton University Press, Princeton, New Jersey. 260 pp.

Thies W, Kalko EKV. 2004. Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, ***Carollia perspicillata*** and ***C. castanea*** (Phyllostomidae). Oikos 104:362-376

Thomas DW. 1988. Analysis of diets of plant-visiting bats, in: Kunz, TH. (Ed.), Ecological and Behavioral Methods for the Study of Bats, pp. 211-220. Smithsonian Institution Press, Washington DC.

Tschapka M. 2004. Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. Journal of Zoology, 263: 7-21.

Vleut I, Levy-Tacher SI, Galindo-González J, de Boer WF, Ramírez-Marcial N. 2012. Tropical rainforest matrix quality affects bat assemblage structure in secondary forest patches. Journal of Mammalogy doi: http://dx.doi.org/10.1644/12-MAMM-A-005.1

Voight CC, Voight-Heuke SL, Kretzschmar AS. 2012. Isotopic evidence for seed transfer from successional areas into forests by short-fruit bats (*Carollia* spp.; Phyllostomidae). Journal of Tropical Ecology 28: 181-186.

Wendeln MC, Runkle JR, Kalko EKV. 2000. Nutritional Values of 14 Fig Species and Bat Feeding Preferences in Panama. Biotropica, 32: 489-501

Whitmore TC. 1989. Canopy gaps and the two major groups of forest trees. Ecology, 70: 536-538.

Wulms M. 2009. Bats as indicator species of forest recovery in areas of secondary forest along a gradient of time since abandonment in Lacanhá, Chansayab, Chiapas, Mexico. Dissertation, University Van Hall, Larenstein

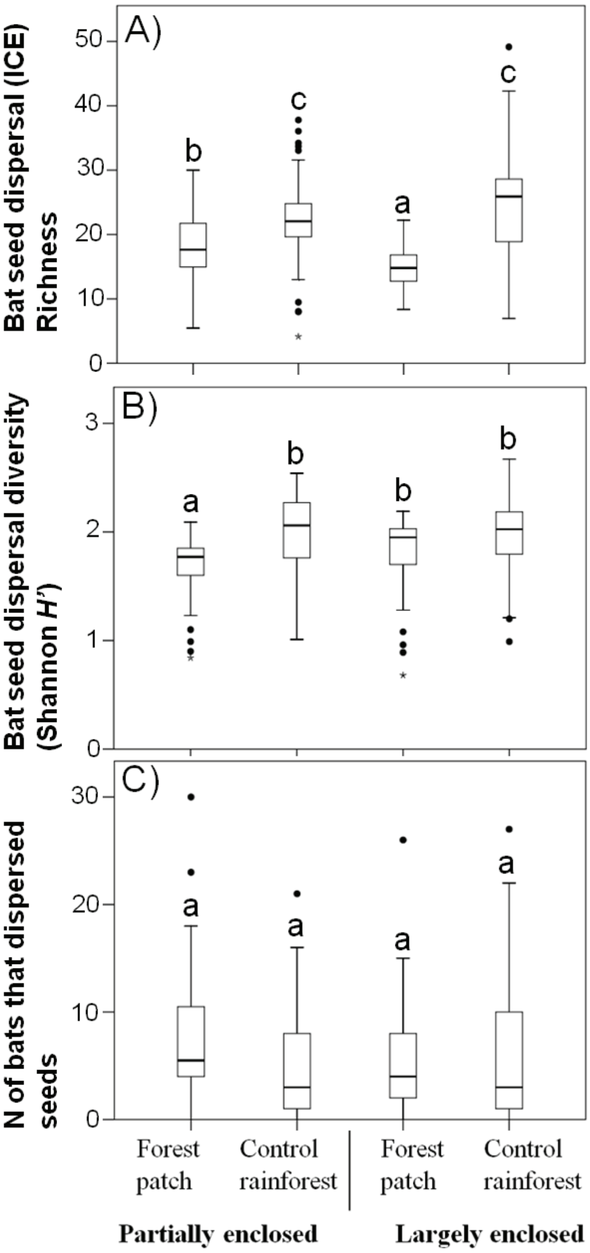

Fig. 1 Box plots representing; A) species richness (ICE) and B) Shannon *H'* diversity index of seeds dispersed by bats C) the number of bats with seeds in feces or carrying fruits. Box plots with equal letters are not significantly different; based on a Kruskal-Wallis and a post hoc Mann-Whitney *U* test with Bonferroni correction. Black dots represent outliers, and asterisks extreme cases of outliers.

