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Diversidad de Murciélagos Filostómidos en Estadios Sucesionales de Bosques Neotropicales Secos

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTOR EN CIENCIAS

PRESENTA

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Dr. Isidro Ávila Martínez
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Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 14 de febrero del 2011, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **LUIS DANIEL AVILA CABADILLA** con número de cuenta **506472477,** con la tesis titulada: **"Diversidad de Murciélagos Filostómidos en Estadios Sucesionales de Bosques Neotropicales Secos"**, bajo la dirección de la **Dra. Kathryn E. Stoner Smith.**

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Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
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A mi esposa Mary, mi media naranja

A mis padres Tere y Luis, por su amor, ejemplo y apoyo

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RESUMEN

Los bosques neotropicales están siendo rápidamente modificados por actividades como la ganadería y la agricultura, mismas que provocan el reemplazo de la vegetación original por un mosaico de parches de vegetación en diferentes estadios de sucesión, campos agrícolas y pastizales. Es imprescindible, por tanto, entender como se distribuyen los diferentes taxa en este paisaje transformado y cuales son los factores que determinan su distribución. Especial atención requieren aquellos taxa que juegan un papel clave en el funcionamiento de los ecosistemas, como los murciélagos filostómidos (MF), quienes, mediante servicios tales como la polinización, dispersión de semillas y depredación de insectos, posibilitan la reproducción de las plantas, la regeneración de los bosques, el control de la herbivoría y el movimiento y reciclado de nutrientes.

Uno de los sistemas más amenazados y menos estudiados en el neotrópico, es el bosque tropical seco (BTS), en el que prácticamente no se ha documentado la respuesta de los MF a la transformación del hábitat. La información existente al respecto, ha sido generada principalmente en bosques tropicales húmedos y lluviosos y no se puede extrapolar hacia los BTS debido a los atributos estructurales y funcionales únicos de este sistema. El presente trabajo tiene por objetivo evaluar la presencia y abundancia de los MF, a nivel poblacional, de ensamble y de ensamblaje, en parches de vegetación que representan diferentes estadios sucesionales del BTS, determinando así, cómo responden estos murciélagos a la variaciones en los atributos del hábitat, tanto a nivel local, como a nivel de paisaje. Asimismo, nos enfocamos a discutir las implicaciones de nuestros resultados para la conservación de los MF en los paisajes antropogénicos.

Para esto, primeramente, documentamos las variaciones en riqueza, diversidad y abundancia de MF a lo largo de una cronosecuencia sucesional en el BTS de la reserva de la biosfera Chamela-Cuixmala (RBCC), Jalisco, México (Capítulo 2). Esta cronosecuencia comprendió 4 estadios sucesionales: inicial (pastizales), temprano, intermedio y tardío. La mayor riqueza de especies se presentó en el estadio tardío. Los cambios en riqueza de especies entre los estadios sucesionales siguieron un patrón aditivo en donde las especies encontradas en un estadio sucesional dado incluían a todas las especies encontradas en el estadio sucesional previo más otras especies no registradas en los estadios anteriores. Por otra parte, la diversidad y abundancia de MF no difirieron significativamente entre estadios sucesionales, encontrándose una gran variación intra-estadio.

Posteriormente, con el fin de identificar posibles patrones inherentes al BTS en la respuesta de los MF a la transformación del hábitat, comparamos la presencia y abundancia de estos murciélagos en diferentes estadios sucesionales de tres BTS (Capítulo 3), localizados a lo largo de un gradiente latitudinal: 1) RBCC en México, 2) Hato Piñeiro (HP) en Venezuela y 3) Parque Estadual da Mata Seca (PEMS) en Brasil. En este sistema evaluamos si la respuesta de los MF a la sucesión vegetal está modulada por la marcada estacionalidad en el régimen de precipitación característica de los BTS. En general, encontramos un alto nivel de especificidad en la respuesta de los MF, siendo ésta particular de las especies, los gremios tróficos, las estaciones del año y la región. Además, encontramos que sólo unos pocos taxa están tan fuertemente asociados a un determinado estadio sucesional, que pueden ser considerados como taxa indicadores de ese estadio. Estas asociaciones taxa-estadio variaron, sin embargo, con las estaciones del año. Así, la respuesta de los MF a la transformación del BTS puede estar modulada por: 1) las condiciones ambientales características de cada región, 2) particularidades en la conducta y requerimientos ecológicos de las especies de cada región, 3) la composición, estructura y patrones fenológicos de

los ensamblajes de plantas que ocurren en los diferentes estadios sucesionales y 4) la composición y configuración del paisaje en cada una de las regiones.

Finalmente, con el fin de explicar la gran variación inter e intra-estadio sucesional en la presencia y abundancia de los MF, evaluamos las relaciones causales entre dicha variación (a nivel de población, ensamble y ensamblaje) y las variaciones en los atributos del hábitat, tanto a nivel local (complejidad estructural de la vegetación), como a nivel de paisaje (cobertura de la vegetación riparia y del bosque seco, área promedio de los parches de vegetación y diversidad de tipos de parches) en la RBCC. Los atributos del paisaje se midieron en dos escalas correspondientes a circunferencias de 500 y 1000 m de radio centradas en el sitio de muestreo. Los resultados muestran que: 1) las variaciones en los atributos del hábitat, tanto a nivel local como de paisaje, explican las variaciones en la presencia y abundancia de MF a lo largo de la cronosecuencia, 2) la respuesta de los MF a los cambios en los atributos del hábitat es dependiente de la escala, 3) la asociación entre los atributos del paisaje y la abundancia de los MF es gremio-específica, así, la variación en la abundancia de frugívoros está asociada con la variación en la cobertura de la vegetación riparia, mientras que la variación en la abundancia de nectarívoros está asociada con la variación en la cobertura del bosque seco, y 4) la variación en la composición específica y abundancia de los ensamblajes está asociada a la variación en la cobertura de la vegetación riparia; esto debido al predominio de las especies frugívoras en dichos ensamblajes.

Dada la alta variación inherente a los paisajes tropicales actuales y en particular a los paisajes transformados del BTS, sólo la consideración y estudio de varios factores a la vez (atributos del hábitat, estacionalidad, latitud, matriz de vegetación, etc.), nos permitió vislumbrar cuáles son los factores que modulan las respuestas de los MF a la perturbación y en que forma lo hacen. Aunque no se detectaron patrones claros en estas respuestas, resultó evidente que las estrategias de conservación de los MF y de sus servicios ecosistémicos en el BTS, requieren de la preservación tanto de la vegetación conservada como de la vegetación secundaria, ya que un gran porcentaje de estos murciélagos usan (e impactan) ambos tipos de vegetación. Especial interés se le debe prestar a la vegetación riparia que resulta determinante para la conservación de un gran número de MF que ocurren en el BTS.

En general, se requiere todavía de estudios provenientes de diferentes regiones, con diferentes especies y regímenes de perturbación, para poder proyectar escenarios hacia un espectro más amplio de paisajes antropogénicos. Se requiere, sobre todo, que la comunidad científica tome conciencia plena de la urgencia de conocer la respuesta de la biota del BTS a la creciente perturbación. El estudio y conocimiento de la dinámica sucesional y de regeneración natural de este sistema nos permitirá generar acciones de manejo y conservación que contrarresten los efectos de la transformación de nuestros paisajes tropicales.

ABSTRACT

Neotropical forests are being increasingly modified by activities as cattle raising and agriculture provoking the replacement of the original vegetation by a mosaic of patches of different successional stages, agricultural fields and pasture lands. In this context, it is indispensable to understand the distribution of taxa across the transformed landscapes and which factors are determining this distribution. Special emphasis deserve those taxa playing key roles in the ecosystem functioning such as Phyllostomid bats (PB). These bats perform activities as pollination, seed dispersal and insect predation which make possible plant reproduction, forest regeneration, herbivory control and translocation and recycling of nutrients.

The tropical dry forest (TDF) is one of the most endangered neotropical systems. As it has been poorly studied, the PB response to habitat transformation is practically unknown in this system. Available information to this respect has been mostly generated in tropical moist and rain forest and cannot be extrapolated to TDF because this system presents unique structural and functional attributes. In this study we aim to evaluate the PB occurrence, at population, ensemble and assemblage level, in TDF vegetation patches of different successional stages, determining in this way, how PB respond to variation on habitat attributes at local and landscape level. We also discuss the implications of our results for the PB conservation in anthropogenic landscapes.

First of all, we documented the PB variation in species richness, diversity and abundance across a successional chronosequence in the TDF of the Chamela-Cuixmala Biosphere Reserve (CCBR), Jalisco, Mexico (Chapter 2). The chronosequence included four successional stages: initial (pastures), early, intermediate and late. The highest species richness was registered in the late stage. Changes in species richness among successional stages followed an additive pattern, where the species occurring in a given successional stage included all species occurring at the previous stage plus other new species. On the other hand, the PB diversity and abundance did not differ significantly among successional stages and both parameters showed high intra-stage variation.

Afterwards, in order to identify potential patterns on the PB response to TDF transformation, we compared bats occurrence in different successional stages of three TDFs (Chapter 3) located across a latitudinal gradient: 1) CCBR, Mexico, 2) Hato Piñeiro (HP), Venezuela and 3) Parque Estadual da Mata Seca (PEMS), Brazil. We evaluated if PB response to succession was modulated by the marked seasonality on the precipitation regime characteristic of TDFs. In general we found high specificity on the PB response as it showed particularities relative to the species, guilds, seasons and regions. Moreover, we found that only a few taxa were so tightly associated to a determined successional stage that could be considered indicators of such stage. However, this taxa-stage association changed between seasons in all cases. We concluded that PB response to TDF transformation could be modulated by: 1) the environmental conditions of each region, 2) particularities of the behavior and ecological requirements of the regional species, 3) the composition, structure and phenological patterns of plant assemblages occurring in the different successional stages and 4) the regional landscape composition and configuration.

Finally, in order to explain the high inter and intra-stage variation in PB occurrence, we evaluated the causal/explanatory relationships between such variation (at the assemblage, ensemble and population level) and the variation on habitat attributes at both local (vegetation structural complexity) and landscape level (percentage of forest cover, mean patch area and diversity of patch types) in the CCBR. Landscape attributes were analyzed at two scales through

500 and 1000 m circumferences centered on each sampling site. Our results indicate that: 1) variations in habitat attributes, at local and landscape level, explain the variations in PB occurrence across the chronosequence, 2) PB response to changes in habitat attributes is scale-dependent, 3) the association between landscape attributes and PB occurrence is guild-specific as the variation in frugivores abundance is associated to the variation in riparian vegetation cover, while the variation in nectarivores abundance is associated to the variation in TDF cover, and 4) the variation in assemblage's species composition and abundance is related to the variation in riparian vegetation cover probably because these assemblages are dominated by frugivorous bats.

Provided that tropical landscapes, and specially the TDF transformed landscapes, are highly heterogeneous, we needed to consider several factors simultaneously (habitat attributes, seasonality, latitud, vegetation matrix, etc) to elucidate which factors modulate PB responses to disturbance and how they do it. Even when clear patterns concerning these responses did not emerge, we found that conservation of PB and their ecosystem services require the preservation of conserved and secondary vegetation as a high proportion of these bats use (and impact on) both types of vegetation. Special attention must be paid to the preservation of riparian vegetation as it determines the conservation of numerous PB species occurring in the TDF.

In order to understand the dynamics of a wider range of anthropogenic landscapes, we need to perform studies in different regions with different species pools and disturbance regimes. Above all, we need the attention of the scientific community as it is urgent to understand the response of the TDF biota to increasing habitat transformation. By understanding the natural regeneration and successional dynamics operating in this system, we will be able to generate conservation actions and counteract the effects of transformation on our tropical landscapes.

CAPÍTULO 1

Introducción

INTRODUCCIÓN

Los bosques tropicales albergan gran parte de la diversidad del planeta, probablemente más de la mitad de las especies (Whitmore 1990, Heywood 1995, Primack et al. 2001a). Sin embargo, la alta tasa de pérdida y transformación de estos ecosistemas está poniendo en gran riesgo el mantenimiento de su biodiversidad (FAO 2009). Los paisajes tropicales, en la actualidad, están generalmente compuestos por un mosaico de vegetación en diferentes estadios sucesionales debido al efecto combinado de las perturbaciones naturales y humanas. La actividades humanas, en particular, están alterando de forma acelerada y a gran escala la estructura natural de estos paisajes y el curso de sus procesos ecológicos ya que provocan la remoción de una gran porción de la cobertura vegetal, la formación de parches de vegetación cada vez más pequeños, el incremento del efecto de borde, la invasión de especies exóticas, la alteración de las condiciones ambientales y una disminución en la capacidad del sistema para recuperarse de la perturbación (Benitez-Malvido 1998, Chazdon et al. 2007, Gascon et al. 2004, Hilty et al. 2006, Laurance y Bierregaard 1997, Maass 1995).

Los bosques neotropicales en específico, se encuentran altamente amenazados por actividades como la agricultura, la ganadería y la explotación forestal, las cuales han provocado que una gran parte de su área original haya sido reemplazada por un complejo mosaico de bosques secundarios, campos agrícolas, campos ganaderos y asentamientos humanos (Nepstad et al. 1999, Primack et al. 2001b, Sanchez-Azofeifa et al., 2005, Chazdon et al. 2007, Quesada et al. 2009). Estos paisajes transformados serán el hábitat predominante para la vida silvestre en el futuro cercano (Hilty et al 2006, Quesada et al. 2009) y esto ha llevado a la comunidad científica a reconocer que es extremadamente urgente generar un conocimiento adecuado acerca de la respuesta de estos sistemas a la perturbación (Gascon et al. 2004). Particularmente, es necesario entender los procesos ecológicos que están operando en los paisajes transformados y determinar que factores modulan la distribución y el desempeño de la biota (Gascon et al. 2004), poniendo especial atención en aquellos taxa que juegan un papel crítico en el funcionamiento de los ecosistemas (Cosson et al. 1999b, Jordán 2009).

El bosque tropical seco

Uno de los ecosistemas neotropicales más ampliamente distribuido (Portillo-Quintero y Sánchez-Azofeifa 2010) es el bosque tropical seco (BTS), ecosistema altamente estacional que alberga una alta diversidad y un gran número de especies endémicas (Ceballos 1995, Gentry 1995, Dirzo y Trejo 2001). Históricamente, el BTS ha sido un hábitat preferido para los asentamientos humanos y la agricultura y por tanto constituye uno de los sistemas neotropicales más transformados y amenazados (Trejo y Dirzo 2000, Quesada y Stoner 2004, Sánchez-Azofeifa 2005). Sin embargo, es poca la atención que la comunidad científica ha prestado a estos bosques en comparación con otros sistemas neotropicales como los bosques húmedos y lluviosos (Sanchez-Azofeifa et al. 2005). Consecuentemente, el BTS se encuentra poco representado en las áreas naturales protegidas y su área original se ha reducido en un 66% a causa de la presión antropogénica (Miles et al. 2006, Portillo-Quintero y Sánchez-Azofeifa 2010). Dado este escenario, es necesario entender el proceso de sucesión ecológica que subyace a la regeneración natural de este sistema, tomando en cuenta que éste presenta características estructurales y funcionales únicas que determinan una respuesta también única a la perturbación humana (Bongers et al. 2009). Esta respuesta es, por ejemplo, marcadamente distinta a la de otros sistemas tropicales como los bosques húmedos y lluviosos, cuyo desempeño es frecuentemente usado para inferir el comportamiento de los BTS, aún cuando no es extrapolable a los mismos (Avila-Cabadilla et al. 2009).

Específicamente, los BTS se diferencian de los bosques tropicales húmedos y lluviosos en aspectos como: 1) el régimen de precipitación, que en el BTS (≈500-2000 mm por año) es marcadamente estacional dando lugar a una severa época seca que puede durar entre 3 y 8 meses en dependencia de la posición latitudinal (Holdridge 1947, Murphy y Lugo 1986, Sánchez-Azofeifa et al. 2005), 2) la fenología, ya que al menos el 50% de los árboles del BTS pierden sus hojas durante la época seca como consecuencia de la marcada estacionalidad en el régimen de precipitación (Bullock y Solis-Magallanes 1990, Sanchez-Azofeifa et al. 2005), 3) la estructura de la vegetación, pues la escasa disponibilidad de agua en el BTS ocasiona que su vegetación presente una menor altura del dosel, área basal, número de estratos, tasa de crecimiento y productividad primaria en general (Murphy y Lugo 1986, Bullock 1995, Holbrook et al. 1995, Martínez-Yrízar 1995), y 4) la composición específica de los estadios iniciales de la sucesión, mismos que en el BTS están dominados por especies anemocóricas y autocóricas y no por las especies zoocóricas características de los estadios iniciales de los bosques tropicales húmedos y lluviosos (Bullock 1995, Gentry 1995, Vieira y Scariot 2006).

El estudio de la sucesión ecológica.

Se conoce como proceso de sucesión ecológica o secundaria a la serie de cambios secuenciales, no estacionales, que se presentan en los atributos de las comunidades (p.ej. composición y estructura), así como en las funciones generales de un ecosistema después de una perturbación mayor, misma que provoca la remoción completa o casi completa de los individuos que conforman las comunidades (Pickett y White 1985, Chazdon et al. 2007, Martínez-Ramos y García-Orth 2007). En el caso del neotrópico, la perturbación más frecuente ha sido la remoción de la vegetación en áreas que posteriormente serán usadas para agricultura o ganadería extensiva (Chazdon et al. 2007).

El estudio de la sucesión ecológica nos permite conocer aspectos cruciales de la dinámica de los ecosistemas tales como: 1) el periodo de tiempo necesario para su recuperación, 2) los patrones y tasas de cambio en la estructura y composición de las comunidades durante el proceso sucesional, 3) los cambios en las interacciones bióticas, 4) los cambios en el ciclo de nutrientes y la productividad del ecosistema y 5) el efecto de los diferentes tipos de perturbación en todos estos aspectos (Charles-Dominique 1986, Margalef 1963, Odum 1969, Chazdon et al. 2007).

Históricamente, los modelos de sucesión ecológica tanto para zonas templadas (Cowles 1899, Clements 1916, Gleason 1926, Tansley 1935, Clements 1936, Egler 1954, Connell y Slatyer 1977, Grime 1977, Tilman 1985) como tropicales (Gómez-Pompa et al. 1972, Bazzaz y Pickett 1980, Chazdon et al. 2007, Martínez-Ramos y García-Orth 2007, Chazdon et al. 2008), se han basado en la dinámica de las comunidades vegetales, siendo muy poco los modelos que consideran la dinámica de las comunidades de animales (p.ej.. Fox 1990). Este sesgo en la generación del conocimiento se debe, principalmente, a la facilidad de muestrear las comunidades de plantas que, por su naturaleza sedentaria, son más fáciles de estudiar que los animales.

En el neotrópico, la mayoría de los estudios sobre sucesión ecológica se han centrado también en las comunidades de plantas, principalmente en aquellas de los bosques tropicales lluviosos (Bazzaz y Pickett 1980, Gómez-Pompa y Vázquez-Yanes 1981, Guariguata y Ostertag 2001, Chazdon et al. 2007, Martínez-Ramos y García-Orth 2007, Chazdon et al. 2008). Así, tanto los cambios en los atributos de las comunidades animales a lo largo de la sucesión, como el papel que estas comunidades juegan en el proceso sucesional, han sido poco estudiados en estos sistemas (Muscarella y Fleming, 2007). En tiempos recientes se ha acrecentado el esfuerzo para documentar estos aspectos (aves: Borges, 2007; reptiles: Rios-Lopéz y Mitchell, 2007; murciélagos: Castro-Luna et al., 2007; Mancina et al., 2007; Willig et al., 2007) y muchos de los estudios realizados al respecto han mostrado que, aun cuando frecuentemente se asume que las comunidades animales “siguen” pasivamente a las comunidades de plantas durante el proceso sucesional, los animales juegan un papel activo en dicho proceso vía dispersión de semillas, dispersión de hongo micorrízicos, polinización, herbivoría y descomposición de materia orgánica (Charles-Dominique 1986, Gorchov et al. 1993, Muscarella y Fleming 2007).

La sucesión ecológica involucra una compleja interacción de procesos (Odum 1969). Por tanto, un mejor entendimiento del proceso sucesional requiere del estudio simultáneo de varios componentes de los ecosistemas, incluyendo, por supuesto, a las comunidades animales que interactúan con las comunidades vegetales durante este proceso. El estudio de los cambios en las comunidades de animales a lo largo de la sucesión del BTS, en donde dichos cambios no han sido documentados, resulta entonces indispensable para generar información crucial que nos auxilie en el manejo y conservación de este sistema.

Grupos clave en el neotrópico: los murciélagos filostómidos

Con el objetivo de mantener los procesos ecológicos y con ello preservar una fracción importante de la biodiversidad en los paisajes tropicales contemporáneos, debemos estudiar a aquellos taxa que sean claves en el mantenimiento de estos procesos. Los murciélagos, por ejemplo, son considerados un componente importante de la biodiversidad así como un grupo clave dentro del neotrópico (Aguirre et al. 2003). Debido a su gran radiación evolutiva, estos animales ocupan la mayoría de los niveles tróficos ya que incluyen desde consumidores primarios hasta consumidores terciarios (folívoros, nectarívoros, polinívoros, frugívoros, insectívoros, animalívoros y sanguívoros, Hutson et al. 2001). Los murciélagos son particularmente importantes en el funcionamiento de los ecosistemas ya que interactúan con un diverso espectro de organismos y regulan procesos ecológicos complejos (Bernard y Fenton 2002, Estrada et al. 1993a, Fleming 1988, Hutson et al. 2001). Proveen, por ejemplo, diferentes servicios ecológicos tales como: 1) dispersión de semillas, 2) polinización, 3) control de poblaciones de invertebrados y vertebrados pequeños y 4) reciclaje y transformación de nutrientes y energía (Charles-Dominique 1986, Fleming 1982, 1988, Gorchov et al. 1993, Kalka et al. 2008, Muscarella y Fleming 2007, Valiente-Banuet et al. 2004, Whitaker 1993, Williams-Guillén et al. 2008).