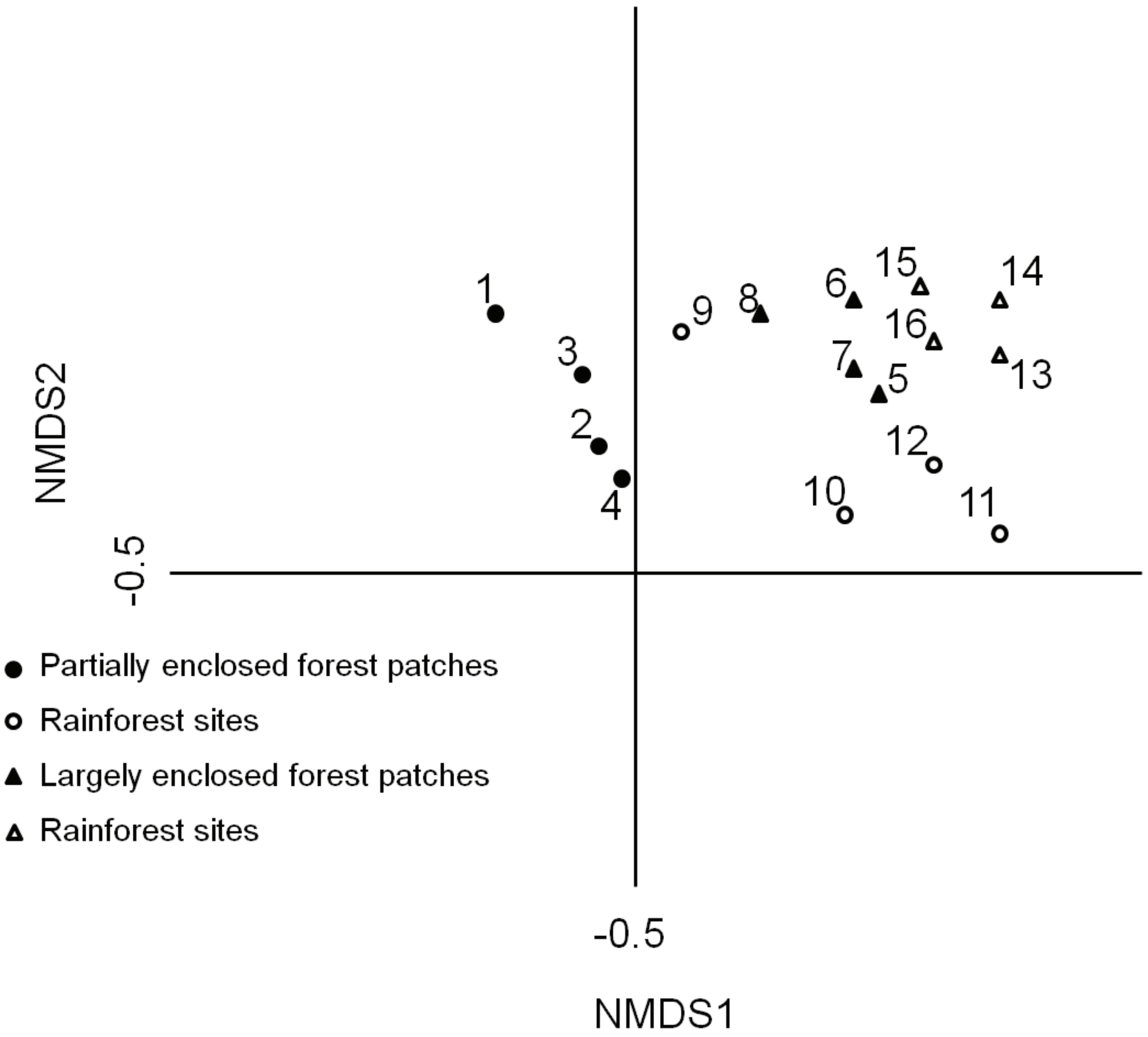

Fig. 2 NMDS ordination of the study sites based on frequency of bats per dispersed seed species, based on Bray–Curtis dissimilarities (Stress = 8.542). Circles represent partially enclosed forest patches (closed) and the nearby rainforest sites (open), while triangles represent largely enclosed forest patches (open) and its nearby rainforest sites (closed).

Table 1. Mean abundance (± AAD (average of absolute deviation)) of all frugivorous bats that dispersed seeds categorized per life form (tree and shrub) and successional stage (early or late). Differences between treatments are expressed by different bold letters, based on Kruskal-Wallis and post hoc Mann-Whitney U test with Bonferroni correction.

	Partially enclosed				**Largely enclosed**			
	Forest patch		**Control rainforest**		**Forest patch**		**Control rainforest**	
Early successional trees	0.98 ± 0.98	**a**	1.13 ± 1.30	**a**	1.77 ± 1.92	**a**	1.92 ± 2.03	**a**
Early successional shrubs	5.44 ± 3.96	**b**	2.46 ± 2.30	**a**	2.71 ± 1.73	**a**	1.88 ± 1.65	**a**
Late successional trees	0.10 ± 0.19	**a**	1.08 ± 1.01	**c**	0.38 ± 0.53	**b**	1.35 ± 1.39	**c**
Late successional shrubs	0.33 ± 0.51	**a**	0.17 ± 0.31	**a**	0.23 ± 0.39	**a**	0.13 ± 0.23	**a**

Plant species	**Successional stage**	**Life form**	**Bat species**							
			C. s.		*C. p.*		*A. j.*		*A. l.*	
			N	*%*	*N*	*%*	*N*	*%*	*N*	*%*
*Brosimum alicastrum**	Late	Tree	0	0	0	0	0	0	8	4
*Calophyllum brasiliense var.j**	Late	Tree	0	0	0	0	0	0	2	1
Cecropia obtusifolia	Early	Tree	9	4	15	5	22	26	94	50
Cecropia peltata	Early	Tree	3	1	15	5	12	14	19	10
Ficus maxima	Late	Tree	0	0	0	0	26	31	13	7
Ficus americana	Late	Tree	0	0	0	0	12	14	12	6
Ficus spp 1	Late	Tree	0	0	0	0	5	6	1	1
Ficus spp 2	Late	Tree	0	0	0	0	4	5	21	11
Piper aduncum	Early	Shrub	55	23	86	28	1	1	1	1
Piper aeruginosibaccum	Late	Shrub	9	4	26	8	0	0	1	1
Piper auritum	Early	Shrub	88	37	89	29	1	1	5	3
Piper hispidum	Late	Shrub	37	16	50	16	2	2	2	1
Piper umbellata	Early	Shrub	7	3	4	1	0	0	0	0
Piper aequale	Late	shrub	1	0	3	1	0	0	0	0
Prunus salicifolia	Early	Tree	0	0	2	1	0	0	2	1
*Quararibea funebris**	Late	Tree	0	0	0	0	0	0	5	3
Family Solanacea 1	Early	Shrub	0	0	0	0	0	0	0	0
Family Solanacea 2	Early	Shrub	0	0	0	0	0	0	1	1
Solanum erianthum	Early	Shrub	12	5	13	4	0	0	0	0
Solanum torvum	Early	Shrub	4	2	0	0	0	0	0	0

Spp uni.1	1	0	0	0	0	0	0	0
Spp uni.2	2	1	0	0	0	0	0	0
Spp uni.3	1	0	0	0	0	0	0	0
Spp uni.4	0	0	2	1	0	0	0	0
Spp uni.5	0	0	1	0	0	0	0	0
Spp uni.6	3	1	1	0	0	0	0	0
Spp uni.7	1	0	0	0	0	0	0	0
Spp uni.8	3	1	5	2	0	0	0	0
Total	**236**		**312**		**85**		**187**	
Total species	**16**		**14**		**9**		**15**	

Table 2. Number of plant species registered from bat seeds dispersed by the four most abundant bat species (*C. s.* = *Carollia sowelli*. *C. p.* = *Carollia perspicillata*. *A. j.* = *Artibeus jamaicensis* and *A. l.* = *A. lituratus*). Successional categories and life form follows Greig (1993), Guevara (1997), Levy-Tacher and Aguirre-Rivera (2005), Pennington and Sarukhán (2005). *shows fruits only found carried by bats.