En el neotrópico, los murciélagos polinizan presumiblemente 573 especies de plantas y dispersan las semillas de otras 549 especies (Geiselman et al. 2002 onward, Lovoba et al. 2009). De este modo, este grupo contribuye al mantenimiento de la diversidad vegetal, conectando poblaciones de plantas distantes entre sí vía transporte de polen y semillas, acción que además promueve la regeneración natural en las áreas degradadas (Fleming 1988, Fleming et al. 2009, Lovoba et al. 2009). Es ampliamente reconocido que los murciélagos juegan un papel relevante en la sucesión de los sistemas tropicales porque muchas de las semillas que dispersan provienen de plantas pioneras que son particularmente importantes durante las etapas tempranas de la sucesión. De hecho, en los bosques húmedos y lluviosos, casi la mitad de las plantas pioneras más abundantes en términos de densidad, biomasa y área basal, son dispersadas por murciélagos (p. ej. *Solanum*, *Cecropia*, *Piper*, *Vismia*, Fleming, 1988; Charles-Dominique, 1986; Gorchov, 1993; Muscarella y Fleming, 2007, Lovoba et al. 2009). Los murciélagos insectívoros, además, pueden reducir significativamente los niveles de herbivoría en los bosques neotropicales, ya que cada noche pueden llegar a consumir más de 1.5 veces su peso corporal en insectos (McNab 1982, Estrada et al. 1993a, Kalka et al. 2008).

Una de las familias de murciélagos más importantes dentro del neotrópico es la Phyllostomidae, que es la familia más diversa (Hutson et al. 2001) tanto taxonómica (151 especies) como funcionalmente (mayoría de gremios tróficos incluyendo a todos los nectarívoros y frugívoros). Los murciélagos filostómidos presentan hábitos especializados de alimentación, refugio y selección de hábitat que los hacen indicadores de la alteración de los ecosistemas (Fenton et al., 1992; Medellín et al., 2000; Clarke et al., 2005a, Jones et al. 2009). Son considerados también un grupo clave al proveer servicios ecológicos importantes mediante la dispersión de semillas, la polinización y el control de poblaciones de animales (Whitaker 1993, Hutson et al. 2001, Geiselman et al. 2002 onward, Kalka et al. 2008, Williams-Guillén et al. 2008, Lovoba et al. 2009).

En este contexto, resulta indispensable evaluar el efecto de la perturbación antropogénica sobre los murciélagos filostómidos del BTS e identificar cuáles son los factores que determinan su presencia y abundancia en los diferentes estadios sucesionales de este sistema. Esto constituiría una base científica primordial para la preservación de este importante grupo dentro de los paisajes transformados del BTS y contribuiría al conocimiento de cómo los diferentes procesos ecológicos en los que los filostómidos tienen un papel preponderante, podrían verse afectados durante el proceso sucesional de estos bosques.

Estudio del efecto de la perturbación del BTS sobre los murciélagos filostómidos.

En esta tesis, precisamente, se evaluaron los cambios que experimentan los ensamblajes de filostómidos en diferentes estadios sucesionales del BTS y se valoraron como las variaciones en algunos atributos bióticos y abióticos del hábitat pudieran estar determinando la presencia y abundancia de estos murciélagos en dichos estadios.

Cabe señalar que, en adelante, para nombrar a un conjunto de especies filogenéticamente relacionadas que coexisten en un lugar determinado, utilizaremos el término “ensamblaje”, mientras que para nombrar al subconjunto de especies de un ensamblaje que pertenecen a un mismo grupo funcional (p.ej. gremio trófico), utilizaremos el término “ensamble” (del inglés “ensemble”) siguiendo a Fauth et al. (1996).

Inicialmente, evaluamos el cambio en diversos atributos de los ensamblajes (composición, riqueza y densidad de especies, abundancia, equitatividad, diversidad) y ensambles de filostómidos (abundancia), a lo largo de un gradiente sucesional del BTS y discutimos la implicación de estos cambios para el manejo y conservación de este grupo y sus servicios ecológicos en los bosques neotropicales secos en general.

Posteriormente, examinamos si existen patrones en la presencia y abundancia de los filostómidos a lo largo de gradientes sucesionales del BTS, estudiando para ello tres BTS ubicados en diferentes latitudes (México, Venezuela y Brasil). La consideración de varios BTS en un gradiente latitudinal, nos permitió evaluar si existe una respuesta consistente de los filostómidos a las transformaciones del hábitat en este sistema, aún cuando varíe la composición del pool regional de especies (tanto de murciélagos como de plantas) y las condiciones climáticas (p.ej. duración de la época de seca). Ya que los BTS son ecosistemas altamente estacionales, en donde los ensamblajes de murciélagos pueden experimentar cambios significativos en la disponibilidad de recursos (p.ej. refugio y alimento) entre la estación seca y la estación lluviosa (Stoner 2001, 2002 y 2005, Avila-Cabadilla et al. 2009), evaluamos además como la estacionalidad puede determinar la presencia y abundancia de los murciélagos filostómidos en los diferentes estadios sucesionales.

Por último, dado que se detectó una gran influencia de diferentes elementos del paisaje en la presencia y abundancia de los filostómidos a lo largo de los gradientes sucesionales del BTS, evaluamos el efecto de la variación en los atributos del paisaje (p.ej. configuración espacial y composición del paisaje) en dicha presencia y abundancia, usando para ello diferentes escalas espaciales que correspondiesen al grado de movilidad de estos organismos.

Objetivos.

Los objetivos principales de este estudio son:

1) Documentar los cambios en los atributos de los ensamblajes de murciélagos filostómidos que se presentan en diferentes estadios sucesionales de un BTS y discutir las implicaciones de éstos cambios para el manejo y conservación tanto de los filostómidos como de los servicios ecológicos que proveen a este ecosistema (Capítulo 2).
2) Determinar, considerando el efecto de la estacionalidad, la existencia de patrones inherentes a los bosques neotropicales secos en la presencia y abundancia de los murciélagos filostómidos en diferentes estadios sucesionales (Capítulo 3).
3) Identificar relaciones causales entre los atributos del hábitat (a escala local y de paisaje) y la presencia y abundancia de los murciélagos filostómidos en diferentes estadios sucesionales de un BTS. Discutir, asimismo, las implicaciones de esta relación para la conservación de este grupo en los paisajes antropogénicos del BTS (Capítulo 4).

Relevancia

Este estudio representa el primer esfuerzo en evaluar cambios en los ensamblajes de murciélagos a lo largo de gradientes sucesionales del BTS. A pesar del papel tan importante que juegan los murciélagos en los sistemas tropicales y particularmente en su proceso sucesional, la mayoría de los estudios que han documentado la respuesta de los murciélagos neotropicales a la alteración de su hábitat, se han realizado en el contexto de la perturbación o de la fragmentación *per se*. Solo unos pocos estudios han evaluado esta respuesta en el marco de la sucesión (p.ej. Castro-Luna et al. 2007, de la Peña-Cuéllar 2010) y todos ellos lo han hecho en bosques húmedos y lluviosos cuyo comportamiento, como se dijo anteriormente, no es extrapolable al BTS debido a las marcadas diferencias que ambos sistemas presentan en cuanto a estacionalidad, estructura de la vegetación, composición de especies y disponibilidad de recursos quiropterocóricos y quiropterofílicos (Mooney et al. 1995, Murphy y Lugo 1986, Gentry 1995, Viera y Scariot 2006, Bullock 1995). Por tanto, este estudio aporta información novedosa y crucial para el conocimiento, manejo y conservación de los BTS.

La mayoría de los estudios que han abordado la respuesta de los murciélagos a la alteración del hábitat, han combinado datos de diferentes estaciones del año (lluvia y secas), o bien, han analizado los datos de una sola estación. Esto puede opacar información importante sobre dicha respuesta, haciendo difícil la discriminación entre patrones y casualidad (Klinbeig y Willig 2010). Nuestros resultados contribuirán entonces al conocimiento de cómo la variación estacional modula la presencia y abundancia de los filostómidos en los sistemas tropicales.

En síntesis, este estudio constituye un esfuerzo de evaluación integral de los factores que determinan la presencia y abundancia de los filostómidos en los paisajes tropicales transformados. Esto al considerar entre estos factores no sólo la estacionalidad y el efecto de la variación local en los atributos del hábitat, sino también el efecto de la variación en los atributos del paisaje a diferentes escalas. La caracterización cuantitativa de los atributos del paisaje permite identificar con mayor precisión aquellos factores que afectan la presencia y abundancia de los filostómidos en áreas de BTS con diferentes niveles de perturbación, al tiempo que proporciona una visión más integral de la dinámica que opera en estos paisajes transformados. Esta tesis representa el primer estudio de esta naturaleza realizado en el BTS.

CAPÍTULO 2

Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest.

RESUMEN

Los estudios relacionados con la dinámica sucesional de los sistemas tropicales han estado mayormente enfocados en comunidades de plantas y han sido conducidos principalmente en áreas tropicales húmedas o lluviosas. En este estudio, nosotros documentamos los cambios que sufren los ensamblajes de murciélagos entre diferentes estadios sucesionales de un bosque neotropical seco. Nos enfocamos específicamente en la familia Phyllostomidae, una familia rica en especies que comprende la mayoría de los gremios tróficos registrados en los murciélagos neotropicales, incluyendo a los nectarívoros y frugívoros, a quienes se les reconoce un papel importante en los procesos de reproducción de las plantas y en la regeneración del bosque. Para determinar las variaciones en la riqueza, diversidad y abundancia de las especies de filostómidos durante el proceso sucesional, se muestrearon los respectivos ensamblajes usando redes de niebla en 12 sitios pertenecientes a 4 estadios sucesionales con diferentes edades de abandono: pastizal (0 años), temprano (3 a 5 años), intermedio (8 a 12 años) y tardío (>50 años). Un esfuerzo de captura de 142 noches, usando cinco redes de niebla por noche, arrojo 606 filostomidos pertenecientes a 16 especies. El estadio tardío mostró la mayor riqueza de especies ya que en él se encontraron todas las especies registradas en este estudio (16 especies en comparación con 9 para los estadios temprano e intermedio y 4 para pastizales) y fue el único en donde se presentaron las especies raras. Las especies encontradas en cualquier estadio sucesional, fueron una suma de las especies encontradas en el estadio previo y otras adicionales. Este patrón aditivo pudiera estar determinado por la abundancia natural de las especies dado que las especies abundantes se encontraron en más estadios sucesionales que las especies raras. La riqueza y abundancia de murciélagos fue significativamente menor en los pastizales, independientemente del gremio trófico considerado. En consecuencia, los pastizales no fueron tomados en cuenta para la mayoría de los análisis estadísticos. La diversidad y abundancia de los filostómidos no difirió de manera significativa entre los estadios sucesionales temprano, intermedio y maduro. Sin embargo, a nivel de gremios tróficos, los murciélagos nectarívoros fueron más abundantes en el estadio temprano que en el tardío, probablemente como consecuencia de las diferencias en la disponibilidad de alimento. En conclusión, las áreas del bosque reconocidas como estadios tardíos en este estudio, son los reservorios más importantes de la riqueza de especies. La vegetación secundaria presenta también ensamblajes diversos de murciélagos, mientras que en los pastizales solo se presentan unas cuantas especies abundantes y vágiles que ocasionalmente cruzan este hábitat. Por tanto, sugerimos que las

políticas de uso de suelo en esta región se enfoquen en mantener la conectividad de los mosaicos de vegetación secundaria y madura, para asegurar la conservación de la diversidad de murciélagos y de sus interacciones ecológicas.

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Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest

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A B S T R A C T

Studies on successional dynamics in tropical systems have mostly focused on plant communities and mainly have been conducted in tropical humid areas. Here, we document changes in the structure of bat assemblages among secondary successional stages of a neotropical dry forest. We specifically focused on the speciose phyllostomid bat family, comprising most of the foraging guilds found among neotropical bats, including nectarivores and frugivores that play important roles in processes of plant reproduction and forest regeneration. To investigate bat species richness, diversity and abundance during successionnal processes, we mist-netted bat assemblages in 12 sites belonging to 4 different successional stages, namely pastures (0 yrs), early (3–5 yrs), intermediate (8–12 yrs) and late successional stage (>50 yrs). A capture effort of 142 nights using five mist-nets per night yielded 606 phyllostomid bats belonging to 16 species. Late stage was the most speciose sustaining all species found in the study (16 species against 9 for early and intermediate stages and 4 in pastures), and was the only environment where rare species occurred. Species found within any one successional stage were a combination of species found at the previous stage plus additional ones. This additive pattern appeared to be driven by the natural abundance of species, as the abundant species were found across more succesisonal stages than rarer species. Bats were significantly less speciose and less abundant in pastures, regardless of the foraging guild. Bat diversity and abundance did not differ significantly among early, intermediate and late stages. However, nectarivores were more abundant in early compared to late stage, probably as a consequence of differences in patterns of food availability. We conclude that areas of forest, recognized as late stage in our study, are the most important reservoirs of species richness. Secondary vegetation also contains diverse bat assemblages, while pastures only harbour a few abundant and vagile species occasionally crossing this habitat. We suggest that land-use regulations in this region focus on maintaining connectivity of a mosaic of areas of secondary and mature vegetation to insure the conservation of bat diversity as well as their important ecological interactions.

R E S U M E N

Los estudios relacionados con la dinámica sucesional de los sistemas tropicales han estado mayormente enfocados en comunidades de plantas y han sido conducidos principalmente en áreas tropicales húmedas o lluviosas. En este estudio, nosotros documentamos los cambios que sufren los ensamblajes de murciélagos entre diferentes estadios sucesionales de un bosque neotropical seco. Nos enfocamos específicamente en la familia Phyllostomidae, una familia rica en especies que comprende la mayoría de los gremios tróficos registrados en los murciélagos neotropicales, incluyendo a los nectarívoros y frugívoros, a quienes se les reconoce un papel importante en los procesos de reproducción de las plantas y la regeneración del bosque. Para determinar las variaciones en la riqueza, diversidad y abundancia de las especies de filostómidos durante el proceso sucesional, se muestrearon los respectivos ensamblajes usando redes de niebla en 12 sitios pertenecientes a 4 estadios sucesionales con diferentes edades de abandono: pastizal (0 años), temprano (3 a 5 años), intermedio (8 a 12 años) y tardio (>50 años). Un esfuerzo de captura de 142 noches, usando cinco redes de niebla por noche, arrojo 606 filostomidos

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pertenecientes a 16 especies. El estadio tardío mostró la mayor riqueza de especies ya que en el se encontraron todas las especies registradas en este estudio (16 especies en comparación con 9 para los estadios temprano e intermedio y 4 para pastizales) y fue el único en donde se presentaron las especies raras. Las especies encontradas en cualquier estadio sucesional, fueron una suma de las especies encontradas en el estadio previo y otras adicionales. Este patrón aditivo pudiera estar determinado por la abundancia natural de las especies dado que las especies abundantes se encontraron en más estadios sucesionales que las especies raras. La riqueza y abundancia de murciélagos fue significativamente menor en los pastizales, independientemente del gremio trófico considerado. En consecuencia, los pastizales no fueron tomados en cuenta para la mayoría de los análisis estadísticos. La diversidad y abundancia de los filostómidos no difirió de manera significativa entre los estadios sucesionales temprano, intermedio y maduro. Sin embargo, a nivel de gremios tróficos, los murciélagos nectarívoros fueron más abundantes en el estadio temprano que en el tardío, probablemente como consecuencia de las diferencias en la disponibilidad de alimento. En conclusión, las áreas del bosque reconocidas como estadios tardíos en este estudio, son los reservorios más importantes de la riqueza de especies. La vegetación secundaria presenta también ensamblajes diversos de murciélagos, mientras que los pastizales solo se presentan unas cuantas especies abundantes y vágiles que ocasionalmente cruzan este hábitat. Por tanto, sugerimos que las políticas de uso de suelo en esta región se enfoquen en mantener la conectividad de los mosaicos de vegetación secundaria y madura para asegurar la conservación de la diversidad de murciélagos así como sus interacciones ecológicas.

1. Introduction

“An understanding of ecological succession provides a basis for resolving man’s conflict with nature” (Odum, 1969, p. 262).

In the neotropics, bat communities may be considered as a keystone group. They provide important ecological services in ecosystems through their role in seed dispersal, pollination, and control of invertebrate and small vertebrate populations (Whitaker, 1993; Hutson et al., 2001; Geiselman et al., 2007; Kalka et al., 2008; Williams-Guillén et al., 2008). Neotropical bats visit and presumably pollinate 573 species and disperse seeds from 516 species (Geiselman et al., 2007). Moreover, it has been demonstrated that insect predation by bats can significantly decrease herbivory levels in a neotropical rain forest (Kalka et al., 2008). Additionally, bats play an important role during the successional process because they disperse several species (i.e. *Solanum*, *Cecropia*, *Piper* and *Vismia*) which are dominant in secondary vegetation of moist and rainforest in terms of density, basal area and biomass (Gorchov et al., 1993; Fleming, 1988; Charles-Dominique, 1986; Muscarella and Fleming, 2007).

Despite the important role of bats in tropical ecosystems and in the successional process in particular, most studies documenting how neotropical bat communities respond to habitat modifications have been performed in the context of habitat disturbance and fragmentation (Table 1). Only a few studies have attempted to document the recovery of bat assemblages during secondary succession of neotropical forests (Table 1) and these have been conducted in moist and rain forests. At present, no single study has evaluated changes in bat communities in tropical dry forests (TDFs) during succession.

Current knowledge on how secondary succession affects bat communities in tropical moist/rain forests cannot be extrapolated to communities inhabiting TDFs because of the uniqueness of this ecosystem. Tropical dry forests are, indeed, quite different from tropical moist/rain forests in several major aspects including: (1) strong seasonality of abiotic conditions, i.e. water availability (Mooney et al., 1995); (2) forest structure, i.e. smaller canopy height, basal area and number of strata (Murphy and Lugo, 1986); (3) species composition, i.e. the flora is a depauperate subset of the one present in moist/rain forests (Gentry, 1995); and (4) plant species composition in early successional stages are dominated by anemochorous and autochorous plants instead of zoochorous plants occurring in early successional moist/rain forests (Bullock, 1995; Gentry, 1995; Vieira and Scariot, 2006). As a consequence of this, chiropterochoric resource availability is lower in the early sucesional stages of TDFs. Considering these differences, it is likely that changes in TDF bat communities will be different from those described for tropical moist/rain forests.

The main objective of this study was to document the composition and structure of phyllostomid bat assemblages occurring in different successional stages of a TDF. We focus on Phyllostomidae because of their ecological importance in neotropical ecosystems (discussed above) and because this is the most speciose (151 species), and functionally diverse bat family in the Neotropics which includes most of the foraging guilds recognized for bats (Hutson et al., 2001). Additionally, their specialized requirements for food, roosting sites, and habitat selection, make them a useful indicator of habitat change (Fenton et al., 1992; Medellín et al., 2000; Clarke et al., 2005a,b).

Analyses were performed at both the assemblage and guild level. First we compare the phyllostomid bat assemblages occurring in different successional stages considering the following community attributes: species richness, species density, evenness and diversity. Next, we compare the abundance of the most speciose guilds, frugivores and nectarivores, among different successional stages. Finally, we discuss the implications of our results for the management and conservation of phyllostomid bats and their ecological services in mosaics of conserved and secondary TDFs.

We expect the most diverse phyllostomid bat assemblages to occur in the late successional stages because these present the most diverse and structurally complex vegetation within TDF (Chazdon et al., 2007). We also expect fewer frugivores and nectarivores in the early successional stages because these are frequently dominated by grasses and anemocorous plants that do not constitute food sources for these animals (Vieira and Scariot, 2006).

2. Methods

2.1. Study area and sampling sites

The study was performed in and surrounding the Chamela-Cuixmala Biosphere Reserve (CCBR) (19°22′–19°35′N, 104°56′–105°03′W), located in the central western coast of México in the state of Jalisco. The CCBR consists of primarily mature forest and has an extension of 13,200 ha, where the predominant vegetation type is TDF (Lott, 1993). This region presents a markedly seasonal

Table 1

Summary of most studies performed in the Neotropics about the effect of habitat modification and secondary succession on bat assemblages. Forest type (RF: rain forest, MF: moist forest). Assemblage attributes (*S*: species richness, Sp.D.: species density, Div.: diversity, Ab.: total abundance). Effects (NS: non-significant difference, (<): decrease, (>): increase, I: higher values in the intermediate successional stages). The effect of disturbance/fragmentation on bat assemblages was determined by comparing disturbed areas with mature forest. The effect of succession on bat assemblages was analyzed as the tendency found in assemblage attributes during this process.

Main subject and site	Forest type	Effects				Reference
		S	Sp.D.	Div.	Ab.	
Disturbance/fragmentation						
Quintana Roo, México	RF	–	NS	<[a]	NS	Fenton et al. (1992)
Veracruz, México	RF	<	–	–	–	Estrada et al. (1993)
Parana, Brazil	MF	<	–	–	>	dos Reis and Muller (1995)
French Guiana	RF	<	–	–	>	Brosset et al. (1996)
French Guiana	RF	–	<	<[a]	<	Cosson et al. (1999a,b)
Petén, Guatemala	RF	NS	–	–	–	Schulze et al. (2000)
Veracruz, México	RF	<	–	–	<	Estrada and Coates-Estrada (2001)
French Guiana	RF	–	<	–	<	Pons and Cosson (2002)
Veracruz, México	RF	<	>	>[a]	>	Estrada and Coates-Estrada (2002)
Canindeyú, Paraguay	MF	>	–	–	–	Gorresen and Willig, 2004
Quindío, Colombia	MF	<	–	–	–	Numa et al. (2005)
Trinidad, Republic of Trinidad and Tobago	MF	NS	–	<[b]	>	Clarke et al. (2005a)
Bahia, Brazil	RF	<	–	<[a]	–	Faria et al. (2006)
Pará, Brazil	MF	NS	–	–	NS	Bernard and Fenton (2007)
Matagalpa, Nicaragua	MF	–	<	NS[a]	<	Medina et al. (2007)
Succession						
Chiapas, México	RF	>	–	>	–	Medellín et al. (2000)
Trinidad, Republic of Trinidad and Tobago	MF	NS	–	NS[b]	I	Clarke et al. (2005b)
Tabasco, México	RF	–	NS	NS[a]	NS	Castro-Luna et al. (2007)
Pinar del Río, Cuba	MF	NS	–	I[a]	<	Mancina et al. (2007)[c]
Iquitos, Perú	RF	–	–	–	–	Willig et al. (2007)[d]

[a] Shannon index as a measure of diversity.

[b] Alpha of Fisher index as a measure of diversity.

[c] The sequence of secondary stages was established according to the degree of perturbation, instead of the number of years since abandonment.

[d] Although the authors discuss about the effects of habitat conversion on bat biodiversity from a community perspective, they do not analyze directly the effect of this disturbance on assemblages attributes.

pattern of rainfall (García-Oliva et al., 2002). Average annual precipitation based on 30 years (1977–2006) is 763 ± 258 (SD) mm and occurs mainly during the months June–October (http://www.ibiologia.unam.mx/ebchamela/index.html). Accumulated precipitation and months that received rainfall, respectively, during the years in which data were collected were: 2004, 652 mm, June–October; 2005, 384 mm, July–August, and 2006, 387 mm, June–October (http://www.ibiologia.unam.mx/ebchamela/index.html).

We used a chronosequence approach where time is substituted by space. Each set of study sites has different ages of abandonment, allowing inference of the successional process along time. We selected twelve sampling sites representing four successional stages (three sampling sites per treatment): 3 pastures, 3 early stage sites (3–5 years), 3 intermediate stage sites (8–12 years), and 3 late stage sites (at least 50 years old; Fig. 1). Each sampling site (with the exception of the late stage sites) consisted of a 120 m × 90 m plot embedded within a matrix of vegetation of the same kind and surrounded by fire breaks and fences to keep cattle out.

The massive use of the forest in this region started in 1943 when the Mexican government initiated a program “March to the Sea”, encouraging agriculture, cattle raising and tourism development (Castillo et al., 2005). The secondary vegetation sites used in this project were selected based on information about time since last major disturbance (i.e. cutting, clearing and fire) obtained from interviews with cultivators. Only sites that had been completely abandoned for an identified period of time were included. Cultivators indicated that secondary vegetation occurred mainly when economic restrictions limited their continued use as agricultural or pasture fields.

The land use history of each of the selected sites is quite similar. Forest was first removed through slash and burn, and lands were

Fig. 1. Aspect photos of the four successional stages in which bats were sampled in the region of the Chamela-Cuixmala Biosphere Reserve. Pictures were taken in the dry season to better illustrate differences in vegetation structure among stage (P: pastures, E: early, I: intermediate and L: late stage).

subsequently used for maize and bean production during approximately two years. Lands were then converted into cattle pastures and were burned approximately every two years, before the rainy season, to foster grass production. In order to select sampling sites with the most homogeneous conditions, all the sites used in this study were located on slopes of small hills, at a mean height of 223 m.a.s.l. (range 178–320), with a slope ranging from 15° to 25°. We avoided north facing slopes because they can show higher heterogeinity in insolation and plant community composition in relation to altitude (Balvanera et al., 2002). The sites with secondary vegetation were located around the mature forest protected by the CCBR at a distance of 1000–5000 m.

The pasture sites were used for cattle raising until the beginning of this study. These areas did not present evidence of high erosion level that would impede the successional process. The associated vegetation consists of mainly non-native grasses with a few shrubs and treelets mostly of the species *Croton pseudoniveus*, *Acacia farnesiana*, *Lonchocarpus constrictus* and *Cordia alliodora*. Treelets were maintained in the pastures to be used for fencing or to provide shade for cattle. Early stage sites (3–5 years) are characterized by a greater presence of shrubs and the permanence of some non-native grasses. Taller woody plants average 5 m in height and are dominated by *A. farnesiana*, *Bauhinia subrotundifolia*, *L. constrictus* and *Ceasalpinia eriostachys*. The intermediate stage sites (8–12 years) share some similarities with late stage sites in terms of stem density (DBH > 1 cm) and average height of the tallest trees (10 m), but woody plant species richness is still 15% lower than that of the late stage. The most common woody plants are *Cnidosculus spinosus*, *L. constrictus*, *Croton roxanae*, and *Caesalpinia caladenia*. Two of the three late stage sites are located within the reserve and one is located in private property connected to the reserve by continuous forest; all three are located approximately 1000 m from the closest border. These sites have been protected from public access and have not suffered any kind of disturbance for at least 50 years. In these sites the average height of the tallest trees is 10 m and the most common woody plants are *Apoplanesia paniculata*, *C. roxanae*, *Piptadenia constricta* and *Thouinia paucidentata* (Chazdon et al., 2007; P. Balvanera, G. Ibarra-Manríquez, A. Pérez-Jiménez and M. Martinez-Ramos, unpublished data).

2.2. Bat sampling

Bats were surveyed at all sites using the same standardized sampling methods each night. Two small nets (6 m long × 2.6 m high), two medium nets (9 m long × 2.6 m high) and one large net (12 m long × 2.6 m high) were set at ground level in natural corridors that represented flyways for bats. Nets were placed within and surrounding each study plot, at a distance not shorter than 30–50 m between them and opened at dusk for five consecutive hours; this period of time corresponds to peak foraging hours for most phyllostomid bats (Fenton and Kunz, 1977). Although this technique is biased towards sampling bats flying at ground level and inappropriate for many tropical moist/rain forests (Bernard et al., 2001), because of the lower canopy height in the studied TDF (maximum mean of mature forest: 15 m) this method is adequate for this study site.

Sites were sampled approximately every 46 ± 15 (SD) days from June 2004 to August 2006, with the exception of the pasture sites which were sampled less than the other sites due to a very low capture rate. In our analyses we only include samples performed on non-rainy and moonless nights ($n = 20$, 39, 40 and 43 for pastures, early, intermediate and late stages, respectively) in order to reduce variation in capture success. To avoid biases due to trap-shy behavior of bats, each site was sampled a single night at a time. The order of sampling for every plot was randomized during each sampling period.

Nets were checked approximately every 30 min and bats were temporarily stored in cloth bags for processing. Bats were identified to species using a dichotomous key (Timm and Laval, 1998), and individually numbered aluminum bands were placed on their forearm. We used the classification of Koopman (1993) for bat families, subfamilies and genera. The species were classified into four feeding guilds using the classification used by Timm and Laval (1998): frugivores, nectarivores, gleaning insectivores and sanguivores.

2.3. Analyses

2.3.1. Bat sampling completeness

We assessed the completeness of the bat survey by calculating the percentage of the total estimated species richness that effectively was covered by samples. Total species richness was estimated by computing the mean of the first and second order Jackknife index. The Jackknife procedure is a technique for reducing the bias of estimates (Colwell and Coddington, 1994), which helps to deal with small samples (<100 individuals per site). Ninety percent of completeness was considered as a satisfactory level of sampling efficiency (Moreno and Halffter, 2001).

2.3.2. Analyses at the assemblage level

Rank-abundance (dominace-diversity) graphs were built for each sampling site following the methodology described by Feinsinger (2001). These graphs constitute a useful tool for visualizing some attributes of the assemblage such as species richness (number of points), evenness (slope), number of rare species (tail of the curve) and relative abundance of each species (order of the species in the graph), and have been proposed as an alternative way of comparing communities (Feinsinger, 2001).

For the comparison of species richness among successional stages, we computed individual-based rarefaction curves (Gotelli and Colwell, 2001), after pooling all capture data by successional stage (EstimateS software, Version 8, Copyright R. K Colwell: http://viceroy.eeb.uconn.edu/estimates). The 95% confidence intervals of the moment-based estimator of species richness (Sobs Mao Tau), were used to determine if significant differences existed among successional stages (Colwell et al., 2004). We also computed species density (number of species captured per sampling night) and bat abundance (number of individuals captured per sampling night) and compared their variations among the four successional stages, sampling sites and between seasons using generalized linear models (GLMs, GENMOD procedure; SAS, 2000). The model used successional stage, sampling site (nested within successional stage) and season (dry *vs.* rainy) as categorical independent variables (main effects) and species density and abundance, respectively, as response variables for each analysis. A negative binomial distribution associated with a log-link function was specified as it appeared to be the error distribution that best describes the structure of our count data. The negative binomial distribution has been previously proposed as an appropriate underlying distribution for statistical analyses of frequency count data (White and Bennetts, 1996). The least-square mean (LSMEAN) and confidence limits corresponding to each of the main effect categories, as well as the likelihood ratio statistic (p-value based on the Chi-square distribution) were computed in order to pinpoint significant differences between pairs of categories (SAS, 2000).

Two other computed measures of species diversity were the probability of interspecific encounter (PIE), which is an indicator of evenness proposed by Hurlbert (1971), and the Shannon diversity index (H) (Magurran, 2004). To allow direct comparison among sites with different capture numbers, all indicators were standardized (individual-based) with rarefaction methods, using 1000 random reorganizations of sample orders (Gotelli and Graves, 1996). The Shannon diversity index was computed with EstimateS software (Version 7.51; Colwell, 2005) and the PIE index was computed with EcoSim software (Version 7.72; Gotelli and Entsminger, 2004). Mean diversity indices for a given capture number where compared among successional stages using the nonparametric Kruskal–Wallis test.

Finally, in order to explain the change in species composition during the successional process, we used binomial regressions to test if the ubiquity of bats (proportion of secondary successional stages and sites in which each species occurs) was significantly related to their natural abundance in late stage mature forest. Natural abundance was calculated as the average number of the total individuals captured within the three sites representing the late stage. Regressions where performed with the R software (RDCT, 2006 R Development Core Team, 2006) following Faraway (2006).

2.3.3. Analyses at the guild level

The abundance (number of individuals captured per sampling night) of the most represented guilds (frugivores and nectarivores) was computed and compared among the four successional stages, samplings sites and between seasons using generalized linear models (GENMOD procedure; SAS, 2000) as explained above.

3. Results

One hundred and forty-two sampling nights at the 12 sites resulted in a 5964 net-m-night capture effort and led to the capture of 929 individuals comprising 22 species and 4 families (Table 2). Phyllostomidae was the most speciose and abundant family, with 16 species (72.7% of all species) and 606 individuals (65.2% of all captures). The non-phyllostomid bats captured belong to the families Mormoopidae (3 species), Vespertilionidae (2) and Molossidae (1), and represented 32.8%, 1.8% and 0.1% of the total

Table 2

Number of individuals captured at each study site. Successional stages (P: pastures, E: early, I: intermediate and L: late stage). Guild (AI: aerial insectivorous, GI: gleaning insectivorous, F: frugivorous; N: nectarivorous; and S: sangivorous).

	Guild	Successional stage												Total
		Pasture			Early			Intermediate			Late			
		P1	P2	P3	E1	E2	E3	I1	I2	I3	L1	L2	L3	
Mormoopidae[a]														
Pteronotus davyi[b]	AI	0	1	0	0	0	0	0	0	0	1	0	1	3
Pteronotus parnellii[b]	AI	16	10	0	57	13	12	35	5	2	54	30	65	299
Mormoops megalophylla[b]	AI	0	0	0	0	0	0	0	0	0	0	0	3	3
Phyllostomidae[a]														
Phyllostominae[c]														
Micronycteris microtis[b]	GI	0	0	0	0	0	0	0	0	0	0	0	1	1
Glossophaginae[c]														
Glossophaga soricina[b]	N	2	1	0	27	3	28	2	8	6	4	0	21	102
Glossophaga commissarisi[b]	N	0	0	0	3	1	16	0	4	1	0	0	4	29
Leptonycteris yerbabuenae[b,d]	N	0	0	0	13	0	15	0	3	1	3	0	0	35
Choeroniscus godmani[b]	N	0	0	0	0	0	0	0	0	0	0	0	1	1
Musonycteris harrisoni[b]	N	0	0	0	0	0	0	0	0	0	1	0	0	1
Carolliinae[c]														
Carollia sp.[b,e]	F	0	0	0	0	0	0	0	0	0	0	0	7	7
Stenodermatinae[c]														
Artibeus jamaicensis[b]	F	0	1	5	8	11	14	11	32	22	6	1	112	223
Artibeus watsoni[b]	F	0	1	1	0	0	3	1	7	0	1	0	1	15
Artibeus intermedius[b]	F	0	0	1	1	2	0	2	4	2	0	4	21	37
Artibeus phaeotis[b]	F	0	0	0	5	0	1	0	1	4	0	1	13	25
Artibeus lituratus[b]	F	0	0	0	0	0	0	0	0	0	0	1	2	3
Sturnira lilium[b]	F	0	0	0	0	1	4	0	3	0	0	0	5	13
Centurio senex[b]	F	0	0	0	0	0	0	0	0	0	0	1	0	1
Chiroderma salvini[b]	F	0	0	0	0	0	0	0	0	0	0	1	0	1
Desmodontinae[c]														
Desmodus rotundus[b]	S	0	0	0	2	1	6	6	2	13	14	0	68	112
Vespertilionidae[a]														
Lasiurus blossevillii[b]	AI	0	0	0	0	0	0	1	0	0	0	1	0	2
Rhogeessa parvula[b]	AI	0	1	0	0	0	2	0	5	1	0	0	6	15
Molossidae[a]														
Molossus rufus[b]	AI	0	0	0	0	0	0	0	0	0	0	0	1	1
Total abundance		18	15	7	116	32	101	58	74	52	84	40	332	929
Phyllostomid abundance		2	3	7	59	19	87	22	64	49	29	9	256	606
Observed number of phyllostomid species		1	3	3	7	6	8	5	9	7	6	6	12	16
Completeness		90	94	91	94	90	95	93	96	96	94	94	95	90-96
Number of samples		4	8	8	15	10	14	15	15	10	16	9	18	142

[a] Family.

[b] Species.

[c] Subfamily.

[d] *Leptonycteris curasoae*, *sensu* Ceballos and Miranda (1986), was considered as *Leptonycteris yerbabuenae* based on Russell and Wilson (2006).

[e] The specimens of the genus *Carollia* were registered as *Carollia* sp. because none of them fit the morphological description of *Carollia subrufa*, the unique species of this genus reported for the study area (Ceballos and Miranda, 1986).

captures respectively. The results presented are based on the phyllostomid bat data.

3.1. Bat sampling completeness

The sampling effort was considered sufficient to characterize the phyllostomid bat assemblage given that completeness reaches 90–96% at all sites (Table 2).

3.2. Assemblage level

Captures were dominated by three species: *Artibeus jamaicensis* (36.8%), *Desmodus rotundus* (18.5%) and *Glossophaga soricina* (16.8%), which together represented 72.1% of the phyllostomid bats. *A. jamaicensis* and *G. soricina* were dominant in most of the sampling sites (Fig. 2). Eight species presented an intermediate level of abundance (from 0.5% to 6.1% of all phyllostomid bats) and five rare species were represented by a single individual (Table 2). All the rare species (*Micronycteris microtis*, *Choeroniscus godmani*, *Musonycteris harrisoni*, *Centurio senex*, *Chiroderma salvini*), as well as two of the species with an intermediate level of abundance (*Artibeus lituratus* and *Carollia* sp.), were exclusively captured in the mature forest (Table 2).

Phyllostomid species richness varied from 1 to 12 among sites, and totaled 4 in pastures, 9 in early, 9 in intermediate and 16 in late stages (Fig. 2). The individual-based rarefaction curves (Fig. 3), suggest that we sampled all species occurring in early and intermediate stages after about 100 captures, as curves reached a asymptote with a negligible confidence interval. Late stage samples, on the contrary, did not reach a ceiling and eventually attained significantly higher species richness than other sites after about 130 captures, as shown by the non-overlapping confidence intervals.

In pastures, due to the paucity of captures, the corresponding rarefaction curves did not provide valuable information. Nevertheless, GLMs performed on species density and bat abundance revealed strong differences between pastures and all other successional stages (species density: $\chi^2 = 28.72$, df = 3, $p = <0.001$, bat abundance: $\chi^2 = 29.16$, df = 3, $p = <0.001$), where pastures presented the lowest values for both parameters (Fig. 4). The species density and bat abundance were also significantly different between sampling sites ($\chi^2 = 42.44$, df = 8, $p = <0.001$; $\chi^2 = 55.62$, df = 8, $p = <0.001$, respectively), and season ($\chi^2 = 28.20.44$, df = 1, $p = <0.001$; $\chi^2 = 31.32$, df = 1, $p = <0.001$, respectively). The successional stages that presented significant differences between sampling sites were: (1) intermediate and late stages for species density and (2) early, intermediate and late stages for bat abundance (Fig. 4). The dry season presented the lowest value for both species density and bat abundance.

The diversity index values of PIE and *H*, could not be adequately documented for pastures. In spite of the pattern of increasing species richness observed during the process of succession (4 in pastures, 9 in early, 9 in intermediate, 16 in late) the diversity index values were statistically indistinguishable among the three successional stages and among sampling sites (Table 3). The standard error values corresponding to each stage indicate that in all cases the highest variation among sampling sites occurred in the late stage (Table 3).

The level of species ubiquity found in secondary sites was explained by the species' natural abundance. The natural abundance of species was positively related to the number of secondary sites (binomial logit regression, $\chi^2 = 37.62$. df = 14, $p < 0.001$), and secondary stages ($\chi^2 = 10.4$, df = 14, $p = 0.001$) in which the species occur. Removing the 3 most abundant species from the analysis, in order to determine if the results were biased by them, did not alter this pattern (site numbers: $\chi^2 = 14.78$, df = 11, $p < 0.001$; stage numbers: $\chi^2 = 9.56$, df = 11, $p = 0.002$).

3.3. Guild level

Frugivorous (56.3% of species and 53.6% of individuals) and nectarivorous bats (31.1% and 27.7%) accounted for the highest

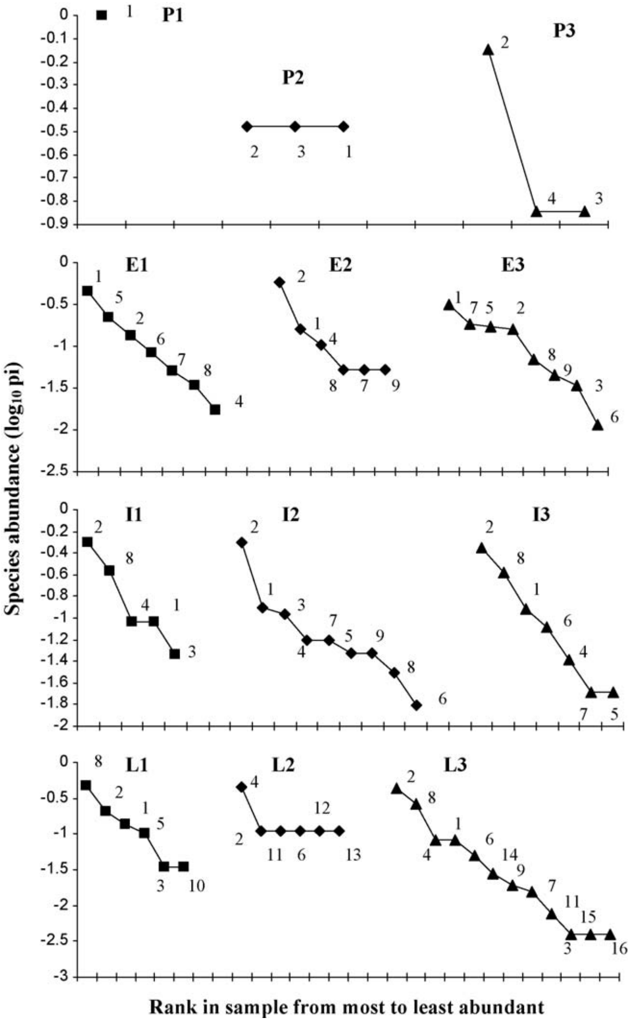

Fig. 2. Rank-abundance (dominance-diversity) graph of species captured at Chamela-Cuixmala in all sampled sites. Numbers represent species captured. 1: *Glossophaga soricina*, 2: *Artibeus jamaicensis*, 3: *Artibeus watsoni*, 4: *Artibeus intermedius*, 5: *Leptonycteris yerbabuenae*, 6: *Artibeus phaeotis*, 7: *Glossophaga commissarisi*, 8: *Desmodus rotundus*, 9: *Sturnira lilium*, 10: *Musonycteris harrisoni*, 11: *Artibeus lituratus*, 12: *Centurio senex*, 13: *Chiroderma salvini*, 14: *Carollia* sp., 15: *Choeroniscus godmani*, 16: *Micronycteris microtis*. P1–P3: pasture's sampling sites, E1–E3: early stage's sampling sites, I1–I3: intermediate stage's sampling sites, L1–L3: late stage's sampling sites. pi: relative abundance of each species.

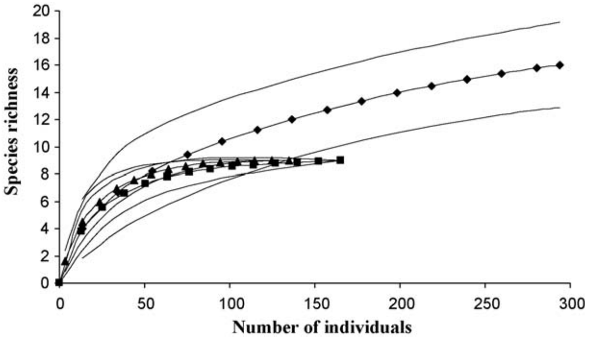

Fig. 3. Individual-based rarefaction curves (*sensus* Gotelli and Colwell, 2001) for early (triangle), intermediate (square), and late (rhombus), successional stages. Simple lines delineate the 95% confidence intervals.