	DII			
	1	2	3	4
C. s.	1.95	0.58	1.13	0.67
C. p.	2.92	1.04	1.32	0.63
A. j.	0.07	0.94	0.64	1.15
A. l.	0.07	0.30	0.45	0.59
Total	**5.01**	**2.86**	**3.85**	**3.04**

Table 3. Disperser Importance Index (DII) values of two small and two large frugivorous bat species per treatment (1= partially enclosed patch, 2=control rainforest, 3=largely enclosed patch, 4= control rainforest) per bat species (*C. s.* = *Carollia sowelli*, *C. p*. = *Carollia perspicillata*, *A. j*. = *Artibeus jamaicensis* and *A. l.* = *A. lituratus*).

Appendix 1 Number of captures per frugivorous bat species per treatment.

	Partially enclosed		Largely enclosed			
Species	**Forest patch**	**Rainforest**	**Forest patch**	**Rainforest**	**Total**	**% of total**
Artibeus jamaicensis	19	138	81	171	409	16.65
Artibeus lituratus	15	181	93	155	444	18.07
Artibeus phaeotis	25	27	21	26	99	4.03
Artibeus toltecus	4	5	9	4	22	0.90
Artibeus watsoni	10	24	24	20	78	3.17
Carollia perspicillata	185	80	90	109	464	18.88
Carollia sowelli	150	87	70	75	382	15.55
Centurio senex		5	8	3	16	0.65
Chiroderma villosum				2	2	0.08
Glossophaga commissarisi	13	35	21	26	95	3.87
Glossophaga soricina	17	23	29	54	123	5.01
Lichonycteris obscura		1			1	0.04
Phyllostomus discolor		17	4	12	33	1.34
Phyllostomus stenops			2	1	3	0.12
Platyrrhinus helleri	4	6	5	8	23	0.94
Sturnira lilium	87	44	53	35	219	8.91
Uroderma bilobatum	8	8	3	7	26	1.06
Vampyressa pusilla		6	2	3	11	0.45
Vampyrodes caracciolii		5		2	7	0.28
Total	**537**	**692**	**515**	**713**	**2457**	

Capítulo IV

Discusión general

Discusión

En los terrenos comunales de Lacanhá, a nivel de paisaje existe una matriz de selva, con una variedad de bosques secundarios de diferentes etapas sucesionales y áreas agrícolas, que podrían permitir una alta diversidad biológica según la hipótesis de disturbio intermedio (HDI). En este sentido la diversidad de murciélagos podría ser favorecida en un paisaje constituido por una matriz de selva perforada por parches con distintos niveles de disturbio. La cercanía de estas condiciones permite que la gran mayoría de murciélagos se refugien en la selva, desde donde pueden dirigirse a sus áreas de forrajeo según su preferencia alimenticia.

Nuestros resultados se restringen a estudios a nivel de parcela donde se encontró una alta diversidad en una condición de bajo disturbio. Esta alta diversidad en la selva podría responder a la influencia de los parches de diferentes etapas sucesionales aledaños a esta, que permiten el mantenimiento de especies de murciélagos dependientes de áreas con mayor disturbio.

La comunidad de murciélagos en la selva

En la primera parte de la investigación se encontró la mayor diversidad y riqueza de murciélagos en la selva, el área de menor nivel de disturbio. Las especies de murciélagos más abundantes en esta condición fueron *Artibeus jamaicensis* y *Artibeus lituratus,* reconocidas por su capacidad de adaptarse a paisajes transformados, aprovechando los frutos disponibles de los árboles aislados (Fenton et al. 1992, Schulze et al. 2000, Galindo-González y Sosa 2003, Galindo-González 2004). Sin embargo, estas especies también pueden ser favorecidas en un área predominantemente selvática al poder alimentarse de los frutos de los árboles de la etapa sucesional tardía.

Las especies de murciélagos carnívoros-insectívoros son reconocidas como indicadoras de condiciones prístinas, o de bajo disturbio según la HDI (Estrada y Coates-Estrada 2002, Schulze et al. 2000). Estas especies dependen de la selva por la variedad y abundancia de recursos que esta condición les ofrece (Gorresen y Willig 2004). En particular, dos especies de carnívoros-insectívoros de mayor tamaño, *Vampyrum spectrum* y *Chrotopterus auritus,* fueron capturadas exclusivamente en la selva, mientras que otras especies de carnívoros-insectívoros más pequeños, como *Mimon bennettii*, *Trachops cirrhosus y Tonatia saurophila,* también dependen de la selva, pero esporádicamente han sido encontradas en áreas de bosque secundario (Galindo-González 2004). El patrón de ocurrencia de estos murciélagos fue similar en nuestro estudio, pero únicamente fueron capturados en los parches de bosque secundario con mayor proporción de selva. Es probable que el tránsito de estas especies por los parches de bosque secundario sea favorecido cuando la proporción de selva es alta.

La comunidad de murciélagos en parches de bosque secundarios rodeados mayormente por selva

La diversidad y abundancia de murciélagos fueron similares en la selva y en los parches de bosque secundario con mayor proporción de selva circundante. Sin embargo, la riqueza y la contribución a la diversidad total de los murciélagos fue menor en estos bosques secundarios en relación a la selva. Las mismas especies de murciélagos frugívoros encontradas abundantemente en la selva (*Artibeus* *jamaicensis* y *A. lituratus*) también lo fueron en los parches de bosque secundario mayormente rodeado por selva. Evidentemente, la proporción de selva favorece el movimiento de estas especies hacia áreas de bosque secundario. El bosque secundario puede proveer recursos para estas especies y la proporción de selva alrededor permite la cercanía hacia posibles refugios y perchas más seguras (Castro-Luna et al. 2007b, Soriano y Ochoa 2001). El hábitat preferencial de estas especies es la condición de bajo disturbio, sin embargo pueden aprovechar los bosques secundarios sin depender de ellos para sobrevivir.

La comunidad de murciélagos en parches de bosque secundarios rodeados parcialmente por selva

Los parches de bosque secundario con menor proporción de selva presentaron menor diversidad, riqueza y contribución a la diversidad total de los murciélagos que la selva y los parches de bosque secundario con mayor proporción de selva circundante. Se encontró una alta abundancia de pocas especies de murciélagos como *Carollia perspicillata*, *C. sowelli*, y *Sturnira lilium,* conocidas por su preferencia alimenticia hacia los frutos de Piperaceae y Solanaceae, generalmente encontrados en áreas abiertas con alto disturbio o de bosque secundario incipiente (Greig 1993, Fleming 2004, Williams-Guillén y Perfecto 2010). La alta abundancia de estas pequeñas especies de murciélagos probablemente se debe a la mayor conectividad que existe en los parches parcialmente rodeados por selva con otros bosques secundarios y áreas agrícolas. Así, los murciélagos frugívoros pequeños son atraídos por las áreas de mayor disturbio, debido a que en estas condiciones abundan sus recursos alimenticios. Estos pequeños murciélagos están bien adaptados a las condiciones de mayor disturbio con disponibilidad de recursos por arbustos de etapa sucesional temprana, pero tienen un rango de hábitat pequeño, es decir que su refugio debe estar cercano a múltiples áreas de forrajeo (Bonaccorso et al. 2007, Heithaus y Fleming 1978). El hábitat preferencial de estas especies es la condición de mayor disturbio, sin embargo pueden aprovechar la selva sin depender de ella para sobrevivir. Este grupo de murciélagos puede ser un buen ejemplo de las especies favorecidas por el disturbio intermedio, las cuales permiten el aumento de la diversidad a nivel de paisaje.

Variables estructurales de la vegetación y la comunidad de murciélagos

Aparte de la proporción de la selva alrededor de los parches, también las similitudes o diferencias estructurales de la vegetación pueden afectar el movimiento de murciélagos (Gascon et al. 1999). En nuestro caso evaluamos varios atributos (la apertura de dosel, el área basal, la diversidad, la densidad y la altura de los árboles) para reconocer las diferencias estructurales entre los parches de bosque secundario y la selva. Sin embargo, de estas variables sólo la apertura del dosel presentó una diferencia significativa, inversamente proporcional a la abundancia de los murciélagos. Es probable que un dosel más cerrado presente una condición que brinde una mayor protección a los murciélagos de sus depredadores, así como una mayor cantidad de lugares de refugio (Evelyn et al. 2003). Al respecto, se desconoce el efecto de la presencia de depredadores sobre el comportamiento de forrajeo de los murciélagos, y en particular en los trópicos (Baxter et al. 2006). En regiones templadas existe evidencia de murciélagos insectívoros que evitan los claros y pasan por sus bordes con cobertura de vegetación para evitar a las aves de presa o murciélagos carnívoros de mayor tamaño (Limpens y Kapteyn 1991, Furlonger et al. 1987, Grindal y Brigham 1999). En el presente estudio fue posible capturar murciélagos carnívoros como *Vampyrum spectrum* y *Chrotopterus auritus* en la selva, que son conocidos por alimentarse de murciélagos pequeños, y escuchar y capturar búhos en los bosques secundarios.

El efecto de la matriz de selva sobre la dispersión de semillas por murciélagos

De todos los murciélagos el grupo de los frugívoros fue el más diverso en cada una de las distintas condiciones estudiadas. Los murciélagos frugívoros son importantes dispersores de semillas que contribuyen al desarrollo de la sucesión vegetal en los ecosistemas tropicales (Muscarella y Fleming 2007). En la segunda parte de la investigación se encontró una diversidad más alta de semillas dispersadas por murciélagos en selva y parches de bosques secundarios con mayor proporción de selva. Sin embargo, la riqueza de semillas dispersadas fue mayor en selva y parches de bosques secundarios con menor proporción de selva circundante. La alta diversidad y riqueza de semillas dispersadas en la selva probablemente es causada por la alta disponibilidad de refugios y su cercanía hacia áreas de forrajeo. Así, los murciélagos que regresan a su refugio en la selva transportan una alta variedad de semillas de las distintas etapas sucesionales. Áreas con mayor disturbio, como los parches de bosques secundarios, pueden ofrecer una alta variedad y disponibilidad de recursos para murciélagos frugívoros por su predilección hacia frutos de arbustos y árboles de la etapa sucesional temprana (Galindo-González 2003). La disponibilidad de estos frutos es constante a lo largo del año en baja densidad y tienen una distribución espacial agregada (Gentry 1974, Fleming y Heithaus 1981). En la selva, la distribución dispersa de árboles con frutos y su producción masiva provoca que los murciélagos que forrajean en ellos, normalmente de mayor tamaño, viajen grandes distancias para consumir sus frutos, con lo cual aumenta la probabilidad de que las semillas sean dispersadas lejos de los árboles parentales.

La mayoría de las semillas dispersadas por los murciélagos frugívoros en todas las condiciones fueron de árboles y arbustos de la etapa sucesional temprana. Estos resultados concuerdan con otros estudios sobre la importancia de murciélagos frugívoros para favorecer la sucesión en áreas de etapa sucesional temprana (Galindo-Gonzalez 2003, Medellín y Gaona 1999, Muscarella y Fleming 2007). En la selva, con mayor disponibilidad de frutos de la etapa sucesional avanzada, se encontró una mayor cantidad de murciélagos que dispersaron semillas de especies de la etapa sucesional tardía que en parches de bosque secundario. Sin embargo, los parches de bosque secundario completamente rodeado por selva fueron positivamente afectados por la selva, y se encontró una mayor dispersión de semillas de esta etapa sucesional por los murciélagos frugívoros que en parches de bosque secundario con menor proporción de selva alrededor. De esta manera, la proporción de selva afectó positivamente a la cantidad de murciélagos que dispersan semillas de especies tardías hacia el bosque secundario mayormente rodeado. Este proceso adquiere mayor relevancia tomando en cuenta que en ninguna de las dos condiciones de bosque secundario se registraron árboles de fases sucesionales tardías.

Murciélagos dispersores de semillas en selva y bosque secundario mayormente rodeado por selva

Las especies *Artibeus lituratus* y *A. jamaicensis* fueron las más abundantes y las principales dispersoras de semillas en la selva y parches de bosque secundario mayormente rodeado por selva. Estas especies han sido encontradas como especialistas consumidoras de frutos de *Ficus* spp. (Fleming 1986), pero últimamente fueron clasificadas como generalistas, al incluir en su dieta frutos de *Cecropia* (Passos y Passamani 2003, Da Silva *et al.* 2008). Para estos murciélagos grandes la disponibilidad de frutos de *C. obtusifolia* puede funcionar como una alternativa en periodos de baja abundancia de frutos de *Ficus* spp*.,* debido a que *C. obtusifolia* cuenta con una disponibilidad de frutos casi todo el año en los parches de bosque secundario (Estrada y Coates-Estrada 1985). En nuestro estudio, *C. obtusifolia* fue el árbol más dispersado por *A. lituratus* y en menor proporción lo hizo con *Ficus máxima*, *Ficus americana* y dos otras especies de Ficus, en contraste con *A. jamaicensis* que dispersaron más del 50% de frutos de *Ficus* spp. *Artibeus jamaicensis* y *A. lituratus* dispersaron semillas de especies de árboles de diferentes etapas sucesionales (*Cecropia*, *Ficus spp*, *Brosimum alicastrum*, *Quararibea funebris*), y por lo tanto sus contribuciones hacia el desarrollo de bosques de diferentes etapas sucesionales puede ser considerado mayor en comparación con la dispersión de semillas por parte de las especies del género *Carollia*.