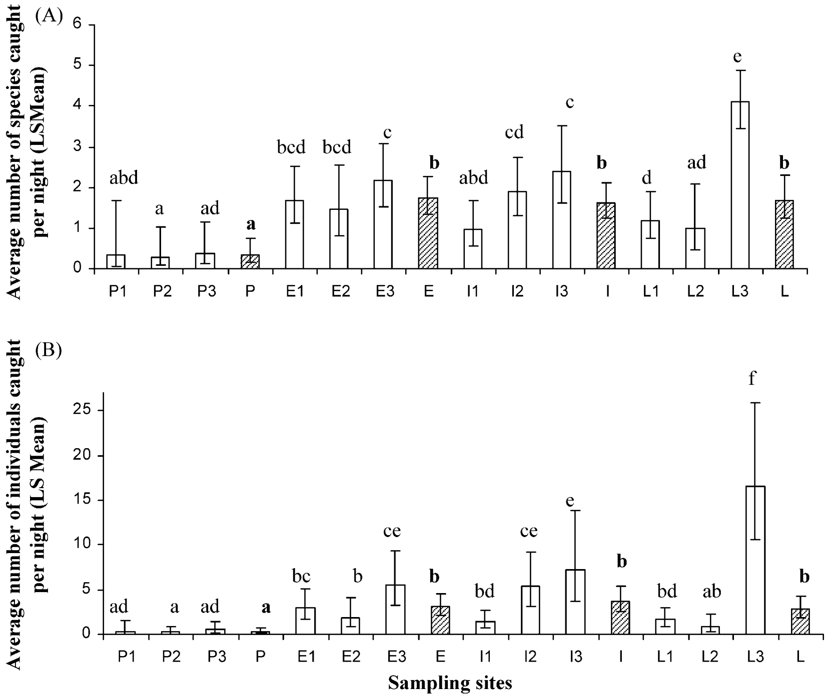

Fig. 4. Average number of species (A) and number of individuals (B) of phyllostomid bats captured each night (species density and bat abundance, respectively), at the different sampling sites (open bars) and successional stages (shaded bars) (±95% confidence intervals). Bars sharing a letter are not significantly different ($p > 0.05$). P: pastures, E: early, I: intermediate and L: late stage.

percentage of both captured species and individuals (Table 2). The other two guilds recognized in the pool of captured species were represented by just one (sanguivores: *D. rotundus* and gleaning insectivores: *M. microtis*), with 112 individuals of *D. rotundus* and just 1 of *M. microtis* captured (Table 2).

The number of foraging guilds represented in bat assemblages was higher in the late successional stage (pastures: 2, early stage: 3, intermediate stage: 3 and late stage: 4). No sanguivorous bats were captured in the pastures and the only gleaning insectivore was captured in the late stage.

The number of frugivorous species in the assemblages increases towards the late successional stage, ranging from 3 in pastures, 5 in early stage, 5 in intermediate stage, to 9 in late stage (Table 2). Four frugivorous species were exclusively captured in the late stage: *Carollia* sp., *A. lituratus*, *C. senex* and *C. salvini* (Fig. 2). The mean number of frugivores captured per sampling night was not significantly different among successional stages (GLM, $\chi^2 = 3.73$, df = 2, $p = 0.1552$), but it differed among sites ($\chi^2 = 51.98$, df = 6, $p = <0.0001$) and between seasons ($\chi^2 = 20.38$, df = 1, $p = <0.0001$) (Fig. 5). The successional stages in which there were differences among sampling sites were the intermediate and late. The dry season presented lower numbers of frugivores captured per sampling night.

As in the case of frugivorous bats, the number of nectarivorous species increased toward the late stage (pasture: 1, early stage: 3, intermediate stage: 3, late stage: 5) (Table 2). Two species were exclusively captured in the late stage (*C. godmani* and *M. harrisoni*) (Fig. 2). The abundance of nectarivorous bats captured per night was significantly different among successional stages ($\chi^2 = 6.15$, df = 2, $p = 0.0463$), sampling sites ($\chi^2 = 21.51$, df = 6, $p = 0.0015$), and season ($\chi^2 = 9.57$, df = 1, $p = 0.0020$; Fig. 5). More nectarivores were captured, on average, in the early stage and in the rainy season; however, significant differences among sampling sites were only found in the late successional stage. Pastures could not be statistically compared in the analysis of frugivores and nectarivores because many zeros in the datasets precluded the calculation of the likelihood ratio statistic for all comparisons.

Table 3
Rarified diversity index values (confidence intervals in parenthesis) for each sampling site. The Chi^2 and *p*-values presented are from the Kruskal–Wallis test used to compare the successional stages. All indices were rarified at 19 individuals. The pasture stage and the L2 site were not considered in the analyses due to the low number of collected individuals. Indexes (PIE: evenness index; *H*: Shannon diversity index).

Successional stages and sites	Diversity index	
	PIE	*H*
Early stage		
E1	0.59 (0.53–0.73)	1.22 (0.69–1.75)
E2	0.65 (0.65–0.65)	1.13 (0.76–1.50)
E3	0.56 (0.39–0.76)	1.21 (0.47–1.95)
Mean ± SE	0.62 ± 0.04	1.19 ± 0.05
Intermediate stage		
I1	0.68 (0.61–0.75)	1.12 (0.67–1.57)
I2	0.63 (0.43–0.78)	1.17 (0.70–1.64)
I3	0.70 (0.53–0.84)	1.21 (0.74–1.68)
Mean ± SE	0.67 ± 0.03	1.17 ± 0.05
Late stage		
L1	0.67 (0.53–0.75)	1.16 (0.65–1.67)
L3	0.88 (0.59–1.15)	1.47 (0.82–2.12)
Mean ± SE	0.76 ± 0.12	1.32 ± 0.22
Chi^2; *p*	4.03; 0.13	0.90; 0.64

4. Discussion

4.1. Assemblage level

As expected, results suggest differences among bat assemblages in different successional stages of TDF. Bat assemblages with lower species richness, species density and bat abundance (Figs. 2 and 4) were found in pastures, while assemblages with higher species richness were found in later successioanl stages. Bat assemblages in pastures were composed of only four species occurring in low abundance (Fig. 2). Indeed, due to the low number of captured

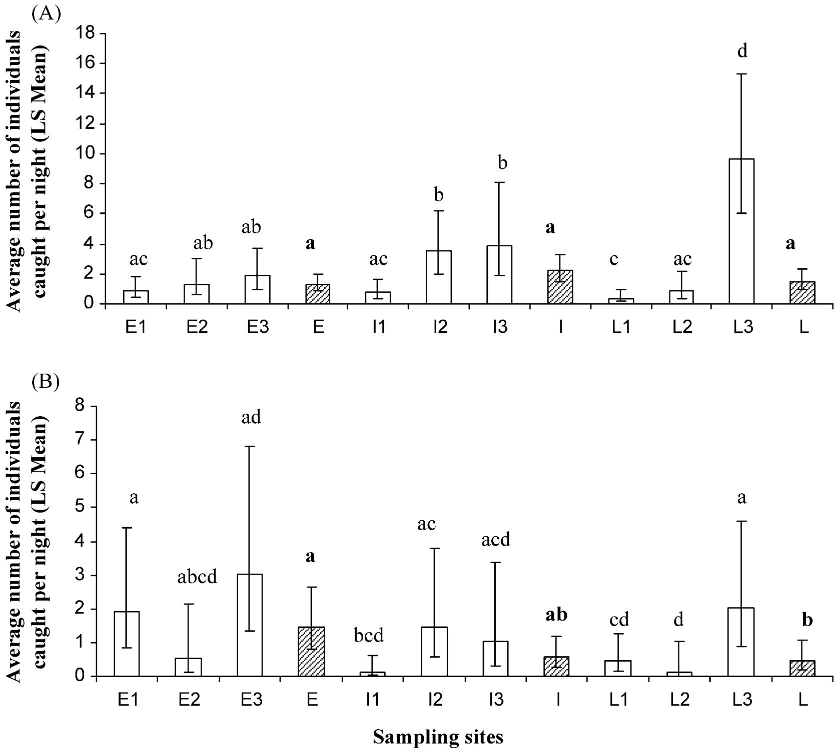

Fig. 5. Average number of fugivorous (A) and nectarivorous bats (B) captured each night at the different sampling sites (open bars) and successional stages (shaded bars) (±95% confidence intervals). Bars sharing a letter are not significantly different ($p > 0.05$). P: pastures, E: early, I: intermediate and L: late stage.

individuals and species in this stage, it was impossible to consider pastures in most of the quantitative analyses. A similar low capture rate of bats in pastures was found in a study evaluating the effects of forest fragmentation on bat assemblages in tropical rain forest (Estrada et al., 1993).

The depauperate phyllostomid bat community found in pastures may be a consequence of the scarcity of food resources, as well as the simplicity of the vegetation structure characteristic of this stage (Chazdon et al., 2007). Most of the phyllostomid bats inhabiting the region are frugivores and nectarivores that cannot obtain food, roost or shelter in the pastures where introduced grasses constitute the most important component of the vegetation. Several studies have documented how the presence and density of trees can determine the presence and abundance of bats in pastures because trees may provide roost, shelter and food (Galindo-González and Sosa, 2003; Lumsden and Bennett, 2005; Medina et al., 2007). In addition to scarcity of resources in pastures, some bats may avoid open areas to avoid predation pressure or because they are not adapted to cover large distances among food patches while foraging (Henry et al., 2007). The size of pasture plots and structure of the surrounding landscape may further influence local bat abundances and is an issue which warrants further research.

The late stage showed the bat assemblage with the highest species richness (all the phyllostomid species reported in this study), where 7 species, including all the rare ones (species represented by a single individual), were exclusively found in this stage. Again, this result may be a consequence of the differences among successional stages in terms of vegetation structure and composition, which determine the habitat quality and resource availability for this group. The vegetation in late stages presents the highest diversity and structural complexity in relation to other successional stages (Chazdon et al., 2007), consequently it shows higher resource availability. This condition would favor the presence of richer bat species assemblages. Similar results were also found in a subtropical moist forest (dos Reis and Muller, 1995) and a tropical rain forest (Medellín et al., 2000). In both studies, the authors found that the most specious bat assemblages occurred in the most diverse and structurally complex habitats.

There were no significant variations in species density, bat abundance and other diversity indicators (PIE, H) among the bat assemblages occurring in early, intermediate and late stages. L3 had the highest values of the late stage sites; however, the great variations among sampling sites, particularly in the late stage, did not allow the detection of any differences among stages. Similar results were also found by Castro-Luna et al. (2007), when comparing bat assemblages associated with different successional stages in a tropical rain forest. These authors argued that similarities in diversity found among assemblages may be a consequence of compensation, implying that competition among species for limiting resources is an important factor structuring such assemblages.

When pooling all the species captured per successional stage we found that the species within any successional stage were a combination of the species found at the previous stage plus new ones. Furthermore, we found a strong relationship between the natural abundance and ubiquity of species. The most abundant species in the late successional stage also occurred in more secondary stages and sites than the least abundant species, which were only found in the late succession stage. This pattern may be explained by the fact that the species that occur naturally at low abundance may be more sensitive to habitat modification due to an increased risk of local stochastic extinction (Davies et al., 2000; Henle et al., 2004). In contrast, species that occur naturally at high abundance could be less susceptible to habitat disturbance due to their generalist requirements or because their probability to arrive to modified areas is higher compared to less abundant species (Cosson et al., 1999a,b). Several other studies have found that the naturally most abundant species are also more abundant in disturbed areas (Estrada et al., 1993; Willig et al., 2007; Meyer et al., 2008) and that the rare species are mostly associated with mature forest (Brosset et al., 1996). Several of the rare species reported here (*C. senex*, *M. harrisoni*, *M. microtis*), already have been identified as rare species or mature forest dwelling species in previous studies (Fenton et al., 1992; Estrada et al., 1993; Stoner et al., 2002; Schulze et al., 2000).

Significant variation in both species density and abundance was found between the dry and rainy season, where the highest values were registered during the rainy season. This variation corresponds to the marked seasonality in the availability of resources typical of TDF (Bullock, 1995). According to Stoner (2005), in Chamela TDF the highest peaks of chiropterochoric and chiropterophilic resources occur during the rainy season.

4.2. Guild level

Frugivores and nectarivores constitute the trophic guilds best represented in our bat assemblages. The absence of omnivores, carnivores and the scarcity of gleaning insectivores, represented in this study by a single individual (*M. microtis*), can be a consequence of the isolation of Chamela TDF from tropical rain forest. According to Ceballos (1995), a significant part of the TDF fauna is a subset of the tropical moist/rain forest fauna. The TDF located along the western coast of Mexico is tenuously connected to the southern tropical moist forest (Ceballos, 1995). Indeed, Stoner (2005), based on the species composition and guild structure of the Chamela bat community, suggests that this one is more similar to simpler neotropical savanna communities.

No significant variation was found in the abundance of frugivorous bats among the early, intermediate and late stages. Nevertheless, a significant site effect was detected for frugivore abundance. The late site L3, for example, showed the highest abundance. This site is located near humid areas (riparian and semideciduous forest) where some species of the genus *Ficus*, *Brosimum* and *Piper* occur; these species constitute some of the most important food sources for neotropical frugivorous bats (Geiselman et al., 2007).

In contrast to results obtained in tropical humid and rain forests (e.g. Brosset et al., 1996; Schulze et al., 2000), the abundance of frugivorous bats in Chamela TDF was not higher in areas of secondary successional vegetation. This divergence may be a consequence of distinct plant community composition among the early stages of these forests. In tropical dry forest, for example, early successional stages are dominated by anemochorous plants which do not constitute food resources for frugivorous bats (Vieira and Scariot, 2006). In contrast, in wetter tropical ecosystems, chiropterochoric species such as *Cecropia* spp., *Piper* spp., *Solanum* spp., and *Vismia* spp., are dominant in early stages and constitute the bulk of the diets of most frugivorous bats (Brosset et al., 1996; Fleming, 1988).

Nectarivores reached their highest abundance in the early stage. This may be due to the presence of several *Crescentia alata* (Bignoniaceae) trees close to the early stage sites. These trees represent an important food source for nectarivorous bats in the region (Stoner et al., 2003). Additionally, two of the most abundant species of woody plants found in the early stages (Mimosaceae: *A. farnesiana*, Bignoniaceae: *C. alliodora*), have been reported as chiropterophilic species (Tellez and Ortega, 1999).

A significant effect of seasonality on the abundance of frugivores and nectarivores was detected in this study. The same result was obtained in a previous study performed in the region by Stoner (2005), which states that the strong seasonality in resource availability provokes the seasonal change in the abundance of these guilds.

When comparing our results with previous studies performed in tropical moist/rain forest we find several similarities between these systems including: (1) phyllostomid assemblages occurring in pastures are depauperate in relation to the ones occurring in later stages; (2) a large proportion of species occur in secondary habitats; (3) the most preserved forest showed the highest species richness; and (4) the natural abundance of species can significantly explain their ubiquity in transformed habitats. The main dissimilarity we found between our study in TDF and previous studies in moist/rain forest is that the abundance of frugivorous bats in more humid environments is higher in secondary habitats while in the Chamela TDF this did not occur.

4.3. Implications for management and recommendations for future research

According to our data, the definitive loss of TDF mature vegetation could provoke a significant reduction in phyllostomid bat diversity. Rare species would be more affected because they are most tightly associated with this habitat. Nevertheless, our data also show that secondary vegetation provides important habitat for many phyllostomid species. Based on this information we recognize the importance of both of these habitat types. Since it is unrealistic to exclusively maintain intact mature forest in this region, we suggest that land-use regulations focus on maintaining connectivity of a mosaic of areas of secondary and mature vegetation. This would help to preserve the diversity of bats in the region as well as their important ecological interactions (pollination and seed dispersal). Our data also suggest that pastures dominating this landscape would cause a strong reduction in the diversity of this important group of animals.

Changes observed in phyllostomid bat assemblage in different successional stages may ultimately have consequences for the regeneration of plant communities in these areas. For example, the most dramatic changes of bat assemblages along succession were observed in pastures. Here, the significant reduction in phyllostomid diversity and abundance could affect the arrival of chiropterochoric species, as well as the reproduction of the chiropterophilic species found in these areas. The dominance of pastures in a transformed landscape, and the associated change in phyllostomid bat assemblage also may result in a reduction of gene flow among chiropterochorous and chiropterophyllic plants occurring in surrounding fragments of vegetation. Nevertheless, it must be noted that most of the species capable of germinating and establishing in pastures are anemochorous because they can better resist the dryness and strong irradiation found in pastures (Vieira and Scariot, 2006). More detailed studies documenting the distribution and abundance of bat-pollinated and bat-dispersed species in different successional stages of TDF, as well as genetic studies documenting gene flow, will provide important information for better understanding the consequences of changes in bat assemblages among successional stages.

This is the first study to document changes in bat assemblages along successional stages in TDF. To determine if our results represent a general pattern for TDF of if they are site specific, studies in other TDFs must be conducted to help recognize patterns in phyllostomid bat assemblages. Considering the high inter-site variation found in phyllostomid assemblages among our sampling sites, future studies should include greater numbers of sites per successional stage. Additionally, the detection of local and landscape-level factors determining the presence/abundance of bats in each successional stage should be evaluated. This knowledge will constitute a scientific basis for the proper management of modified landscapes. Studies supplying such information are extremely important given that species habitat specificity and the impact of human disturbance on their populations are unknown for most bat species (Fenton, 1997).

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CAPÍTULO 3

Patterns of phyllostomid bat occurrence in different successional stages of Neotropical dry forests: incorporating the seasonality effect

RESUMEN

Los bosques tropicales secos (BTS) se encuentran entre los ecosistemas tropicales más amenazados y están siendo modificados de forma creciente por actividades humanas como la ganadería y la agricultura, mismas que provocan el reemplazamiento de la vegetación natural por un complejo mosaico de parches de vegetación en diferentes estadios sucesionales, campos agrícolas y pastizales. En este contexto, se hace extremadamente necesario entender cómo los diferentes taxa responden a las modificaciones del hábitat. Especial atención deben de recibir aquellos taxa que juegan un papel crítico en los ecosistemas, como los murciélagos filostómidos, quienes facilitan el flujo génico entre las poblaciones de plantas y promueven la regeneración de los bosques. En este estudio buscamos identificar patrones potenciales en la presencia y abundancia de los murciélagos filostómidos a lo largo de diferentes estadios sucesionales del BTS. La respuesta de estos murciélagos a la sucesión se evaluó tanto a nivel poblacional y de ensamble (abundancia), como a nivel de ensamblaje (riqueza de especies, composición específica y composición de gremios tróficos). Para ello, muestreamos con redes de niebla los ensamblajes de murciélagos en 12 sitios, representando 4 diferentes estadios sucesionales (inicial, temprano, intermedio y tardío) en 3 BTSs localizados a través de un gradiente latitudinal: 1) la reserva de la biosfera Chamela-Cuixmala (RBCC), México, 2) Hato Piñero (HP), Venezuela y 3) el parque estatal de Mata Seca (PEMS), Brasil. En este sistema de estudio evaluamos también cómo la marcada estacionalidad en el régimen de precipitación de estos bosques modula la presencia y abundancia de los murciélagos. En la RBCC se capturaron 606 filostómidos, clasificados en 15 especies, 11 géneros, 5 subfamilias y 4 gremios tróficos. En HP, la captura ascendió a 996 individuos, clasificados en 30 especies, 17 géneros, 5 subfamilias y 6 gremios tróficos, mientras que en el PEMS se registraron un total de 808 individuos clasificados en 21 especies, 16 géneros, 5 subfamilias y 6 gremios tróficos. En general, encontramos una gran especificidad en la respuesta de los murciélagos filostómidos, siendo ésta particular de las especies, gremios tróficos, estaciones y regiones. Considerando la incidencia y abundancia en la cual los taxa (especies, géneros, subfamilias) se presentaron en los diferentes estadios sucesionales, detectamos que solamente unos pocos de ellos estuvieron tan fuertemente asociados a un determinado estadio, que pudieron ser considerados como taxa indicadores de ese estadio. Estas asociaciones, sin embargo, variaron con la estación del año. Mediante el análisis de la estructura espacial filogenética de los ensamblajes, se detectó, en dos de las tres regiones estudiadas (RBCC y HP), que los ensamblajes presentaban

un agrupamiento filogenético significativo durante la época de lluvia. Este resultado sugiere que cambios estacionales pueden estar ocurriendo en los procesos que subyacen a la conformación de los ensamblajes. Consideramos, entonces, extremadamente necesario tomar en cuenta la variación en las condiciones ambientales cuando se estudian ecosistemas estacionales. También es necesario hacer énfasis en el estudio de los patrones fenológicos de las plantas, debido a que éstos parecen modular la diversidad y abundancia de recursos en estos sistemas. Concluimos que la alta especificidad en la respuesta de los filostómidos a las transformaciones del BTS puede deberse a: 1) las condiciones ambientales distintivas de cada región, 2) la conducta y requerimientos ecológicos específicos de las especies que se presentan en la región, 3) la composición, estructura y patrones fenológicos de los ensamblajes de plantas que ocurren en los diferentes estadios sucesionales y 4) la composición y configuración del paisaje de la región. Como la presencia y abundancia de estas especies tan vágiles puede estar determinada significativamente por los atributos del paisaje, en aras de alcanzar un mejor entendimiento acerca de los factores que determinan la presencia y abundancia de los filostómidos en los paisajes antropogénicos, recomendamos extender el foco de atención de los estudios más allá de la caracterización del hábitat a escala local (p.ej. clasificación del hábitat en diferentes estadios sucesionales) para incluir su caracterización a nivel de paisaje (composición y configuración).

Patterns of phyllostomid bat occurrence in different successional stages of Neotropical dry forests: incorporating the seasonality effect

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Key words

Phyllostomid bat, Successional stages, Seasonal variation, Tropical dry forest.