Murciélagos dispersores de semillas en bosque secundario parcialmente rodeado por selva

Dos murciélagos pequeños (*Carollia sowelli* y *C. perspicillata*) fueron los dispersores más importantes en el bosque secundario parcialmente rodeado por selva. Su dieta consistió de semillas de *Piper* y aunque varias especies de este género son tolerantes a la sombra (*P. hispidum* y *P. aeruginosibaccum*; Greig 1993), las especies de *Piper* más dispersadas por estos murciélagos fueron *P. aduncum* y *P. auritum*, arbustos propios de etapas sucesionales tempranas (Greig 1993). La abundancia de plantas con frutos maduros de estas dos especies de *Piper* estuvo positivamente relacionada con la cantidad de murciélagos dispersores de estas semillas en parches parcialmente rodeados por selva. Debemos considerar que estos parches y su entorno (áreas agrícolas y bosque secundario), son una amplia y abundante fuente de forrajeo para las especies de *Carollia*. Estas dos especies han sido encontradas a lo largo de distintas etapas sucesionales, con un mayor abundancia en etapas intermedias (Medellín et al. 2000, Castro-Luna et al. 2007, de la Peña et al. 2012). Así, es probable que la presencia de estas especies en un sitio no sólo dependerá de la abundancia de alimento, sino también de la cobertura de dosel para disminuir la posibilidad de depredación o la distancia entre áreas de forrajeo y refugio. Estos factores sumados a otros más pueden reducir el costo energético (Heithaus y Fleming 1978), prefiriendo el área de forrajeo más cercana al refugio.

El manejo tradicional Lacandón y las aplicaciones para la restauración

El manejo tradicional de los recursos naturales por los lacandones implica un conocimiento detallado de la flora y fauna y sus interacciones, a partir del cual han manejado la selva por generaciones sin destruirla (Nations y Nigh 1980, De Vos 1988). El fomento de la diversidad mediante prácticas tradicionales lacandonas es evidente en sus esquemas de producción, así como en las acciones para la restauración de áreas degradadas (Nations y Nigh 1980, Aronson et al. 2007, Douterlungne et al. 2010). A partir de nuestros resultados podemos concluir que la vegetación en los terrenos comunales de Lacanha-Chansayab, resultante de su aprovechamiento mediante el sistema de rtq, genera un paisaje humanizado de disturbio intermedio que permite la presencia de una alta diversidad de murciélagos y la dispersión de semillas de varias especies; gran parte de ellas, arbustos y árboles de la selva neotropical, dependen de los frugívoros para la dispersión de sus semillas (Howe y Smallwood 1982). Desde esta perspectiva, la dispersión de semillas por murciélagos del proceso puede considerarse como un elemento que favorece o acelera la regeneración en los bosques secundarios (Elliot et al. en prensa). Para entender la importancia que puede tener la dispersión de semillas en la restauración de áreas degradadas, se requiere conocer a sus dispersores y las características de la vegetación que los sustenta (Wunderle 1997). La llegada de dispersores y por lo tanto su contribución para la regeneración depende de la complejidad, estructura, composición y disponibilidad de recursos del entorno vegetal en que habitan (Wunderle 1997). También la configuración del paisaje, la distribución espacial de las áreas en diferentes etapas sucesionales, puede ser un factor importante en el desplazamiento de estos dispersores de semillas, sin embargo, aún existe poca evidencia al respecto (Castro-Luna et al. 2007, Vargas-Contreras et al. 2009). En este estudio se encontró que la mayor proporción de selva alrededor de los bosques secundarios puede proveer refugios y recursos alimenticios importantes para los murciélagos, así como favorecer la dispersión de semillas de especies de etapas sucesionales avanzadas. La cercanía y proporción de selva alrededor los bosques secundarios permiten que especies de murciélagos como *Artibeus* pero tambien *Sturnira* y *Carollia,* con una alta diversidad alimenticia, tengan el potencial de contribuir al enriquecimiento florístico en áreas degradadas o dañadas y ayudar a acelerar el proceso de sucesión en los bosques secundarios. Estudios como éste, enfocados a evaluar la dispersión de semillas en áreas degradadas con diferentes proporciones de selva, representan un primer paso para reconocer la importancia de la selva para promover el movimiento de murciélagos y la dispersión de semillas en bosques secundarios en proceso de sucesión.

Los parches de bosque secundario fueron dominados por árboles de *O. pyramidale*, una especie con características estructurales específicas, como una copa angosta y pocas ramas creando un dosel relativamente abierto (Galia-Selaya et al. 2008). El dosel abierto puede favorecer la entrada de luz hacia el sotobosque, promoviendo el crecimiento de arbustos con alimento para varias especies de murciélagos frugívoros (ej. Piperaceae y Solonaceae); además el néctar de las flores de *O. pyramidale* se conoce como un recurso importante para varias especies de murciélagos nectarívoros (Heithaus et al. 1975, Tschapka 2004). Sin embargo, se requiere la comparación de la comunidad de murciélagos en bosques secundarios dominados por *O. pyramidale* con bosques secundarios sin dominancia de esta especie para poder entender el efecto de las características estructurales específicas y la disponibilidad de recursos sobre el movimiento de los murciélagos.

Factores determinantes en la comunidad de murciélagos

Una matriz de selva con parches de bosque secundario, genera un paisaje heterogéneo el cual implica una serie de factores determinantes para el movimiento de los murciélagos. En primera instancia, esta condición puede aumentar la cantidad de nichos para los murciélagos en comparación con un área homogénea de selva o de pastizal (Castro-Luna et al. 2007a). La mayor proporción de selva alrededor de estos parches, es otro factor importante que afecta positivamente la diversidad y riqueza de murciélagos en los parches de bosque secundario. Por otra parte, el bosque secundario no resultó ser un obstáculo o factor determinante para la mayoría de las especies murciélagos encontrados, siempre y cuando el parche estuviera rodeado mayormente por selva. Anteriormente se ha mencionado la importancia de la estructura y composición de la vegetación como factores que determinan la comunidad de murciélagos en un área dada (Crome y Richards 1988, Medellín et al. 2000, Kalko y Handley 2001, Gorresen y Willig 2004, Ford et al. 2005, Castro-Luna et al. 2007). Aunque se encontraron diferencias estructurales entre los sitios de la selva y los parches de bosque secundario, solo la apertura del dosel resultó de ser determinante en la abundancia de murciélagos. Sin embargo, hay que considerar que las diferencias estructurales entre los parches de selva y bosque secundario podrían requerir de muestreos más amplios para poder encontrar una relación entre estas variables y la comunidad de murciélagos. Por lo tanto se requiere ampliar el estudio sobre la importancia de la proporción de selva para bosque secundario dentro de un espectro sucesional mayor.

Los parches de bosque secundario presentaron una diversidad y riqueza de disponibilidad de frutos que coincidieron con las especies que fueron dispersadas por los murciélagos frugívoros y que no fueron encontradas en la selva. La disponibilidad de estos frutos permitió una mayor abundancia de varias especies de murciélagos frugívoros como *Carollia* en los parches de bosque secundario. Aparte de este estudio, pocos han encontrado la importancia que puede tener la disponibilidad de frutos como factor determinante para los murciélagos frugívoros (Vargas-Contreras 2009).

Conclusiones

La comunidad de Lacanhá-Chansayab cuenta con un paisaje que consiste de una matriz de selva interrumpida por pequeñas perforaciones o parches de áreas agrícolas y de bosque secundario en diferentes etapas sucesionales. Esta condición es singular y exclusiva en el contexto regional y permite que prevalezca un disturbio intermedio que promueve una alta diversidad de murciélagos. En particular, la selva de Lacanhá, cuenta con una mayor diversidad, riqueza y contribución a la diversidad total de los murciélagos en relación con los bosques secundarios. Además, la proporción de selva alrededor de los parches de bosque secundario afectó positivamente la diversidad, riqueza y contribución a la diversidad total de los murciélagos. El movimiento de las especies raras (escasas o infrecuentes) de murciélagos, dependientes de la selva hacia parches de bosque secundario, fue favorecido por la proporción de selva en torno a los bosques secundarios. La apertura del dosel fue mayor en los bosques secundarios, lo cual afectó negativamente la abundancia de murciélagos.

La proporción de selva alrededor de los bosques secundarios no sólo afectó la diversidad y riqueza de murciélagos, sino también facilitó el paso de frugívoros grandes, capaces de dispersar semillas de árboles de la etapa sucesional tardía hacia los bosques secundarios. La dispersión de semillas por los murciélagos pequeños en áreas con menor proporción de selva fue dominada por especies de etapas sucesionales tempranas. Es probable que el desarrollo sucesional sea favorecido por estos dos procesos.

Recomendaciones

El uso de redes de niebla en el sotobosque es una técnica efectiva y recomendada para la captura de murciélagos frugívoros. Esta técnica además de ser sencilla en su aplicación, permite llevar a cabo comparaciones entre diferentes estudios (Medellín et al. 2000, Schulze et al. 2000, Castro-Luna et al. 2007a). Sin embargo, es posible que las estimaciones de la diversidad y abundancia que realizamos estén sesgadas hacia los murciélagos de la familia Phyllostomidae, debido a que otras familias de murciélagos son capaces de evadir las redes del sotobosque, por lo tanto es posible que el uso del muestreo acústico y redes del dosel podrían ayudar a tener una mejor estimación de la riqueza, diversidad y abundancia de murciélagos. Con el propósito de reconocer la importancia de la selva para estos grupos de murciélagos, se recomienda además enfocar los muestreos en los murciélagos insectívoros y nectarívoros, y su contribución hacia el control de insectos herbívoros y polinizadores en parches de bosque secundario parcialmente y completamente rodeado por selva.

Todavía no existe un método estandarizado para la estimación de disponibilidad de frutos para murciélagos. En este estudio aplicamos un método de conteo de plantas con frutos maduros, que resultó apropiado para arbustos y árboles de frutos con semillas pequeñas, con una distribución agrupada y una producción constante de frutos como son las especies de los géneros *Piper* y *Cecropia*. Sin embargo, este procedimiento resultó inadecuado para la estimación de la disponibilidad de alimento de frutos de árboles con una distribución más dispersa y una producción masiva de frutos en periodos cortos, como se presenta en los árboles de especies de la etapa sucesional tardía (Gentry 1974, Fleming y Heithaus 1981, Fleming et al. 1987). Por lo tanto se recomienda que el método para estimar disponibilidad de frutos para murciélagos tome en cuenta las interacciones entre una o dos especies de murciélagos y una o dos especies de plantas, considerando a su vez su distribución y producción de frutos.

La conservación de grandes áreas de selva permite la abundancia de refugios y recursos que puede mantener una alta diversidad de murciélagos (Fenton et al. 1992, Schulze et al. 2000, Garcia-Estrada et al. 2011). La conversión de pequeñas superficies de selva en áreas de mayor disturbio, permite la creación de nichos que favorecen la diversidad de murciélagos y los servicios ambientales que ellos proveen. El paisaje en la comunidad de Lacanhá es poco común en el contexto regional y por lo tanto las recomendaciones que se derivan de esta investigación, difícilmente serán aplicables para paisajes con mayor disturbio. Sin embargo, nuestros resultados muestran la importancia que tiene la conservación y restauración de áreas con vegetación madura para mantener y brindar áreas de refugio y forrajeo para los murciélagos, y a su vez contar con una fuente de semillas de especies sucesionales intermedias y tardías que puedan ser dispersadas por los murciélagos en áreas de mayor disturbio.