Abstract

Tropical dry forests (TDFs) are among the most endangered tropical ecosystems, being increasingly modified by human activities as cattle raising and agriculture, which provoke the replacement of the natural vegetation by a complex mosaic of patches of different successional stages, agricultural fields and pasturelands. In this context, it is urgent to understand how the different taxa respond to habitat modification. Special emphasis deserve those taxa playing critical roles in the ecosystems as the phyllostomid bats, which facilitate the genetic flow among plant populations and promote forest regeneration. In this study we aim to identify potential patterns on phyllostomid bats occurrence in different TDF successional stages. Occurrence was evaluated at population and ensemble level (abundance) as well as at the assemblage level (species richness and composition, guild composition). Specifically, we mist-netted bat assemblages in 12 sites representing 4 different successional stages (initial, early, intermediate and late) in 3 TDFs located across a latitudinal gradient: 1) the Chamela-Cuixmala biosphere reserve (CCBR), Mexico, 2) Hato Piñeiro (HP), Venezuela and 3) the Parque Estadual da Mata Seca (PEMS), Brazil. We also evaluated how the marked seasonality of the TDFs precipitation regime modulates bats occurrence. In CCBR we captured 606 phyllostomids classified in 15 species, 11 genera, 5 subfamilies and 4 broad guilds. In HP captures ascended to 996 individuals classified in 30 species, 17 genera, 5 subfamilies and 6 broad guild while in PEMS a total of 808 individuals classified in 21 species, 16 genera, 5 subfamilies and 6 broad guilds were registered. In general we found high specificity on the phyllostomid bat occurrence as it showed particularities relative to the species, guilds, seasons and regions. Considering the incidence and abundance in which taxa occur in the different successional stages, we found that only a few of them were so tightly associated to a given stage that could be considered indicators of such stage. However, this association changed between seasons in all cases. By analyzing the spatial phylogenetic structure

of the assemblages, we detected phylogenetic clustering during the rainy season of two of the three regions. This finding points toward a seasonal change on the processes underlying the conformation of such assemblages. We then consider extremely necessary to account for variations in environmental conditions when studying seasonal ecosystems. It is also necessary to emphasize on the study of plant phenological patterns as they appear to modulate the resources abundance and diversity in these systems. We concluded that the high specificity of phyllostomid bats response to TDF transformation could arise from: 1) the distinctive environmental conditions of each region, 2) the specific behavior and ecological requirements of the regional bat species, 3) the composition, structure and phenological patterns of plant assemblages occurring in the different successional stages and 4) the regional landscape composition and configuration. As the occurrence of vagile species could be significantly determined by the landscapes attributes, in order to reach a better understanding about phyllostomids occurrence in anthropogenic landscapes, we strongly recommend to extend the focus of the studies beyond the characterization of the habitat at a local scale (i.e. classification of different successional stages) to include its characterization at a landscape level (composition and configuration).

1. Introduction

In the Neotropics, the natural landscape has been increasingly modified by human activities such as cattle raising and agriculture (Skole and Tucker 1993, Maass 1995, Nepstad et al. 1999, Primack et al. 2001, Quesada and Stoner 2004), provoking the replacement of natural vegetation by a complex mosaic of patches of different successional stages, agricultural fields and pasturelands (Sanchez-Azofeifa et al. 2005, Chazdon et al. 2007, Quesada et al. 2009). In fact, in several countries that present more than 2 % of annual deforestation (Primack *et al*. 2001), transformed landscape likely will be the predominant habitat available for wildlife in the near future (Hilty et al. 2006, Quesada et al. 2009). Consequently, it is urgent to determine which factors shape the distribution and performance of biota in Neotropical landscapes transformed by human activities, paying special attention to taxa participating in critical ecosystem functioning (Cosson et al. 1999, Jordán 2009).

In the Neotropics, bats are considered a key-stone group due to the ecological services they provide: seed dispersal, pollination, control of invertebrate and small vertebrate populations and recycling and translocation of nutrients and energy (Fleming 1982, Charles-Dominique 1986, Fleming 1988, Gorchov et al. 1993, Whitaker 1993, Valiente-Banuet et al. 2004, Muscarella and Fleming 2007, Kalka et al. 2008, Williams-Guillén et al. 2008). Bats favor the maintenance of plant diversity as they facilitategene flow among distant plant populations and the dispersion of plant species across the landscape, via pollen and seed translocation (Fleming 1988, Fleming et al. 2009, Lovoba et al. 2009). In fact, in some depauperae tropical areas, it has been suggested that bats can promote forest regeneration as nearly half of the most abundant pioneer plants are presumably dispersed by them (i.e. *Solanum*, *Cecropia*, *Piper*, *Vismia*, Charles-Dominique 1986, Gorchov et al. 1993). Insectivorous bats can significantly reduce forest herbivory levels as well (Kalka et al. 2008).

In tropical environments, bats deal with seasonal fluctuations of key resources (i.e. food, roost) and climate conditions (i.e. humidity, temperature) through behavioral and physiological adaptations. Examples of this are changes in diet breadth, type of food, food intake rate, patterns of habitat use, defense of feeding areas as well as migratory behavior (Heithaus et al. 1975, Whitaker and Black 1976, Bonaccorso 1979, Thomas 1983, Fleming and Heithaus 1986, Arroyo-Cabrales et al. 1987, Cockrum 1991, Wilkinson and Flemings 1996, Herrera et al 2001, Tschapka 2004, Ayala-Berdon et al. 2009). Indeed, tropical bats have the capacity to enter in torpor as a response to energetic restrictions and as a mechanism for avoiding dehydration in arid zones (Geiser 2004, Kelm and Helversen 2007).

One of the most endangered and seasonal ecosystems within the Neotropics is the tropical dry forest (TDF), a preferred zone for agriculture and human settlements (Quesada & Stoner 2004, Sánchez-Azofeifa 2005), that is distributed along most of the latitudinal gradient of the Neotropical region (approximate extension 519,597 km^2 according to Portillo-Quintero and Sánchez-Azofeifa 2010). TDFs are characterized by a marked seasonality in the precipitation regime and a severe dry season (DS) which can last from three to eight months, depending on the latitudinal position. TDFs nearest to the latitudinal limit of the tropics present the longest DS (Murphy and Lugo 1986, Sanchez-Azofeifa et al. 2005). Deciduousness is characteristic of TDF vegetation with at least 50% of the trees losing their leaves during the DS (Bullock and Solis-Magallanes 1990, Sanchez-Azofeifa et al. 2005). In spite of being one of the most endangered ecosystems (66% reduction in its original area, Portillo-Quintero and Sanchez-Azofeifa 2010), TDF is one of the least protected habitats (Miles *et al*. 2006) and has historically received little scientific attention in comparison to other Neotropical systems (Sanchez-Azofeifa et al. 2005).

As plant phenological patterns and primary productivity are strongly seasonal in TDFs, bats occurring in these systems have to deal with significant seasonal changes in terms of vegetation structure and type and amount of food. Kalacska et al. (2005), for example, report significant differences between seasons in canopy openness, plant area index (PAI) and leaf area index (LAI) of three TDFs. These changes on vegetation structure could significantly impact the activity of several bat species found in the Neotropics, especially those belonging to the family Phyllostomid which strongly depend on highly cluttered space for foraging and are sensitive to change in vegetation structure (Kalko et al. 1996, Cosson et al. 1999). Insect consuming bats also can experience significant changes in food availability between seasons as precipitation, primary productivity and insect abundance and diversity are positively related in the tropics (Wolda 1978, Frith and Frith 1985, Martínez-Yrizar et al. 1996 and Pescador-Rubio et al. 2002). Nectarivorous and frugivorous bats face significant variations in food availability as well, due to the pronounced seasonality in the flowering and fruiting of trees and shrubs (Frankie et al. 1974, Fleming 1988, Stoner et al. 2003). Seasonal differences in chiropterophilic and chiropterocoric resources were reported by Stoner (2005) in two TDFs (Mexico and Costa Rica), where the highest peaks of chiropteophilic resources occurred during the DS and at the beginning of the RS, whereas the highest number of canopy trees with fruits occurred during the RS.

The response of bats to seasonality provokes marked seasonal changes in their assemblages and ensembles. Stoner (2001, 2002, and 2005) and Avila-Cabadilla et al. (2009), for example, found significant changes in frugivore and nectarivore abundance between the TDFs seasons. In spite of this seasonal variation in bat assemblages and ensembles, most of the studies addressing bat response to habitat alteration, have combined data across seasons or analyzed data from a single season (Klingbeil and Willig 2010). These approaches may obscure important features about bat response, making difficult the discrimination between casualty and patterns. Klingbeil and Willig (2010), for example, report seasonal differences in the response of bat assemblages and ensembles to variation of landscape attributes (composition and configuration) in an evergreen forest of the Amazon.

1.1. Study Focus and objectives

The main goal of this study was to identify and explain potential patterns of phyllostomid bat occurrence in different successional stages representing the transformed landscapes of TDF, incorporating the effect of seasonality. For this purpose we studied a latitudinal gradient of Neotropical dry forests. First, we documented the seasonal changes on the attributes of phyllostomid assemblages (species composition, structure, species richness and abundance) along the gradient. Second, considering the seasonality, we compared the assemblages (species richness, species and guild composition), ensembles (abundance) and populations (abundance) occurring at the different successional stages. Third, we evaluated the seasonal distribution of species, genera and subfamilies in the different successional stages in order to identify successional/seasonal indicator taxa. Finally, by evaluating assemblage spatial phylogenetic structure, we discussed the possible mechanisms determining phyllostomid assemblage composition, as well as the seasonal differences in such mechanisms. A chronosequence approach was used as a baseline for this study where we contrasted the data from three Neotropical dry forests spanning a wide gradient in latitude (Mexico, Venezuela and Brazil) and dryness, and differing in their bat species pools.

We focus on phyllostomid bats for the following reasons: 1) they constitute the bat family with the greatest diversity, both taxonomical and functional in the Neotropics (Hutson et al. 2001), 2) they show specialized requirements for food, roosting sites and habitat selection that make them useful indicators of habitat change (Jones et al. 2009), and 3) they include the vast majority of Neotropical nectarivores and frugivores, guilds that play critical roles in ecosystem functioning (Hutson et al. 2001, Geiselman et al. 2002 onward, Lovoba et al. 2009).

We predict that: 1) Seasonal variations in phyllostomid assemblages will occur as a consequence of the marked seasonality of TDFs. 2) Assemblages in different successional stages will differ in terms of composition and structure. Greater differences will occur between the preserved forests and the secondary vegetation as gleaning insectivores and carnivores, mainly belonging to the subfamily Phyllostominae, are tightly associated with the preserved forest (Fenton et al. 1992, Medellín et al. 2000, Jones et al. 2009). In this sense, the region with the highest percentage of species belonging to these guilds will show the greatest difference among the successional assemblages. 3) Because of the above mentioned patterns, taxa belonging to the subfamily Phyllostominae will show a higher probability of being identified as indicators taxa of the most advanced successional stages. 4) Seasonal variations in the mechanisms determining phyllostomid assemblage composition are anticipated as a consequence of the strong seasonal variation in TDF environments.

2. Methods

2.1 Study area and sampling sites

The study was performed in three regions spanning a latitudinal gradient from north to south: 1) The central western coast of Mexico, in and surrounding the Chamela-Cuixmala Biosphere Reserve (hereafter CCBR) located in the state of Jalisco (19°22'–19°35'N, 104°56'–105°03'W, http://www.ibiologia.unam.mx/ebchamela /index.html); 2) The llanos of west-central Venezuela in Hato Piñero (hereafter HP), a natural area located in the state of Cojedes (8°40'–9°00'N, 68°00'–68°18'W, http://www.hatopinero.com/turismo/); and 3) The valley of the São Francisco River in Brazil, in and surrounding the Parque Estadual da Mata Seca (hereafter PEMS) located in the state of Minas Gerais (14°48'– 14°56'S, 43°55'– 44°04'W, IEF 2000).

These regions, with a markedly seasonal pattern of rainfall, represent a gradient of precipitation. In HP average annual precipitation is 1469 mm, with 86% of the rainfall occurring between May–October (Scognamillo et al. 2003). In PEMS average annual precipitation is 818 ± 242 (SD) mm, with most of the rainfall occurring during November–April (Madeira et al. 2009). In CCBR average annual precipitation is 763 ± 258 (SD) mm, with most of the rainfall occurring during June–October (Avila-Cabadilla et al. 2009). Average annual temperature of the three regions is approximately 25°C (http://www.ibiologia.unam.mx/ebchamela/index.html, Antunes 1994, Scognamillo et al. 2003).

In general, the landscape of the three regions is constituted by a mosaic of interdigitated forests and open areas, where vegetation types are defined based on interactions of elevation, substrate and hydrology, being water availability the most relevant source of environmental heterogeneity for plant establishment and growth (Mooney et al. 1995, Murphy and Lugo 1995, Balvanera et al. 2002). Tropical dry forest (sensu Holdridge 1947) constitutes the predominant vegetation type in these regions being mostly associated with rolling hills in CCBR and HP and with flat and nutrient–rich soils in PEMS (Lott 1993, IEF 2000). In all three regions small areas of tropical semi-deciduous forest occur along permanent rivers and temporary creeks. In HP, during the rainy season, up to 80% of the ranch is flooded with water depths ranging from a few centimeters to 1.5 m (Scognamillo et al. 2003).

Agriculture and cattle raising are the most important economic activities in the three regions but tourism is also important in CCBR and HP. As a consequence of these human activities, large areas of these landscapes are covered by cattle ranches, agricultural fields and patches of secondary vegetation representing different successional stages.

We used a chronosequence approach as a baseline for sampling site selection. In each region we selected twelve sampling sites (three sites per treatment) representing four successional stages differing in time since abandonment: pastures, early successional stages (3–5 years), intermediate successional stages (8–12 years in CCBR and 18–25 years on HP and PEMS), and late successional stages (at least 50 years old).

In general, pastures are dominated by non-native grasses and a few shrubs and treelets left standing for fencing and cattle shading. Early successional stage is characterized by an increasing presence of shrubs and the permanence of the non-native grasses and treelets. The height of the 10 tallest woody plants in this stage ranges from 5.00–6.60 m in PEMS and 3.50–7.00 m in CCBR to 0–16 m in HP. The higher heights found in some sites of HP are due to a few high trees left standing. In the intermediate successional stage, the vegetation shows increments in height, basal area and species number with respect to the early stage (Chazdon et al. 2007, Madeira et al. 2009). The height of the 10 tallest woody plants here ranges from 7.00–12.00 m in HP and 10.40 –13.20 m in CCBR to 14.30–15.40 in PEMS. Finally, the late successional sites present, on average, the most structurally complex vegetation and the highest species richness (pers. obs, Chazdon et al. 2007, Madeira et al. 2009, Chazdon et al. 2010). These forests have not suffered any significant human impact for at least 50 years and are now under state and/or national protection. The height of the 10 tallest woody plants in this stage ranges from 9-10 m in CCBR and 20 –22 m in HP to 20.–23 m in PEMS.

2.2 Bat sampling

Bat samplings were carried out employing a standardized set of 2.6 m high mist nets set at ground level. In CCBR, we employed a set of five mist nets— two 6 m, two 9 m and one 12 m long, the total sampling area was of 109 m^2 and the study period comprised from June 2004 to August 2006. In HP and PEMS we employed a set of 10 mist nets of 12 m long each, the total sampling area was of 312 m^2 and the study period comprised from July 2007 to April 2009 and from March 2007 to August 2009, respectively.

Mist nests were located crossing natural or artificial corridors (small corridors expanded with a machete) representing potential flyways for bats. Distance among nets was never shorter than 30 m. Samplings were always performed during the first 5 hours after sunset, the peak foraging time for most phyllostomid bats (Fenton and Kunz 1977). In order to avoid variation in capture success we sampled during non-rainy, non-windy and moonless nights. During each sampling period, the order of sampling for every site was randomized, performing a single sampling at each site in order to avoid biases due to the trap-shy behavior of bats.

Sampling efforts were distributed between the rainy and dry seasons. Seasons were defined in accordance with the precipitation regime during the study period. The RS was considered to begin one month after the first rain, while the DS was considered to begin one month after the last rain (Alvarez-Añorve et al. 2008). In CCBR sites were sampled 5 ± 1.6 (SD) nights during the RS and 9 ± 1.6 (SD) nights during the DS. In HP sites were sampled 4 ± 0.8 (SD) nights during the RS and 4 ± 0.3 (SD) nights during the DS. Finally, in PEMS sites were sampled 4 ± 0.8 (SD) nights during the RS and 7 ± 1.1 (SD) nights during the DS.

During samplings nets were checked every 30 min. All bats captured were stored in cloth bags. Pregnant females and juveniles were processed first and released. Bat species were identified based on the field guides of Timm and Laval (1998) and Medellín et al. (1997). We also considered the study of Nogueira (1998) carried out in Jaíba, Brazil. A small set of voucher specimens (1-5 individuals) belonging to species with uncertain identification were sacrificed and preserved in 70% ethanol for posterior analysis. With the exception of juveniles and non-healthy individuals, all captured bats were marked on their forearm with a numbered aluminum band. Despite the lack of information on possible differences in mist net capture efficiency for different phyllostomid species, we assume that capture data adequately reflect the relative abundance of all phyllostomids. Taxonomic designation of bat species follows Simmons (2005). We assigned bat species to broad guilds based on Kalko et al. (1996), Timm and Laval (1998), Castro-Arellano et al. (2007) and Reis et al. (2007). The recognized broad guilds for phyllostomids were: nectarivores, frugivores, gleaning insectivores, omnivores, carnivores and sanguivores. Our ensembles, sensu Fauth et al. (1996), are composed of phyllostomids belonging to the same guild.

2.3 Vegetation structure

Vegetation structure of each sampling site was characterized within a 0.10 ha (20 x 50 m) plot, considering all woody plants with a diameter at breast height (DBH) $\geq$ 5 cm (Alvarez-Añorve et al. 2008). The vegetation attributes measured were number of individuals, (NI), number of species (NS), and total basal area (BA).

2.4 Analysis

2.4.1 Bat sampling completeness

Sampling completeness per site was evaluated through the percentage of species captured in each site in relation to the site’s estimated species richness. Each season was considered separately. Species richness was estimated by using the first-order jackknife estimator in EstimateS (version 8.2, Colwell 2009). This estimator is based on incidence data considering the number of species occurring in a single sample (Magurran 2004). We selected it because it produces a low biased estimation of species richness even at small samples sizes (< 100 individuals per site, Colwell and Coddington 1994). In accordance with Moreno and Halffert (2001), we considered 90% of completeness a sufficient level of sampling efficiency.

2.4.2 Seasonal intra-site variation of phyllostomid assemblages

We analyzed bat assemblage seasonal variations in terms of species composition, structure, species richness and abundance. For this purpose, in each site we compared the RS phyllostomid assemblages versus the DS phyllostomid assemblages.

As a first step, in order to graphically represent assemblage attributes per site and per season, we built rank-abundance (dominance-diversity) graphs following Feinsinger (2001).We graphed the "$\log_{10}$ pi" (pi being the proportion of individuals of a given species relative to all captured individuals) versus the species ranked from left to right according to their relative abundance. This method allows visualizing some assemblage attributes such as species richness (number of points), evenness (slope), number of rare species (tail of the curve) and species relative abundance (order of the species in the graph). Indeed, plotting the "$\log_{10}$ pi" instead of the total number of captured individuals per species facilitates the comparison between curves differing in their total number of individuals.

In order to compare the species composition of RS and DS assemblages, we carried out a X^2 randomization test in the EcoSim software (version 7.72, Gotelli and Entsminger, 2010) using null models based on 1000 iterations. To compare assemblage structure (species rank distribution) between seasons, we performed the Kolmogorov-Smirnov test (Sokal and Rohlf 1995) in R (v.2.11.1, R Development Core Team, 2010). Species richness was compared by using the first-order jackknife estimator; the lack of overlapping of its 95% confidence intervals was considered an indicator of significant differences between RS and DS assemblages (Colwell et al. 2004). Finally, to compare bat abundance (average number of individuals captured per night) we performed a Monte Carlo permutation test in the R package "coin" (Hothorn et al. 2008, R Development Core Team 2010) generating the reference distribution with 10,000 rearrangements. The Monte Carlo method is useful to analyze unbalanced data as well as variables that are not distributed normally.

2.4.4 Phyllostomid occurrence in different successional stages

2.4.4.1 A metric reflecting the vegetation structural complexity

In order to obtain a continuous synthetic variable summarizing sampling site variation in terms of vegetation structural complexity, we performed a principal component analysis (PCA) considering NI, NS and BA. The new variable (axis 1 scores, Figure 1) was used as an explanatory variable for evaluating phyllostomid response to changes in vegetation structure.

The total variation explained by PCAs axis 1 was 0.93%, 0.86% and 0.94% for CCBR, HP and PEMS, respectively. All vegetation parameters considered in the PCAs were positively correlated with axis 1. The corresponding eigenvector values were: NI= 0.58, NS= 0.58 and BA= 0.57 for CCBR; NI= 0.57, NS= 0.58 and BA= 0.58 for HP, and NI= 0.58, NS= 0.57 and BA= 0.58 for PEMS. All analyses were performed in R v.2.11.1 (R Development Core Team 2010), using the "prcomp" function available in the stats package.

2.4.4.2 Hypotheses tests

Phyllostomid occurrence in the different sucesional stages during the RS and the DS was evaluated at the population, ensemble and assemblage-level. The RS and DS captures were analyzed separately. At the population and ensemble level we used the mean number of captured individuals per site and per season as an indicator of the abundance. Only species and ensembles with at least 10 captured individuals in each season were analyzed. At the assemblage-level, we used as response variables the species richness and four new synthetic variables reflecting the dissimilarities among phyllostomid assemblages in terms of species (two variables) and guild composition (two variables).

These new synthetic variables were the sampling sites scores in the axis 1 and 2 of two bidimensional ordinations obtained by mapping, with the non-metric multidimensional scaling (NMDS), the dissimilarities among phyllostomid assemblages in term of species (ordination 1) and guild composition (ordination 2). Both ordinations were based on Bray-Curtis similarity matrices of species and guilds (Magurran 2004).

The Bray-Curtis distance measure compared the assemblages in terms of species/guilds presence and abundance (Magurran 2004). For calculation of the Bray-Curtis coefficients, site data were standardized to the same abundance by dividing each cell abundance (species or guild abundance) by the total site abundance (total captured individuals in the site). In this way, we compared sampling sites in terms of species or guild proportions, ensuring that differences in total abundance among sites would not influence the results (Kindt and Coe 2005). All phyllostomids, including those scarcely represented (1 or 2 individuals), were considered in the analysis. Recaptures were not included. The degree of relation between each species/guild and the sampling sites was mapped by means of their weighted abundance average per site (Oksanen 2010).