El paisaje en las comunidades alrededor del área de estudio ha sido fragmentado por los sistemas de producción intensivos de ganadería, limitando áreas de forrajeo y posibilidades de refugio para los murciélagos. Aparte de la importancia de conservar fragmentos de selva, que brindan refugios y áreas de forrajeo, se recomienda la restauración de áreas degradadas cercanas a estos fragmentos de selva, con el uso de especies de arbustos y árboles con disponibilidad de frutos para los murciélagos frugívoros. Así, la cercanía de la selva hacia las áreas de restauración puede facilitar la llegada de murciélagos frugívoros pero también incrementar la dispersión de semillas por ellos. El pasado nos ha mostrado que la restauración con la siembra de árboles por sí sola no es suficiente (CONAFOR 2012). Además, la falta de conectividad en el paisaje y la fuente de semillas pueden limitar gravemente la regeneración de especies nativas en comunidades degradadas (Bakker & Berendse 1999). Por lo tanto, se requiere el desarrollo de estrategias como la siembra de plantas con disponibilidad de alimento para los murciélagos, pero también la colocación de refugios artificiales cerca de las áreas degradadas y áreas de restauración para promover el movimiento de dispersores y polinizadores en el paisaje, capaces de promover procesos centrales para el desarrollo de la sucesión de áreas degradadas (Corlett 2002, Young 2000).

Literatura citada

Amram DW. 1937. Eastern Chiapas. Geographical Review, 27:19-36.

Anónimo. 1974. Estudio de gran visión de la zona Lacandona, Chiapas. Comisión de Estudios del Territorio Nacional, Secretarıa de la Presidencia, México City, México.

Anónimo, 1999. Utilización industrial de nuevas especies forestales en el Perú. II Edición. Proyecto OIMT PD 37/88 (I). Organización Internacional de Maderas Tropicales. Yokohana y Lima. 240 p.

Aronson J, Renison D, Rangel-Ch JO, Levy-Tacher SI, Ovalle C, Del Pozo A. 2007. Restauracion del Capital Natural: sin reservas no hay bienes ni servicios. Ecosistemas 16: 15-24.

Bakker, J.P. and Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution 14: 63–68.

Baxter DM, Psyllakis JM, Gillingham MP, O'Brien EL. 2006. Behavioural response of bats to perceived predation risk while foraging. Ethology, 112: 977-983.

Bernard E, Fenton MB. 2003. Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. Biotropica, 35: 262-277.

Bonaccorso FJ, Winkelmann JR, Shin D, Agrawal CI, Aslami N, Bonney C, Hsu A, Jekielek PE, Knox AK, Kopach SJ, Jennings TD, Lasky JR, Menesale SA, Richards JH, Rutland JA, Sessa K, Zhaurova L, Kunz TH. 2007. Evidence for exploitative competition: Comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). Biotropica, 39: 249-256.

Burkey TV. 1989. Extinction in Nature Reserves: The effect of fragmentation and the importance of migration between reserve fragments. Oikos, 55: 75-81.

Breedlove D. E.1973. The phytogeography and vegetation of Chiapas (México). En Graham A (Ed.) Vegetation and vegetational history of northern Latin America. Elsevier. Amsterdam. pp. 145-165.

Castelletta M, Sodhi NS, Subaraj R. 2000. Heavy extinction of forest avifauna in Singapore: Lessons for biodiversity conservation in Southeast Asia. Conservation Biology, 14: 1870-1880.

Castro-Luna AA, Sosa VJ, Castillos-Campos G. 2007a. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. Animal Conservation, 10: 219-228.

Castro-Luna AA, Sosa VJ, Castillo-Campos G. 2007b. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. Acta Chiropterologica, 9: 219-228.

CONAFOR. 2012. Lineamientos de operación para proyectos especiales de conservación y restauración forestal.

Connell JH. 1978. Diversity in tropical rain forests and Coral reefs. Science, 199:1302–1310.

Corlett, R. T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscapes. In Seed Dispersal and Frugivory: Ecology, Evolution and Conservation (eds. D. J. Levey, W. R. Silva and M. Galetti), pp. 451–465. CABI Publishing, New York, New York, USA.

Crome FHJ, Richards GC. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology, 69: 1960–1969.

Da Silva AG, Gaona O, Medellín RA. 2008. Diet and trophic structure in a community of fruit-eating bats in Lacandon forest, Mexico. Journal of Mammalogy, 89: 43–49.

De Vos J. 1988. Viajes al desierta de la soledad: cuando la Selva Lacandona aun era selva. Secretaria de Education Publica. Mexico, D.F.

Diemont SAW, Martin JF, Levy-Tacher SI, Nigh RB, Lopez PR, Golicher JD. 2006. Lacandon Maya forest management: Restoration of soil fertility using native tree species. Ecological Engineering, 28: 205-212.

Douterlungne D, Levy-Tacher SI, Golicher JD, Román-Dañobeytia F. 2010. Applying indigenous knowledge to the restoration of degraded tropical rain forest dominated by bracken. Restoration ecology, 18: 322-329.

Elliott S, Blakesley D, Hardwick, K. in press. Restoring Tropical Forests: a Practical Guide. Kew Publications, London.

Estrada A, Coates-Estrada R. 1985. A preliminary study of resource overlap between howling monkeys (Alouatta palliata) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology 9: 27–37.

Estrada A, Coates-Estrada R. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation 103: 237–245.

Evelyn MJ, Stiles DA, Young RA. 2003. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. Biological Conservation, 115: 463–473.

Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM, Adkins B. 1992. Phyllostomid Bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica, 24: 440-446.

Fleming TH. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. Pp. 105-118. En: Estrada A, Fleming TH (o Eds.), Frugivores and seed dispersal. Dordrecht.

Fleming, TH. 1988. The short-tailed fruit bat, a study in plant-animal interactions. The University of Chi-cago Press, Chicago, 365 pp.

Fleming TH. 2004. Dispersal ecology of neotropical Piper shrubs and treelets. In Piper: a Model Genus for Studies of Phytochemistry. Pp. 58-77. Dyer LA, Palmer ADN (o Eds.) Ecology, and Evolution. Kluwer Academic/Plenum Publishers, New York, NY.

Fleming TH, Heithaus ER. 1981. Frugivorous Bats, Seed Shadows, and the Structure of Tropical Forests. Biotropica 13: 45-53.

Ford WM, Menzel MA, Rodriguez JL, Menzel JM, Johnson JB. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. Biological Conservation, 126: 528–539.

Furlonger CL, Dewar HJ, Fenton MB. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology, 65: 284-288.

Gadgil M, Berkes F, Folke C. 1993. Indigenous knowledge for biodiversity conservation. Ambio, 22: 151–156.

Galia-Selaya N, Oomen, RJ, Netten JJ, Werger MJ, Anten NP. 2008. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. Journal of ecology 96: 1211-1221.

Galindo-González J, Guevara S, Sosa VJ. 2000. Bat- and bird- generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology, 14: 1693-1703.

Galindo-González J, Sosa VJ. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. The Southwestern Naturalist 48: 579-589.

Galindo-González J. 2004. Clasificación de los murciélagos de la región de los Tuxtlas, Veracruz, respeto a su respuesta a la fragmentación del hábitat. Acta Zoologica Mexicana 20: 239-243.

Garcia DME. 1973. Apuntes de climatología. In: García, D.M.E. (Ed.) Modificaciones al sistema de clasificación climática de Cöppen. Instituto de Geografía, Universidad Nacional Autónoma de México, Mexico.

García-Estrada C, Damon A. Sánchez-Hernández C, Soto-Pinto L, Ibarra-Núñez G. 2012. Diets of Frugivorous Bats in Montane Rain Forest and Coffee Plantations in Southeastern Chiapas, Mexico. Biotropica, 44: 394–401

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91: 223-229.

Gentry AH. 1974. Coevolutionary patterns in Central American Bignoniaceae. Annals of the Missouri Botanical Garden, 69: 728-759.

Gorresen PM, Willig MR. 2004. Landscape-scale responses of bats to habitat fragmentation in Atlantic Rainforest of Paraguay. Journal of Mammalogy 85: 688–697.

Gorchov DL, Fernando Cornejo F, Ascorra C, Jaramillo M. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107/108: 339-349.

Greig N. 1993. Regeneration Mode in Neotropical Piper: Habitat and Species Comparisons. Ecology 74: 2125-2135.

Grindal SD, Brigham RM. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. Ecoscience, 6: 25-34.

Heithaus ER, Fleming TH, Opler PA. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology: 841-854.

Heithaus ER, Fleming TH. 1978. Foraging Movements of a Frugivorous Bat, *Carollia perspicillata* (Phyllostomatidae). Ecological monographs. 48: 127-143.

Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics, 13: 201–228

Kalka MB, Smith AR, Kalko, EKV. 2008. Bats limit arthropods and herbivory in a tropical forest. Science, 320: 71.

Kalko EKV, Handley CO Jr. 2001. Neotropical bats in the canopy: diversity, community structure and implications for conservation strategies. Plant Ecology, 153: 319–333.

Kunz TH, Lumsden LF. 2003. Ecology of cavity and foliage roosting bats.Pp. 3-69. En: Kunz TH, Fenton MB. (o Eds), Ecology of bats. The University of Chicago Press, Chicago and London.

Kunz TH, Braun de Torrez E, Bauer D, Lovoba T, Fleming TH. 2011. Ecosystem services provided by bats. Annals of the New York academy of sciences 1233: 1-38.

Levy-Tacher SI. 2000. Sucesión causada por roza-tumba-quema en las selvas de Lacanhá, Chiapas. Tesis profesional, Colegio de Postgraduados.

Levy-Tacher SI, Golicher JD. 2004. How predictive is traditional ecological knowledge? the case of the Lacandon Maya Fallow Enrichment System. Interciencia, 29: 496-503.

Limpens HJGA, Kapteyn K. 1991. Bats, their behaviour and linear landscape elements. Myotis, 29: 39-48.

McClanahan TR. 1986. The effect of a seed source of primary succession in a forest ecosystem. Vegetatio, 65: 175-178.

Miranda F. 1952. La vegetación de Chiapas, primera parte. Ediciones del gobierno del estado, Tuxtla Gutiérrez.

Miranda F, Hernández XE. 1963. Los tipos de vegetación de México y su clasificación. Boletin de la Sociedad Botánica de México, 28: 29-179.

Medellín RA. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology, 8: 788-799.

Medellín RA, Gaona O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica, 31: 478-485.

Medellín RA, Equihua M, Amin MA. 2000. Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests. Conservation Biology 14: 1666-1675.

Mendoza E, Dirzo, R. 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. Biodiversity and Conservation, 8: 1621–1641.

Muench NP. 1978. Los sistemas de producción agrícola en la región Lacandona (Estudio agronómico preliminar). Tesis profesional, Universidad Autónoma Chapingo, México.

Muscarella R, Fleming TH. 2007. The role of frugivorous bats in tropical forest succession. Biological Reviews, 82: 573–590.

Myers N, Mittermeier RA, Mittermeier, CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature, 403: 853–858.

Nations J, Nigh R. 1980. The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. Journal of Anthropological Research, 36: 1-30.

Nowak RM. 1991. Walker's Bats of the World. London: Johns Hopkins University Press.

Passos JG, Passamani DM. 2003. *Artibeus lituratus* (Chiroptera, Phyllostomidae): biologia e dispersao de sementes no Parque do Museu de Biologia Prof. Mello Leitao, Santa Teresa (ES). Natureza, 1: 1–6.

De la Peña-Cuéllar E, Stoner KE, Avilla-Cabadilla LD, Martínez-Ramos M, Estrada A. 2012. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico.

Pennington TD, Sarukhán K. 1986. Manual para la identificación de campo de los principales árboles tropicales de México. Instituto Nacional de Ingestaciones Forestales. SAG. Mexico.

Rodríguez-Herrera B, Medellín RA, Timm RM. 2007. Murciélagos Neotropicales que acampan en hojas. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Schulze MD, Seavy NE, Whitacre DF. 2000. A Comparison of the Phyllostomid Bat Assemblages in Undisturbed Neotropical Forest and in Forest Fragments of a Slash-and-Burn Farming Mosaic in Petén, Guatemala. Biotropica, 32: 174-184.

Sheil D, Burslem DFRP. 2003. Disturbing hypotheses in tropical forests.Trends in Ecology and Evolution 18: 18-26.

Silver WL, Brown S, Lugo AE. 2002. Effects of change in biodiversity on ecosystem function in tropical forests. Conservation biology, 10: 17-24.

Soriano PJ, Ochoa JG. 2001. The consequences of timber exploitation for bat communities in tropical America. Pp. 153-166. En: Fimbel RA, Grajal A, Robinson JG. (o Eds). The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York, NY.

Thies W, Kalko EKV. 2004. Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos, 104: 362-376.

Tschapka M. 2004 Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. Journal of Zoology 263: 7-21.

Vargas-Contreras JA, Medellín RA, Escalona-Segura G, Interián-Sosa L. 2009. Vegetation complexity and bat-plant dispersal in Calakmul, Mexico. Journal of Natural History 43: 219–243.

Williams-Guillén K, Perfecto I. 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. Biotropica 42: 506-613.

Wunderle JM Jr. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99: 223–235.

Young TP. 2000. Restoration ecology and conservation biology. Biological conservation 92: 73-83.