The NMDS is one of the most appropriated ordination methods in community ecology (McCune & Grace 2002) as it can properly handle nonlinear species´ responses (Oksanen 2010), high beta diversity (McCune & Grace 2002) and data not adjusted to a particular underlying model (i.e. multivariate normality), which are common in community datasets (McCune & Grace 2002). The Bray-Curtis coefficient is preferred for analyzing differences in taxa composition as it assigns the same maximum distance to all pairs of sites not sharing any taxon (Kindt and Coe 2005) and can adequately reflect the intuitive ordering of sites (Kindt and Coe 2005).

We assessed the causal-explanatory relationships between all response variables and two explanatory variables, successional stage and vegetation structural complexity (scores of the PCA axis 1), through a hierarchical partitioning analysis (Chevan and Sutherland 1991). This is a regression technique where all possible GLMs combining the explanatory variables are jointly considered, in order to obtain a measure of the independent effect of each explanatory variable. For this purpose, the increment that certain explanatory variables generate in the model fitting is estimated by averaging the variable influence over the whole model (Chevan and Sutherland 1991, Mac Nally 2000). This procedure alleviates problems of multicollinearity between the explanatory variables (Chevan and Sutherland 1991, Mac Nally 2000). The significance ($\alpha = 0.05$) of the relationships between explanatory and response variables was evaluated through the randomization test suggested by Mac Nally (2002).

The abundance data used as response variables at the population and ensemble level, were modeled by using a Poisson error distribution with the log link function, while the response variables generated through NMDS were modeled using the Gaussian error distribution with the identity link function. When needed, the response variables were transformed in order to fit normality. In all cases the goodness of fit was based on log-likelihood.

It should be noted that CCBR pasture sites were not considered in the CCBR hypotheses tests due to the scarce number of samplings performed in them during the DS as a consequence of their very low capture rates. The CCBR late successional site L2 was not considered either in the hypothesis test evaluating the variation in phyllostomid assemblages in terms of species and guild composition, as no individuals was captured at this site during the DS. Zero values in captures result in a meaningless value of the Bray-Curtis coefficient. The HP pasture site P1, was also excluded from the corresponding hypotheses tests due to the small number of samplings performed at this site during the DS. Finally, the PEMS late successional site L3 was not considered in the PEMS hypotheses tests due to logistical problems in vegetation sampling.

All statistical analyses described in this section were performed in R (v.2.11.1, R Development Core Team 2010). We used the vegan package (Oksanen et al. 2011) for the Bray-Curtis coefficient calculation and NMDS ordinations (function “metaMDS” which is based on the function “isoMDS” available in the MASS package, Venables and Ripley 2002). Hierarchical partitioning analysis was performed utilizing the hier.part package (Walsh and Mac Nally 2008).

2.4.5 Phyllostomid bats as indicators of successional stages

Considering separately the DS and the RS, we evaluated if phyllostomid taxa (species, genus and subfamily) were associated with a certain successional stage, and therefore could be considered as indicators of that stage (in each season). For this purpose, we performed the "Indicator value analysis", proposed by Dufrene and Legendre (1997). This analysis was initially proposed as a possible stopping rule for the clustering of species data and has been used by ecologists for identification of indicator taxa (Castro-Luna et al. 2007, Roberts 2010). In general, an indicator value (IV) is assigned to each taxon, in each successional stage, based on the taxon's relative frequency of occurrence (presence-absence matrix) and relative abundance (abundance matrix). We then selected the maximum IV (IV_{max}) for each taxon and identified the corresponding successional stage. The IV_{max} statistical significance was evaluated through a Monte Carlo test based on 1000 iterations.

In accordance with previous studies (Van Resburg et al. 1999, Castro-Luna et al. 2007), we considered as detectors all taxa with an IV_{max} equal or greater than 0.50. Nevertheless, we only considered as indicators those taxa in which this IV_{max} value (equal or greater than 0.50) was statistically significant. Indicator taxa are characteristic of a particular habitat whereas detector taxa exhibit different degrees of preferences for different types of habitat and consequently are useful to indicate habitat change. The analysis was performed in the R package "labdsv, version 1.4-1" (R Development Core Team 2010, Roberts 2010).

2.4.6 Spatial phylogenetic structure of phyllostomid assemblages

In order to answer the question "are species found within a given site more related phylogenetically, on average, than species found in distinct sites?" we tested for spatial phylogenetic structure of phyllostomid assemblages. In this way we evaluated if processes like habitat filtering and competitive exclusion are determining the assembly of phyllostomid assemblages along our successional gradients. Analyses were performed separately for the RS and DS to take into account the sites´ seasonal variations in resource availability and environmental conditions, as well as the possible seasonal variations occurring as a consequence of phyllostomid assemblages.

We used the phylogram of Baker et al. (2003) to establish the taxonomic relationships among phyllostomid species and genera. The correspondent branch lengths were obtained by using the “Distance Tool” available in PDF-XChange-Viewer (version 2) and the scale provided by Baker et al. (2003). To construct proper regional species pools, including all phyllostomid species that can potentially occur in the sampling sites, we considered the species registered in our sampling period plus other species reported by previous studies in each region (for PEMS: Nogueira 1988 and for CCBR: Miranda 2002, Stoner 2005). Most of the species previously reported were registered in our samples as we reached a high level of sampling completeness during the study.

For each region we built a regional “supertree” (Figure 8), which is a phylogram containing the regional species pool and constitutes the base of all subsequent statistical analyses testing for spatial phylogenetic structure. Species not represented in Baker’s phylogram were located substituting the position of their corresponding genera. Regional “supertrees” were built by using Mesquite (v.2.74, Maddison and Maddison 2010) and TreeGraph (v.2.0.45-197 beta, Stöver and Müller 2010) and exported in Newick format for statistical analysis.

We tested for non-random spatial phylogenetic structure following Cavender-Bares et al. (2004). Specifically, we assessed whether there was a significant correlation between the phylogenetic distance of pairs of taxa and their degree of co-ocurrence within the plots. For this purpose we conformed a matrix of phylogenetic distances between species, by summing all branch lengths between each pair of species, as well as a matrix of pairwise values of co-ocurrence, by using the co-ocurrence index DO_{ij} presented by Hardy (2008). This index is considered a standardized version of the “checkerboard score” of Stone and Roberts (1990), and is defined as:

$DO_{ij} = (P_{ij} – P_i*P_j)/(P_i*P_j)$

where P_i, P_j and P_{ij} are, respectively, the proportions of sites where species i, species j and both species occur. This metric is considered a measure of the difference between the observed and expected number of sites where both species are observed, because the product $P_i^*P_j$ can be viewed as the expectation of P_{ij} under independent distribution of species i and j (Hardy 2008). According to the results obtained by Hardy (2008), the correlation analysis based on the DO_{ij} metric are the most robust under most simulated conditions, using a variety of null models. A positive correlation coefficient indicates phylogenetic overdispersion (co-occurring species are phylogenetically distant) and a negative coefficient indicates phylogenetic clustering (co-occurring species are phylogenetically close). The significance of the correlation coefficient was evaluated by comparing the observed correlation coefficient to the distribution of correlation coefficients obtained through six different null models (all the null models available on the R package “Picante”, Kembel et al. 2010) with 1,000 randomizations. These null models were (sensu Picante package): I) **sample.taxa.labels—**shuffle phylogeny tip labels only within the set of taxa in the community, II) **pool.taxa.labels—** shuffle phylogeny tip labels across all the taxa included in the phylogenetic tree, III) **frequency—** randomize the species abundances, maintaining species occurrence frequency, IV)**richness—** randomize species abundances within samples maintaining sample species richness; V) **independentswap—** randomize community data matrix maintaining species occurrence frequency and site species richness by using independent swap, and VI) **trialswap—** randomize community data matrix maintaining species occurrence frequency and site species richness by using trial swap. The null models break down any association between species phylogeny and co-occurrence (Hardy 2008). All statistical analyses were performed in the R package "Picante" (Kembel et al. 2010).

3. Results

3.1 Bat capture description and sampling completeness

In the CCBR, 142 samplings were carried out in total, 62 during the RS and 77 during the DS. In total we captured 606 phyllostomid individuals representing 15 species, 11 genera, 5 subfamilies and 4 broad guilds (Figure 2, also see Avila-Cabadilla et al. 2009). The individuals classified as *Artibeus intermedius* in Avila-Cabadilla et al. (2009) were re-classified as *Artibeus lituratus* based on Redondo et al. (2008) and Hoofer et al. (2008). Nine of the 15 species were captured in both seasons while 6 were exclusively captured during the RS: *Micronycteris microtis*, *Choeroniscus godmani*, *Musonycteris harrisoni*, *Centurio senex*, *Chiroderma salvini* and *Carollia* sp.

In HP, during 94 sampling nights (50 in the RS and 43 in the DS), we captured 996 phyllostomid individuals representing 30 species, 17 genera, 5 subfamilies and 6 broad guilds (Figure 3). Most of the species were captured in both seasons, with the exception of 6 (*Micronycteris hirsuta*, *Mimon bennettii*, *Mimon crenulatum*, *P. stenops*, *Tonatia saurophila*) and 3 species (*A. lituratus*, *M. microtis*, *Vampyrum spectrum*) that were exclusively captured during the DS and the RS respectively.

Finally, in PEMS we conducted 130 samplings (46 during the RS and 84 during the DS), capturing 808 phyllostomid individuals classified in 21 species, 16 genera, 5 subfamilies and 6 broad guilds (Figure 4). Due to dubious differentiation between *Carollia perspicillata* and *Carollia brevicauda*, we decided to group both species into the single taxon *Carollia* spp. This taxon was used as a unit during analyses. Most of the 21 species were captured in both seasons, excluding two species in the RS (*Chiroderma villosum, Mimon bennetti*) and three species (*Anoura geoffroyi*, *Artibeus cinereus*, *Sturnira lilium*) in the the DS.

The sampling effort per region and per season was considered sufficient to adequately characterize the phyllostomid bat assemblages occurring in each of the sampling sites. Completeness reached 90% in all cases. The average completeness values per season were 97% (90 to 100%) during the RS and 97% (93–99%) during the DS for CCBR; 97% (95–100%) during the RS and 97% (94–100%) during the DS for HP; and 98% (91–100%) during the RS and 96% (91–100%) during the DS for PEMS.

Species composition differed among the study regions. The highest differences occurred between Mexico and Brazil which shared only 4 species (Jaccard's index = 0.13); the lowest differences occurred between Venezuela and Brazil which shared 10 species (Jaccard's index = 0.25). Mexican and Venezuelan sites shared 7 species (Jaccard's index = 0.18).

The differences among the study regions were also evident in terms of the percentage of species representing each subfamily and broad guild (representativeness, Figure 5). Although the same 5 subfamilies were represented in the 3 study regions, in CCBR the best represented subfamilies were the Sternodermatinae and Glossophaginae, whereas in HP and PEMS the best represented were the Phyllostominae and Stenodermatinae (Figure 5). The regions also differed in the number, type and representativeness of the broad guilds (Figure 1). Five broad guilds are represented in the Venezuelan and Brazilian samples: omnivores, carnivores, gleaning insectivores, nectarivores, frugivores and sanguivores. Only the last four are present in the Mexican samples. Similarly, there are major differences among the regions in terms of the representativeness of the gleaning insectivores and nectarivores. In the CCBR, the first are poorly represented (just one species), whereas in HP and PEMS they are the second most speciose guild.

Nectarivores, in contrast, constitute one of the most speciose guild in CCBR, but is poorly represented in HP and PEMS. Frugivores are the most speciose guild in all three regions.

3.2 Seasonal intra-site variation of phyllostomid assemblages

For CCBR, the main seasonal variations in phyllostomid assemblages occurred in species richness and abundance. A significant reduction of species richness was detected during the DS in 5 sites: E1, I1, L1, L2, L3 (Figure 6). Bat abundance also showed a significant reduction in 6 of the 9 sites (Figure 7): E1 (*Z*: -2.661, *p*: 0.000), E2 (-2.307, 0.026), E3 (-1.864, 0.024), I1 (-2.37, 0.020), L2 (-2.121, 0.013) and L3 (-2.072, 0.034). A tendency toward a reduction in bat abundance during the DS was observed in the site L1 (*Z*: -1.940, *p*: 0.062), as well. With regard to seasonal variations in species composition, significant variations occurred only in the site E3 as showed by the X^2 randomization test (observed index value (OI) 41.730, mean of simulated indices (SI) 14.817, p: 0001). In most of the sites (E1, E2, E3, I2, I3, L1, and L3), the most abundant species during the RS were also the most abundant species during the DS (Figure 2). Nevertheless, we also identified species exclusively represented in a single season for most of the plots; the highest number of these species occurred during the RS in E1, E2, I1, L1, L2 and L3. Most assemblages were dominated by *Artibeus jamaicensis* and *Glossophaga soricina* during the RS and by *A. jamaicensis* during the DS (Figure 2). The assemblage structure did not show any significant seasonal variation in the CCBR sites.

In the HP, the main seasonal variation in phyllostomid assemblages occurred in the species composition of 8 sites: P2 (OI: 23.172, SI: 13.017, p: 0.040), P3 (OI: 38.778, SI: 20.902, p: 0.014), E1 (OI: 70.501, SI: 32.762, p: 0.000), E2 (OI: 73.244, SI: 38.641, p: 0.000), E3 (OI: 50.953, SI: 35.504, p: 0.043), I1 (OI: 69.666, SI: 31.148, p: 0.000), I3 (OI: 51.598, SI: 29.216, p: 0.014) and L3 (OI: 98.662, SI: 37.448, p: 0.000). In three sites (L1, L2 and L3) the most abundant species during the RS were also the most abundant during the DS (Figure 3); in four other sites (E2, I1, I2, I3), the most abundant species in one season were among the most abundant species in the other season, but in a different rank order, whereas in the remaining sites (P2, P3, E1, E3) no pattern was detected. Species exclusively represented in a single season occurred in all sites; the highest numbers of these species were registered during the RS (P2, P3, E1, E3, I1, I2, L2, L3). Most of the assemblages were dominated by *Phyllostomus elongatus* during the RS (Figure 3) and with a diverse arrangement of species (*S. lilium*, *Glossophaga longirostris*, *Uroderma bilobatum*, *Platyrrhinus vittatus* and *P. elongatus*) during the DS. Regarding species richness, seasonal variations were only detected in P3 (Figure 6), with the lowest level reached during the DS. A seasonal variation in the assemblage structure was only detected in the L3 site (D: 0.563, p: 0.026). Finally, no significant seasonal variation in bat abundance occurred in the HP sites, but in I3 and L3 we detected a tendency toward reduced abundance in the DS (Z= -1.791, p= 0.087 and Z =1.815, p =0.055 respectively; Figure 7).

In general, for most of the PEMS sites, we did not detect a marked seasonal variation in assemblage attributes. A significant seasonal variation in species composition occurred only in one site, L1 (OI: 78.999, SI: 25.191, p: 0.000). In most sampling sites (P1, P2, E1, E2, E3, I1, I2, I3, L1, L2, L3) the most abundant species in the RS season were among the most abundant in the DS (Figure 4). Species exclusively reported in a single season occurred in almost all sampling sites (P1, E1, E2, I1, I2, I3, L1, L2 and L3) with the highest numbers of these species during the DS (P1, P2, P3, E1, E3, I2, I3, L3). Most of the assemblages were dominated by *Desmodus rotundus* and *Carollia* spp. during the RS and by *Artibeus planirostris*, *Carollia* spp. and *D. rotundus* (Figure 4) during the DS. In relation to species richness, we did not detect significant seasonal changes in most sampling sites (P1, E1, E2, I1, I2, I3, L1 and L2, Figure 6); only four sites (P2, P3, E3, L3) showed changes with the assemblages reaching higher species richness during the DS (Figure 6). Seasonal variations in bat abundance were not detected for any PEMS site (Figure 7);

we only detected a tendency in E2 (Z: -1.732, p: 0.078) toward a reduction in abundance during the DS (Figure 7). Finally, no significant seasonal variation in assemblage structure was registered at any PEMS site.

3.3 Phyllostomid occurrence in different successional stages

Ensemble and species level response

We found different responses among the three regions, specifically between HP versus CCBR and PEMS, concerning the occurrence of frugivorous bats in the different successional stages at both ensemble and population levels. In HP, frugivore abundance (Table 1) was significantly higher in the early successional stage. This stage showed higher total frugivore abundance (during DS), as well as higher abundance of the species *U. bilobatum* (during the RS and DS) and *Uroderma magnirostrum* (during the DS, Appendix 5). However, variations of some frugivorous populations in this region were more tightly associated with variation in vegetation structural complexity than to successional stage (Table 1). This is the case of *A. jamaicensis*, *C. brevicauda* and *P. vittatus* that, during the RS, reached their highest abundance in sites with higher vegetation complexity (Table 1). In contrast, *Sturnira lilium* abuncance was negatively related to structural vegetation complexity during the DS. No marked differences among successional stages in frugivore abundance were observed in the CCBR and PEMS, although highest abundances were always found in late successional sites.

Regarding nectarivore abundance, we detected a similar response in CCBR and PEMS. In both regions nectarivore abundance was significantly different among successional stages (Table 1), being higher at both the ensemble and population level (i.e. *G. soricina*) in the early successional sites (Appendix 4 and 6). These differences occurred during the RS in CCBR and during the DS in PEMS. Nectarivore abundance did not differ among the successional stages of HP.

Gleaning insectivore abundance did not differ among successional stages in PEMS and HP, the two regions in which this variation was evaluated (Table 1). Nevertheless, during the DS of HP the variation in gleaning insectivore abundance was positively related to variations in vegetation structural complexity (Table 1). However, some gleaning insectivorous species tended to be more represented in the early and intermediate sites of this region (i.e. *Lophostoma brasiliense, Trachops cirrhosus*, *Phylloderma stenops*). The unique individual representing this guild in the CCBR was captured during the RS in a late successional site (Figure 2).

The occurrence of the omnivorous bat guild showed different responses between HP and PEMS, the two regions in which they were found. In HP their occurrence was significantly different among successional stages (Table 1) and the highest abundance, at both the ensemble and population level, was achieved in the early and intermediate sites. Higher total abundance in these successional stages occurred during both seasons whereas the abundance of a single species, *P. elongatus,* differed just in the DS (Appendix 5). In PEMS, in contrast, omnivore abundance did not differ among successional stages (Table 1).

The abundance of *D. rotundus,* the unique sanguivorous species analyzed in the three regions, showed different responses among these regions (Table 1). In CCBR, the variation in their abundance was not associated with any explanatory variable; however, in HP, its abundance differed significantly among successional stages during the RS, being greatest in early successional sites (Appendix 5). Finally, in PEMS, the abundance of *D. rotundus,* as well as the abundance of all sanguivores, was significantly higher in sites with higher vegetation structural complexity during the DS (Table 1).

Assemblage level response

The variation among the phyllostomid assemblages occurring in the different successional stages, in terms of species and guild composition, was different for each region (Table 1). In

CCBR, most of the variation was explained by successional stage. The guild composition of late successional assemblages differed significantly during the RS, from that of early and intermediate assemblages (Appendix 3 and 4). The species composition of late successional assemblages also differed significantly from that of early and intermediate assemblages during the RS, but during the DS differences in assemblage species composition were registered between early succession and intermediate-late succession (Appendix 1 and 4). In the case of HP, variations among assemblage species and guild composition were explained by variations of the vegetation structural complexity among sites in both seasons (Table 1). Nevertheless, similar to what we found in CCBR during the RS the differences in assemblage guild composition were also explained by successional stage with late successional assemblages differing significantly from early and intermediate assemblages (Appendix 3 and 5). Finally, in PEMS, assemblage variation in terms of species and guild composition was not significantly related to successional stage vegetation structural complexity (Table 1, Appendix 1, 3).

Assemblage variation in terms of species richness also is explained differently for each study region. Neither the type of successional stage, nor variations in vegetation structural complexity significantly explained the differences in species richness among the CCBR sites (Table 1). In HP, however, early successional sites showed the highest species richness for both seasons (Table 1, Appendix 5). Finally, in PEMS, variation in assemblage species richness was positive and significantly associated with variations in vegetation structural complexity for both seasons (Table 1).

3.4 Phyllostomid bats as indicators of successional stages

In general, we found only a few taxa that can be considered indicators of successional stages (only five taxa, Table 2). In HP, *D. rotundus* and *T. cirrhosus* were tightly associated with the early successional sites during the RS whereas, during the DS, the taxa tightly associated with this stage were *U. magnirostrum* and the genera *Uroderma*. In the dry season *D. rotundus* was tightly associated with the intermediate stage. In PEMS, *Phyllostomus hastatus* was tightly associated with the late successional sites during the DS. Most taxa were indicators during a single season and only *D. rotundus* was an indicator during both seasons.

In general, we identified a greater number of detector taxa than indicator taxa (Table 2). In the CCBR, all detector species were nectarivores (*G. soricina*, *Glossophaga commissarisi*, *Leptonycteris yerbabuenae*) and were associated with the early successional sites. In HP, some frugivores were identified as detector taxa and also were associated with early successional sites (*U. bilobatum*, *U. magnirostrum*, *S. lilium*, *Platyrrhinus helleri*, *C. perspicillata*). Some Phyllostominae species were also associated with early (*T. cirrhosus*), intermediate (*L. brasiliense*) and late successional stages (*Micronycteris nicefori, M. crenulatum*) in this region. Finally, in PEMS, all detector species were associated with the late successional sites. Among them are represented frugivores (*A. planirostris*, *A. cinereus*, *P. stenops*), omnivores (*P. hastatus*, *Phyllostomus discolor*), sanguivores (*D. rotundus* and *Diphylla ecaudata*), nectarivores (*G. soricina*) and carnivores (*Chrotopterus auritus*).

In most cases, species exclusively captured in a given successional stage (asterisks on Table 2) were not recognized as indicator or detector taxa. Only *M. crenulatum* (in HP, DS) and *C. auritus* (in PEMS, RS), exclusively found in late successional sites, were considered detectors.

3.5 Spatial phylogenetic structure in phyllostomid assemblages

In CCBR and HP, we detected, only during the RS, a negative and significant correlation between the phylogenetic distance of pairs of species and their degree of co-occurrence within the plots (Table 3), which is an indication of phylogenetic clustering. On the other hand, in PEMS we did not detect any evidence of spatial phylogenetic structure neither during the RS nor during the DS.

4. Discussion

4.1 Seasonal intra-site variation on phyllostomid assemblages

As expected, we found evidence of seasonal variation in phyllostomid assemblage attributes in the three study regions. These variations occurred at both regional and sampling site levels. In the three regions we found species that were exclusively captured during a single season. In CCBR and HP most of these species were found during the RS whereas in PEMS they were found during the DS.

The seasonal variations found in phyllostomid assemblages could be a consequence of the marked seasonality in the precipitation regime of these TDFs (Scognamillo et al. 2003, Avila-Cabadilla et al. 2009, Madeira et al. 2009). The seasonal change in water availability provokes distinctive plant phenological patterns, changes in the primary productivity (Frankie et al. 1974, Opler et al. 1980, Quesada et al. 2009) and consequently seasonal variations in vegetation structure and bat resource availability (i.e. food and roosts) (Kalacska et al. 2005, Stoner 2005). As mentioned before, bats confront this seasonal variation in key resources through behavioral changes in diet breadth, type of food, patterns of habitat use and defense of feeding areas, as well as through migratory behavior (Heithaus et al. 1975, Whitaker and Black 1976, Bonaccorso 1979, Thomas 1983, Fleming and Heithaus 1986, Arroyo-Cabrales et al. 1987, Cockrum 1991, Wilkinson and Flemings 1996, Herrera et al 2001, Tschapka 2004). These behavioral changes appear to be reflected in the seasonal changes encountered in bat assemblages (i.e. species richness, composition and abundance). However, the nature and intensity of these seasonal variations were different among regions. The most marked variations, for example, were detected in CCBR where species richness and abundance of most assemblages significantly decreased during the DS. In HP and PEMS, in contrast, these parameters did not change between seasons in most of the assemblages. These differences among regions are probably a consequence of their environmental particularities. The CCBR presents the lowest level of precipitation (see methods), as well as the lowest amount of available water across the year–the main source of water around sampling sites consists of temporary rivers and creeks (semi-permanent, seasonally drying water bodies). Migration would be one of the most important behavioral adaptations of CCBR mammals to deal with water and food availability reductions during the DS (Miranda 2002). As bats are one of the mammals with the highest capability of movement (i. e. *A. jamaicensis* covers up to ten kilometers in a single night, Morrison 1978), their seasonal migration to resource rich areas would explain their reduction in species richness and abundance during the DS. Latitudinal migration has in fact been well documented in the region for the species *Leptonycteris yerbabuenae* (Cockrum 1991), whose seasonal migration to northern latitudes is tightly associated with the regional reduction in food availability (Ceballos et al. 1997, Stoner et al. 2003). In contrast, bats inhabiting in HP and PEMS can find permanent sources of water year around in regional rivers and lagoons: Laguna Grande lagoon at HP (located at 100 m from sampling sites) and Lagoa da Prata lagoon and São Francisco river at PEMS (located at 900 m from sampling sites). This would constitute the main reason explaining the non significant seasonal changes in species richness and abundance of HP and PEMS.

Finally, the significant seasonal changes in species composition of HP phyllostomid assemblages, appear to be a distinctive feature of this type of habitat. In 2003, Aguirre et al. reported for a similar environment in Bolivia, forest islands embedded in a seasonally flooded savanna, a high species turnover even among years. This turnover was higher in the group of species relying on seasonal food resources, suggesting that species turnover was explained by variations in food availability.

4.2 Phyllostomid occurrence in different successional stages

We found a high level of specificity in phyllostomid occurrence across the chronosequence depending on the species and guild identity, the season and the region. In general, we detected just a few patterns concerning phyllostomid occurrence across the different successional stages.

Ensembles and populations

The specificity of phyllostomid response to habitat change associated with succession is based on the contrasting ecological requirements among bat species and guilds. For example, frugivore abundance was higher in the early stage at HP but it did not show a marked differentiation among sucesional stages at CCBR or PEMS. The pattern observed in HP, which is the region with the highest average annual precipitation (1469 mm, Scognamillo et al. 2003), is indeed more similar to what has been observed in more humid forests (Brosset et al. 1996, Schulze et al. 2000), where frugivore abundance also is higher in the early successional stages. Several individuals of chiropterochorous species belonging to the genera *Annona*, *Cecropia* and *Ficus* are found in the HP early successional sites (Nassar et al. unpublished data). Chiropterochorous species are common in early succession of tropical wet and rainy forest (Fleming 1988, Charles-Dominique 1986, Brosset et al. 1996). In the Colombian Amazon, for example, individuals from the chiropterochorous genera *Cecropia*, *Miconia*, and *Vismia* accounted for 87% of the stems present in an area abandoned after three years of slash and burn agriculture (Lobova et al. 2009). Moreover, differences in frugivore responses among regions could be explained by differences in regions' environmental characteristics (i.e. precipitation regime) reflected in the species composition of their early successional plant assemblages. In this sense, the absence of this pattern in CCBR and PEMS, the TDFs with the lowest average annual precipitation (763 and 818 mm respectively), would be related to an early successional stage dominated by anemochorous plants (Vieira and Scariot 2006) which do not constitute food resources for frugivorous bats.

Regarding nectarivorous bats, we found a similar response in the two TDFs with the lowest precipitation regime (CCBR and PEMS). In both regions, nectarivore abundance was significantly higher, at both the ensemble and population level (*G. soricina*), in the early successional sites characterized by the presence of shrubs and some non-native grasses. This likely is related to: 1) the capacity of the most abundant nectarivores (CCBR: *G. soricina*, and *L. yerbabuenae;* PEMS: *G. soricina*) to forage and exploit resources in areas where vegetation has a simple structure (Avila-Cabadilla et al. in preparation), and 2) the higher representation of chiropterophilic plants in the early successional stages of both study sites; these plants belong mainly to the genera *Acacia* and *Cordia* (Alvarez and González-Quintero 1970, Alvarez and Sanchez- Casa 1997, Tellez and Ortega 1999, Geiselman et al. 2002 onward).

Contrary to expected, the occurrence of gleaning insectivores did not differ among successional stages in the two regions in which they were analyzed (HP and PEMS). Gleaning insectivore occurrence appears to be more tightly associated with variation in vegetation structural complexity as found in HP (Table 2). This causal/explanatory relationship may be explained by the guilds' high specialization for foraging (gleaning insects from leaves or other surfaces in a highly cluttered space, Kalko et al. 1996) and for roosting (large, shaded leaves, termite nests and hollow trees, Medellín et al. 2000). In fact, we found great variation among sites representing the same successional stage in terms of vegetation structural complexity; in some cases, sites representing different successional stages were more similar in vegetation structure to each other, than sites representing the same successional stage (Figure 17). Moreover, some species thought to be mainly associated with the most advanced sucesional stages, were found in earlier stages (in HP: *L. brasiliense*, *T. cirrhosus*, *P. stenops*) which, as a consequence of specific environmental conditions and land-use history, presented a structurally complex vegetation.

Omnivorous and sanguivorous bat occurrence in the different successional stages showed a high variability among regions. In the case of omnivores, this variability may be associated with the high diversity of food resources they use (Kalko et al. 1996, Reis et al. 2007), as well as regional differences in the type and distribution of such resources. A further detailed analysis of omnivore preferences in each region must be performed in order to identify the "drivers" determining their distribution. On the other hand, factors explaining the inter-regional variation in sanguivore response (*D. rotundus*) to habitat change could be related to the variable distribution of cattle, a non-native source of food preferentially used by *D. rotundus* in anthropogenic tropical landscapes, as well as to differences in the distribution and coverage of riparian vegetation around the sampling sites. Riparian vegetation can determine sanguivore distribution in anthropogenic landscapes (Avila-Cabadilla et al, in preparation) for the following reasons: 1) it offers roosting sites and can be used as stepping stones when bats search for food in the vegetation matrix where cattle occur, 2) it presents a higher availability of sanguivores native food sources—medium and large-sized mammals that concentrate their activities in riparian vegetation when resources are limited in TDF, and 3) farmers concentrate cattle in riparian areas, especially when water availability is scarce.

Assemblages

Although we hypothesized that the regions with a high proportion of Phyllostominae would show greater differences among successional stages, as this subfamily is mainly associated with late succession, the region with the highest proportion of Phyllostominae (HP), did not show differences in assemblage species and guild composition among successional stages On the contrary, the region with the poorest representation of Phyllostominae (CCBR, with only 1 individual of *Micronycteris microtis* which was found in late succession), presented the highest differentiation in assemblage species and guild composition among successional stages.

Our results probably reflect the specific nature of the factors determining the occurrence of most species. In HP, for example, variation among assemblage composition is mainly explained by variations in the vegetation structural complexity; this is congruent with our finding that variation in the abundance of the speciose gleaning insectivores, also is explained by changes in the vegetation structural complexity, and not by the type of successional stage. In the same sense, we found that some of the most abundant frugivores in the region also respond to changes in vegetation structure (*A. jamaicensis*, *C. brevicauda*, and *P. vittatus*, Table 1).

In CCBR, in contrast, the occurrence of several species appears to be determined by successional stage. This is the case of the three most abundant nectarivores which occur in higher abundance in the early stage (Table 1, Figure 2, Avila-Cabadilla et al. in preparation) and of the species exclusively captured in late successional sites (*Carollia* sp., *C. senex*, *C. salvini*, *C. godmani, M. microtis, M. harrisoni,* Figure 2, Avila-Cabadilla et al. 2009). These species together represent 67% of all the species reported in CCBR during our study.

In general, no consistent pattern was detected in relation to phyllostomid species richness in the different successional stages. Whereas in CCBR none of the explanatory variables were significantly related to the variation in species richness, in HP this parameter was explained by successional stage and in PEMS it was explained by vegetation structural complexity. These differences among the regions must be caused by inter-regional variations in other non-measured factors besides the intrinsic attributes of successional stages and sampling sites. These factors are probably mostly associated with attributes of the landscape surrounding the study sites.

In CCBR, we detected a high intra successional stage variation in assemblage species richness. This variation was not explained by differences in vegetation structure among sites. The late successional site, L2, for example, is one of the most preserved and structurally complex sites where rare species, mainly associated with preserved forests (*C. salvini*, *C. senex)* occur (Estrada et al. 1993, Avila-Cabadilla et al. 2009). However, different from that observed in other late successional sites, L2 presents a low species richness which in fact is reduced to zero during the DS. The patterns found for HP, on the other hand, can be related to the proximity of a permanent source of water (Laguna Grande lagoon) to two of the three sites representing the early stage (E1 and E2); both of which are approximately 100 m from the lagoon. This water source is especially important in attracting species from the subfamily Phyllostominae (the most speciose group in the region) because of its higher concentration of prey items (i.e. insects, frogs, and other small vertebrates). In the case of PEMS, the positive relationship detected between assemblage species richness and vegetation structural complexity, is congruent with the findings of Medellín et al. (2000), who also observed this positive relationship. A higher vegetation structural complexity can offer a higher diversity of resources (i.e. food and roosts) allowing for the occurrence of a greater number of species.

4.3 Phyllostomid bats as indicators of successional stages

In general, we found a small number of species that can be considered indicator taxa for a given sucessional stage: *D. rotundus*, *T. cirrhosus*, *U. magnirostrum* and the genus *Uroderma* in HP; *P. hastatus* in PEMS (Table 2) and none in CCBR. Although we hypothesized that several indicator taxa would belong to the subfamily Phyllostominae and consequently would be associated with the late successional stages, only two of six indicator species belong to this subfamily (*T. cirrhosus* and *P. hastatus*).Most indicator taxa, including the Phyllostominae *T. cirrhosus*, were tightly associated with the early and intermediate successional stages. Only the Phyllostominae *P. hastatus* (PEMS, Table 2) was indicative of the late stage. Actually, we found that species exclusively found in late successional stages (Table 2) were not good indicators of this stage. This was mainly due to their low abundance and/or poor incidence (i.e. occurring in just one of the three sites representing this stage). In this sense, Castro-Luna et al. (2007) also found a reduced number of indicator taxa in a tropical moist forest, when evaluating the usefulness of phyllostomid bats as indicators of old-growth forest and patches of secondary vegetation. They concluded that phyllostomids were poor ecological indicators under the disturbance conditions characterizing their study area (which is quite similar to ours).

In this scenario, within a landscape conformed by vegetation patches representing different successional stages, agricultural fields, pasturelands and preserved forests, most bats fail as indicator taxa at a local scale because of their prominent vagility. Phyllostomids have the capacity to move between forest patches and between forest and agricultural islands within the landscape. Estrada et al. (1993) found that 77% of the bat species detected (most of them Phyllostomids) in a tropical rain forest landscape transformed by human activities, were also present in at least one habitat other than the rain forest. They suggest that forest patches and agricultural islands can be used by bats as stepping stones for their movement across the landscape. Some Phyllostomid species such as *A. jamaicensis*, can fly great distances in a single night (8 ± 2 km, Morrison 1978), allowing them to exploit resources in different areas, including those with a certain degree of disturbance (Avila-Cabadilla et al. 2009). Furthermore, the occurrence of bats in a particular vegetation fragment is not exclusively determined by the attributes of the habitat at a local scale (i.e. species composition of plant assemblages, vegetation complexity, fragment area), but also by the constitution of the vegetation matrices around the fragments (specifically by how favourable these matrices are for bat movement) and, ultimately, by the characteristics of the disturbance (i.e. origin, scale, intensity, and duration, Estrada et al. 1993, Gorresen et al. 2005, Bernard and Fenton 2007, Castro-Arellano et al. 2007). In this sense, Klingbeil and Willig (2009) found that the occurrence of frugivores in a fragment was determined by the landscape composition (i.e. percentage of forest, mean patch density) while the abundance of gleaning animalivores was determined by the landscape configuration (i.e. edge density). They suggest that the increase in frugivore abundance in areas with a reduced canopy cover could be explained by the higher occurrence of chiropterochoric plants in such areas, whereas the animalivores abundance was favored in areas with low-contrast edges; these areas allowed them to forage and travel between high quality resources patches.

Although Phyllostominae are characteristic of preserved forests and are considered good indicators of habitat change at a local scale (Fenton et al. 1992, Medellín et al. 2000, Castro-Luna et al. 2007, Jones et al. 2009), we only found a few species belonging to this subfamily that were associated with the late successional stage: *M. nicefori* and *M. crenulatum*, catalogued as detector species in HP; *P. stenops*, *P. discolor* and *C. auritus*, catalogued as detector species in PEMS and *P. hastatus,* catalogued as an indicator species in PEMS as well. The occurrence of this subfamily appears to be affected by non-local factors, as well. For example, in the case of HP, the occurrence of several Phyllostominae (*Micronycteris megalotis, M. microtis, Micronycteris minuta, M. nicefori*, *Micronycteris schmidtorum*, *M. bennettii*, *P. elongatus*, *P. hastatus*, *T. saurophila, T. cirrhosus*, *V. spectrum*, Figure 3) in the early stage can be related to both local habitat attributes (i.e. high vegetation complexity of sites E2 and E3, Figure 1) and landscape attributes (i.e. the small lagoon next to sites E1 and E2). We also found great intra-stage variability in vegetation complexity (Figure 1) that could preclude a high association between the Phyllostomid taxa significantly responding to changes in this parameter (i.e. subfamily Phyllostominae) and a given successional stage.

Nevertheless, the most abundant nectarivorous species *G. soricina, G. commissarisi* and *L. yerbabuenae* can be considered detector species of habitat change in CCBR. These species increase their abundance toward early successional stages, probably due to their capacity for foraging in areas with a simple vegetation structure and to the abundance of chiropterophilic species in these sites. In the same sense, the frugivores *U. bilobatum*, *U. magnirostrum*, *S. lilium*, *P. helleri* and *C. perspicillata*, were also catalogued as detectors in HP as they were moderately associated with the early stage which presents a high abundance of chiropterochoric species (*Annona*, *Cecropia* and *Ficus*).

4.4 Spatial phylogenetic structure in phyllostomid assemblages

The phylogenetic clustering found during the rainy season in CCBR and HP, suggests that during this season some mechanisms generate non-random patterns of phylogenetic structure in phyllostomid assemblages of these regions. These assemblages are constituted by a non-random subset of the regional species pool that could potentially occur in the sampling sites. No evidence of phylogenetic structure was found neither during the DS in these regions nor in PEMS during both seasons.

The phylogenetic clustering observed is probably determined by environmental conditions of the habitat which favor the co-occurrence of phylogenetically related species sharing similar ecological traits (i.e. same type of diet). This assumption is supported by two facts: 1) the phylogenetically related species tend to resemble each other with respect to their type of diet (phylogenetic signal in the trophic guild), and 2) several studies have documented the bats guild-specific response to habitat modification.

The distribution of the type of diet among Phyllostomid species is often confounded with phylogeny as diet categories often represent separate subclades. Giannini and Kalko (2004), for example, found a general agreement between diet and phylogeny when analyzing the trophic structure of a large assemblage of phyllostomid bats: discrete diet groups were compatible with several clades of two phylogenetic hypotheses. In a similar way, we found a phylogenetic signal in the type of diet (trophic guild, Appendix 7) for the three study regions as the phyllostomid species phylogenetically related tended to be categorized in the same trophic guild.

With respect to the guild-specific response of bats to habitat modification, several studies in Neotropical areas have reported a reduction in the occurrence of gleaning insectivores in disturbed habitats (Fenton et al. 1992, Brosset et al 1996, Medellín et al. 2000, Bernard and Fenton 2003, Castro-Arellano et al. 2007), as well as an increment in frugivore abundance (in moist and rain forests) in anthropogenic habitats as a consequence of the higher abundance of chiropterochorous species in these habitats (Brosset et al. 1996, Ochoa 2000, Clarke et al. 2005, Faria 2006, Peters et al. 2006, Mancina et al. 2007). Recently, in the Amazonian, Klingbeil and Willig (2009) found that frugivore abundance responded to variations in landscape composition during the DS and to variations in landscape configuration in the RS, whereas animalivore abundance responded to variations in the landscape configuration during the DS and to variations in the landscape composition during the RS. This constitutes another example of a seasonal-guild specific response to variations in landscape attributes (composition and configuration).

In our case, for CCBR (RS) and PEMS (DS), we detected a higher occurrence of nectarivores in the early successional sites, probably as a consequence of the chiropterophilic species occurring in these sites. In HP (DS), on the other hand, the early sites presented a higher abundance of frugivores probably as a consequence of their chiropterochoric species. At the assemblage level, we found, in CCBR and HP (RS), differences in the guild composition of the assemblages occurring in different successional stages. Note that this is precisely when we also found evidence of spatial phylogenetic structure in these regions (RS).

In general, we found no evidence of negative interactions (competitive exclusion) between sympatric species; these interactions could produce phylogenetic overdispersion in the phyllostomid assemblages. In fact, the mobile nature of bats decreases the intensity, pervasiveness and predominance of this type of interaction (Willig and Moulton, 1989). Consequently, species occurrence and the structure of the assemblages in sites of different successional stages, should be mainly determined by habitat characteristics such as vegetation structure and resource availability, as well as by specific ecological requirements of the species. As Stevens and Willig et al. (2000) pointed out, competitively induced assemblage structure may exist only under narrow temporal and environmental conditions, and would not be characteristic of assemblage organization in most situations. Nevertheless, it is important to note that Moreno et al. (2006) found that frugivorous bat morphological assembly mechanism is different from random patterns. This suggests that some ecological processes, such as competitive exclusion, could determine species richness and structure of bat ensembles at local scale. We could not directly evaluate the spatial phylogenetic structure at the ensemble level because of a low resolution in the phylogenetic tree at the genus level.

4.5 The effect of seasonality on phyllostomid response to habitat change

We have found a marked seasonal specificity on bats' response to habitat change. Most bat responses previously discussed were specific of a determined season (Table 1) and just six were consistent between seasons: 1) the higher abundance of *U. bilobatum* in the early successional stage of HP, 2) the higher abundance of omnivores in this same stage, 3) the higher species richness of the early successional assemblages of HP, 4) the positive association between the variation in assemblage species richness and the variation in the vegetation structure of PEMS sites, 5) the association between the variation in assemblage species and guild composition and the variation in vegetation structure of HP sites, and 6) the differences in assemblage species composition between the early and late successional stages of CCBR.

Additionally, analyzing the incidence and abundance of phyllostomid taxa in sites of different successional stages (indicator value analysis), we encountered that any indicator taxon can function as an indicator of the same successional stage during both seasons. Only a few detector species were moderately associated with the same successional stage independently of the season: *U. bilobatum*, *T. cirrhosus* (early stage) and *L. brasiliense* (late stage) in HP and *C. auritus* (late stage) in PEMS. The association of most of the detectors with a given successional stage was affected by seasonality.

We also have evidence (in CCBR and HP) that the processes determining assemblage species composition at a local scale are affected by seasonality as well. The phylogenetic clustering found in CCBR and HP during the RS shows that assemblage species composition could be determined by the availability of resources as a given resource would attract phylogenetically related species with similar ecological requirements (i.e. type of food).

Plant assemblage species composition and phenological patterns could define the seasonal fluctuations in the abundance and diversity of bat resources (roosts and food) and in the environmental conditions (i.e. vegetation structure) of the successional sites/stages. In this sense, Fernández-Hernández (2008) and Pezzini (2008) reported differences in the frequency, seasonality and duration of plants' leafing, flowering and fruiting, among different successional stages of CCBR and PEMS respectively. These differences may determine seasonal differences in the association between phyllostomids and successional stages or vegetation structural characteristics. Bats can deal with this fluctuation in key resources and environmental conditions, as explained before, through changes in their diet breadth, type of food, food intake rate, patterns of habitat use, and defense of feeding areas, as well as through migratory behavior (Heithaus et al. 1975, Whitaker and Black 1976, Bonaccorso 1979, Thomas 1983, Fleming and Heithaus 1986, Arroyo-Cabrales et al. 1987, Cockrum 1991, Wilkinson and Flemings 1996, Herrera et al 2001, Tschapka 2004). Moreover, seasonal changes in bat foraging behavior and home range size, can also be caused by their seasonal breeding pattern, characteristic of a high percentage of Neotropical phyllostomid bats (Klingbeil and Willig 2010).

The seasonal-specific response of bats to habitat change would then be explained by the markedly seasonal variation in the availability of resources and environmental conditions characteristic of TDFs.

5. Conclusions

In general, we found a high level of specificity in phyllostomid response to habitat change. Climate distinctiveness, the specific ecological requirements and behavior of bat species in each regional species pool, the composition and structure of plant assemblages associated with different successional stages, the particular phenological patterns of these plant assemblages, as well as the specific landscape composition and configuration within each region, constitute important sources of variation determining the absence of solid patterns among the study regions.

Consequently, in order to reach a better understanding about phyllostomid distribution in anthropogenic landscapes, as well as about the ecological processes underlying their assemblages at local scales, we must extend our focus beyond the characterization of their habitat at a local scale (i.e. classification of different successional stages, quantification of the vegetation structure complexity). Future studies should include the characterization of landscape attributes (composition and configuration) because the occurrence of vagile species in a particular area appears to be greatly influenced by these attributes (Estrada et al. 1993, Estrada and Coates-Estrada 2001, Gorresen and Willig 2004, Meyer and Kalko 2008, Klingbeil and Willig 2009, Klingbeil and Willig 2010, Avila-Cabadilla in preparation). Based on our findings, we conclude that, in tropical seasonal environments, it is extremely necessary to account for seasonal variations in environmental conditions and in the abundance and diversity of resources (emphasizing plant phenological patterns). This will allow us to understand the seasonal dynamics in the use of the space by phyllostomid populations, ensembles and assemblages, especially in those regions suffering from severe forest conversion (Klingbeil and Willig 2010).

By adopting this approach, we will gain a better understanding about the ecology and status of bats in the increasingly abundant anthropogenic landscapes. Landscape level patterns emerging from these integrative studies, will allow us to generate models that may be extrapolated to different tropical regions. This would constitute an invaluable tool for the preservation of bat biodiversity and the key ecological processes they perpetuate in transformed landscapes.

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TABLES

Table 1. Percentage of variation explained by successional stage (S_{stage}) and vegetation structural complexity (V_{struct}: sampling sites scores on PCA axis 1) per season, for the response variables analyzed in three regions (CCBR: Chamela-Cuixmala Biosphere Reserve, HP: Hato Piñeiro, and PEMS: Parque Estadual da Mata Seca). Seasons are the rainy season (RS) and the dry season (DS). The response variables at the population level are: ARJAM, ARPLA, ARLIT, ARPHA, PLVIT, STLIL, URBIL, URMAG, CABRE, CAPER, CAspp, GLSOR, GLLON, MICRE, MISAN, PHELO, PHSTE and DEROT which represent the average number of individuals of the species *Artibeus jamaicensis*, *A. planirostris*, *A. lituratus, A. phaeotis*, *Platyrrhinus vittatus*, *Sturnira lilium, Uroderma bilobatum*, *Uroderma magnirostrum*, *Carollia brevicauda*, *C. perspicillata*, *Carollia* spp, *Glossophaga soricina*, *G. longirostris*, *Mimon crenulatum*, *Micronycteris sanborni*, *Phyllostomus elongatus, Phylloderma stenops*, and *Desmodus rotundus* respectively, captured per site per night. At the ensemble level, the response variables are: F, N, GI, O, and S which correspond to the average number of frugivorous, nectarivorous, gleaning insectivorous, omnivorous, and sanguivorous individuals respectively, captured per site per night. At the assemblage level the response variables are: Species (NMDS1), Species (NMDS2), Guild (NMDS1), Guild (NMDS2) and Jack 1. The first four represent the scores of the first and second NMDS axis reflecting site dissimilarities according to the species and guild composition; Jack 1 is the estimator of species richness. Significant relationships appear in bold. Negative relationships among variables are shown in parentheses. R^2_{dev} is the fraction of the total deviance explained by the model considering all explanatory variables, using the Poisson error distribution, and R^2 is the fraction of the total variance in the response variable explained by the model using the normal error distribution.

Table 2. Species, genera and subfamilies of phyllostomid bats considered as indicator and detector taxa in each season at each study region. Species exclusively found in a single successional stage are also presented (*). Seasons and study regions are as in Table 1. Significant p-values (< 0.05) based on Monte Carlos tests with 1000 iterations, appear in bold. SS is the successional stage at which each taxa reach its maximum indicator value (IV): E= early I= intermediate and L= late. Guilds are: N= nectarivores, F= frugivores, GI= gleaning insectivores, C= carnivores, S= sangivores, and O= omnivores.

Table 3. Results of the correlation test between the phylogenetic distance of pairs of taxa and their degree of co-occurrence within the plots in each season at the three study regions. Seasons and study regions are as in Table 1. r: correlation coefficient. Significant relationships employing six null models (I to VI) appear in bold (see the method section for null models description).

Table 1.

Response variable	Guild	n	R^2	Explanatory variable	
				S_{stage}	V_{struct}
CCBR					
RS					
ARJAM	F	9	0.109	56.014	43.986
ARLIT	F	9	0.406	84.957	15.043
ARPHA	F	9	0.274	21.280	78.720
GLSOR	N	9	0.795	**81.649**	18.351 (-)
DEROT	S	9	0.386	86.598	13.402
F		9	0.231	57.805	42.195
N		9	0.723	**79.907**	20.093 (-)
Species (NMDS1)		8	0.515	80.029	19.971 (-)
Species (NMDS2)		8	0.809	**73.786**	26.214 (-)
Guild (NMDS1)		8	0.494	62.957	37.043
Guild (NMDS2)		8	0.795	**76.667**	23.333
Jack1		9	0.450	37.919	62.081
DS					
ARJAM	F	9	0.148	31.247	68.753
ARLIT	F	9	0.710	40.279	59.721
ARPHA	F	9	0.310	53.140	46.860
GLSOR	N	9	0.035	37.213	62.787
DEROT	S	9	0.531	56.360	43.641
F		9	0.151	32.391	67.609
N		9	0.033	17.259	82.741
Species (NMDS1)		8	0.612	**83.060**	16.940
Species (NMDS2)		8	0.235	18.687	81.313
Guild (NMDS1)		8	0.493	82.633	17.367
Guild (NMDS2)		8	0.224	77.950	22.050
Jack1		9	0.141	49.571	50.428

Table 1. continued…

Response variable	Guild	n	R^2	Explanatory variable	
				S_{stage}	V_{struct}
HP					
RS					
ARJAM	F	11	0.903	8.789	**91.211**
CABRE	F	11	0.662	7.631	**92.369**
CAPER	F	11	0.452	2.398	97.602
PLVIT	F	11	0.483	2.264	**97.736**
STLIL	F	11	0.612	35.111	64.889 (-)
URBIL	F	11	0.760	**73.936**	26.064
URMAG	F	11	0.440	10.602	89.398 (-)
GLLON	N	11	0.293	4.636	95.364
PHELO	O	11	0.579	82.433	17.567
DEROT	S	11	0.690	**99.086**	0.914
F		11	0.304	2.341	97.659
N		11	0.312	2.345	97.655
GI		11	0.418	31.505	68.495
O		11	0.729	**98.638**	1.362
Species (NMDS1)		11	0.945	2.363	**97.636**
Species (NMDS2)		11	0.411	2.718	97.281 (-)
Guild (NMDS1)		11	0.192	90.685	9.315
Guild (NMDS2)		11	0.858	**58.686**	**41.314** (-)
Jack1		11	0.484	**90.031**	9.969
DS					
ARJAM	F	11	0.730	88.060	11.940
CABRE	F	11	0.707	43.213	56.787
CAPER	F	11	0.598	46.001	53.999
PLVIT	F	11	0.388	45.905	54.095
STLIL	F	11	0.868	35.694	**64.306** (-)
URBIL	F	11	0.792	**98.841**	1.159
URMAG	F	11	0.847	**94.272**	5.728 (-)
GLLON	N	11	0.111	79.880	20.120
PHELO	O	11	0.356	**96.636**	3.364
DEROT	S	11	0.772	6.683	93.317
F		11	0.615	**99.324**	0.676
N		11	0.219	48.959	51.041
GI		11	0.614	2.151	**97.849**
O		11	0.355	**96.662**	3.338
Species (NMDS1)		11	0.748	5.666	**94.334**
Species (NMDS2)		11	0.187	68.993	31.007
Guild (NMDS1)		11	0.336	66.824	33.176
Guild (NMDS2)		11	0.438	8.227	**91.773**
Jack1		11	0.769	**69.956**	30.043

Table 1. continued**…**

Response variable	**Guild**	**n**	***R*^{2}**	**Explanatory variable** S_{stage}	**Explanatory variable** V_{struct}
PEMS					
RS					
ARPLA	F	11	0.667	4.548	95.452
Caspp	F	11	0.537	50.232	49.768
PHSTE	F	11	0.236	1.390	98.610
GLSOR	N	11	0.626	39.984	60.016
MICRE	GI	11	0.519	7.941	92.059
MISAN	GI	11	0.527	76.143	23.857
DEROT	S	11	0.603	1.066	**98.934**
F		11	0.649	17.290	82.710
N		11	0.711	48.691	51.309
S		11	0.631	1.165	**98.835**
GI		11	0.537	16.460	83.540
O		11	0.463	52.639	47.361
Species (NMDS1)		11	0.365	2.698	97.302 (-)
Species (NMDS2)		11	0.743	61.826	38.173
Guild (NMDS1)		11	0.437	2.461	97.539 (-)
Guild (NMDS2)		11	0.529	258.500	158.500
Jack1		11	0.665	1.763	**98.237**
DS					
ARPLA	F	11	0.648	46.314	53.686
Caspp	F	11	0.537	66.407	33.592
PHSTE	F	11	0.393	47.561	52.439
GLSOR	N	11	0.554	**84.394**	15.606
MICRE	GI	11	0.341	88.855	11.145 (-)
MISAN	GI	11	0.279	95.206	4.794
DEROT	S	11	0.653	2.062	97.938
F		11	0.700	10.950	89.050
N		11	0.375	**97.417**	2.583
S		11	0.673	5.333	94.667
GI		11	0.039	8.557	91.443 (-)
O		11	0.706	45.337	54.663
Species (NMDS1)		11	0.274	2.336	97.663
Species (NMDS2)		11	0.269	56.951 (-)	156.951
Guild (NMDS1)		11	0.264	18.636	81.364
Guild (NMDS2)		11	0.447	0.119 (-)	100.119
Jack1		11	0.679	6.876	**93.124**

Table 2.

Region	Guild	SS	IV	p-value
CCBR				
Species (RS)				
Glossophaga soricina	N	E	0.771	0.118
Glossophaga commissarisi	N	E	0.618	0.182
Leptonycteris yerbabuenae	N	E	0.592	0.196
Micronycteris microtis	GI	L*	0.333	1
Choeroniscus godmani	N	L*	0.333	1
Musonycteris harrisoni	N	L*	0.333	1
Centurio senex	F	L*	0.333	1
Chiroderma salvini	F	L*	0.333	1
Carollia sp	F	L*	0.333	1
Genus (RS)				
Glossophaga	N	E	0.805	0.129
Subfamily (RS)				
Glossophaginae		E	0.817	0.124
HP				
Species (RS)				
Uroderma bilobatum	F	E	0.705	0.080
Artibeus jamaicensis	F	L	0.698	0.166
Lophostoma brasiliense	GI	I	0.667	0.192
Micronycteris nicefori	GI	L	0.600	0.144
Carollia brevicauda	F	L	0.597	0.111
Desmodus rotundus	S	E	0.593	**0.033**
Trachops cirrhosus	GI	E	0.583	**0.049**
Chiroderma salvini	F	L*	0.333	1.000
Vampyrum spectrum	C	E*	0.333	1.000
Species (DS)				
Uroderma magnirostrum	F	E	0.875	**0.030**
Uroderma bilobatum	F	E	0.805	0.064
Desmodus rotundus	S	I	0.759	**0.025**
Sturnira lilium	F	E	0.700	0.103
Platyrrhinus helleri	F	E	0.692	0.061
Artibeus jamaicensis	F	I	0.600	0.145
Carollia perspicillata	F	E	0.500	0.182
Glossophaga soricina	N	L	0.500	0.225
Mimon crenulatum	GI	L*	0.667	0.184
Lophostoma brasiliense	GI	I	0.636	0.096
Trachops cirrhosus	GI	E	0.600	0.101
Phylloderma stenops	F	I*	0.333	1.000
Genus (RS)				
Artibeus	F	L	0.640	0.339
Carollia	F	L	0.556	0.153

Table 2. continued…

Region	Guild	SS	IV	p-value
HP				
Genus (DS)				
Uroderma	F	E	0.826	**0.014**
Mimon	GI	L	0.500	0.232
Subfamily (RS)				
Carollinae		L	0.556	0.157
Subfamily (DS)				
Stenodermatinae		E	0.542	0.079
PEMS				
Species (RS)				
Chrotopterus auritus	C	L*	0.667	0.160
Phylloderma stenops	F	L	0.643	0.064
Desmodus rotundus	S	L	0.614	0.109
Artibeus planirostris	F	L	0.568	0.110
Diphylla ecaudata	S	L	0.533	0.345
Glossophaga soricina	N	L	0.500	0.204
Species (DS)				
Phyllostomus hastatus	O	L	0.847	**0.016**
Artibeus cinereus	F	L	0.667	0.181
Chrotopterus auritus	C	L	0.667	0.201
Phyllostomus discolor	O	L	0.657	0.188
Sturnira lilium	F	P*	0.333	1.000
Anoura geoffroyi	N	E*	0.167	1.000
Genus (DS)				
Phyllostomus	O	L	0.682	0.091
Subfamily (RS)				
Desmodontinae		L	0.550	0.134

Table 3.

Region$_{(SEASON)}$	r	p-value I	II	III	IV	V	VI
CCBR$_{(RS)}$	-0.183	0.110	0.130	**0.017**	**0.043**	**0.008**	**0.008**
CCBR$_{(DS)}$	-0.039	0.397	0.459	0.405	0.419	0.744	0.713
HP$_{(RS)}$	-0.109	0.055*	**0.043**	**0.025**	**0.048**	**0.012**	**0.018**
HP$_{(DS)}$	0.043	0.771	0.782	0.783	0.782	0.695	0.709
PEMS$_{(RS)}$	0.141	0.795	0.804	0.968	0.861	0.993	0.992
PEMS$_{(DS)}$	0.047	0.783	0.745	0.721	0.710	0.486	0.483

***** Marginally significant

FIGURES

Figure 1. Sampling site scores on PCA axis 1 reflecting the site's vegetation structural complexity in the three study regions: The Chamela-Cuixmala Biosphere Reserve (black bars), Hato Piñeiro (gray bars) and Parque Estadual da Mata Seca (white bars). Sampling sites representing different successional stages are: from P1 to P3= pastures, from E1 to E3= early stage, from I1 to I3= intermediate stage and from L1 to L3= late stage.

Figure 2. Rank-abundance curves of the phyllostomid assemblages occurring in the Chamela-Cuixmala Biosphere Reserve sampling sites during the rainy (A) and the dry season (B). Sampling sites are as in figure 1. Numbers represent species captured according to the following list in which the species subfamily (St: Stenodermatinae, Gl: Glossophaginae, Ph: Phyllostominae, Cr: Carolliinae, Ds: Desmodontinae) and foraging guild (F: Frugivore, N: Nectarivore, GI: Gleaning Insectivore, S: Sanguivore) are also specified in parentheses. 1: *Artibeus jamaicensis* (St, F), 2: *A. lituratus* (St, F), 3: *A. watsoni* (St, F), 4: *A. phaeotis* (St, F), 5: *Carollia sp* (Cr, F), 6: *Centurio senex* (St, F), 7: *Chiroderma salvini* (St, F), 8 : *Choeroniscus godmani* (Gl, N), 9: *Desmodus rotundus* (Ds, S), 10: *Glossophaga commissarisi* (Gl, N), 11: *G. soricina* (Gl, N), 12: *Micronycteris microtis* (Ph, GI), 13: *Leptonycteris yerbabuenae* (Gl, N), 14: *Sturnira lilium* (St, F) and 15: *Musonycteris harrisoni* (Gl, N).

Figure 3. Rank-abundance curves of the phyllostomid assemblages occurring in Hato Piñeiro sampling sites during the rainy (A) and the dry season (B). Sampling sites are as in Figure 1. Numbers represent species captured according to the following list in which the species subfamily (St: Stenodermatinae, Gl: Glossophaginae, Ph: Phyllostominae, Cr: Carolliinae, Ds: Desmodontinae) and foraging guild (F: Frugivore, N: Nectarivore, GI: Gleaning Insectivore, C:

Carnivore, O: Omnivore, S: Sanguivore) are also specified in parentheses. 1: *Artibeus jamaicensis* (St, F), 2: *A. lituratus* (St, F), 3: *Carollia brevicauda* (Cr, F), 4: *C. perspicillata* (Cr, F), 5: *Chiroderma salvini* (St, F), 6: *C. villosum* (St, F), 7: *Desmodus rotundus* (Ds, S), 8: *Glossophaga longirostris* (Gl, N), 9: *G. soricina* (Gl, N), 10: *Micronycteris megalotis* (Ph, GI), 11: *M. microtis* (Ph, GI), 12: *M. minuta* (Ph, GI), 13: *M. nicefori* (Ph, GI), 14: *M. schmidtorum* (Ph, GI), 15: *Phyllostomus elongates* (Ph, O), 16: *P. hastatu*s (Ph, O), 17: *Platyrrhinus helleri* (St, F), 18: *P. vittatus* (St, F), 19: *Sphaeronycteris toxophyllum* (St, F), 20: *Sturnira lilium* (St, F), 21: *Lophostoma brasiliense* (Ph, GI), 22: *Trachops cirrhosus* (Ph, GI), 23: *Uroderma bilobatum* (St, F), 24: *U. magnirostrum* (St, F), 25: *Vampyrum spectrum* (Ph, C), 26: *Microncyteris hirsuta* (Ph, GI), 27: *Mimon bennettii* (Ph, GI), 28: *M. crenulatum* (Ph, GI), 29: *Phylloderma stenops* (Ph, F), 30: *Tonatia saurophila* (Ph, GI).

Figure 4. Rank-abundance curves of the phyllostomid assemblages occurring in the Parque Estadual da Mata Seca sampling sites during the rainy (A) and the dry season (B). Sampling sites representing different successional stages are as in Figure 2. Sampling sites are as in Figure 1. Numbers represent species captured according to the following list in which the species subfamily (St: Stenodermatinae, Gl: Glossophaginae, Ph: Phyllostominae, Cr: Carolliinae, Ds: Desmodontinae) and foraging guild (F: Frugivore, N: Nectarivore, GI: Gleaning Insectivore, C: Carnivore, O: Omnivore, S: Sanguivore) are also specified in parentheses. 1: *Artibeus lituratus* (St, F), 2: *A. planirostris* (St, F), 3: *Carollia spp*, grouping *C. brevicauda* and *C. perspicillata* capture data (Cr, F), 4: *Chiroderma villosum* (St, F), 5: *Chrotopterus auritus* (Ph, C), 6: *Desmodus rotundus* (Ds, S), 7: *Diphylla ecaudata* (Ds, S), 8: *Glossophaga soricina* (Gl, N), 9: *Lonchophylla mordax* (Gl, N), 10: *Lophostoma brasiliense* (Ph, GI), 11: *Micronycteris sanborni* (Ph, GI), 12: *Mimon bennettii* (Ph, GI), 13: *M. crenulatum* (Ph, GI), 14: *Phylloderma stenops* (Ph, F), 15:

Phyllostomus discolor (Ph, O), 16: *P. hastatus* (Ph, O), 17: *Tonatia bidens* (Ph, GI), 18: *Anoura geoffroyi* (Gl, N), 19: *A. cinereus* (St, F), 20: *Sturnira lilium* (St, F).

Figure 5. Percentage of the total species number for each subfamily (A) and broad guild (B, F: Frugivore, N: Nectarivore, GI: Gleaning Insectivore, C: Carnivore, O: Omnivore, S: Sanguivore) in the three study regions (CCBR: Chamela-Cuixmala Biosphere Reserve, HP: Hato Piñeiro, and PEMS: Parque Estadual da Mata Seca).

Figure 6. Species richness estimated with the first-order jackknife estimator, per site and per season (triangles= rainy season, circles= dry season), at the three study regions (A= CCBR, B= HP and C= PEMS). Sampling sites are as in Figure 1. Error bars represent the confidence intervals of the estimated values.

Figure 7. Average number of phyllostomid individuals captured each night (±95% confidence intervals), per site and per season (triangles= rainy season, circles= dry season), at the three study regions (A= CCBR, B= HP and C= PEMS). Sampling sites are as in Figure 1.

Figure 8. Baker´s phylograms including just the phyllostomid species present at each study region. Species not captured during samplings are marked with an asterisk. Species and the acronyms used in the phylograms are: *Anoura geoffroyi* (ANGEO), *Artibeus cinereus* (ARCIN), *Artibeus hirsutus* (ARHIR), *Artibeus jamaicensis* (ARJAM), *Artibeus planirostris* (ARPLA), *Artibeus lituratus* (ARLIT), *Artibeus phaeotis* (ARPHA), *Artibeus toltecus* (ARTOL), *Artibeus watsoni* (ARWAT), *Carollia brevicauda* (CABRE), *Carollia perspicillata* (CAPER), *Carollia* sp (CAsp), *Centurio senex* (CESEN), *Chiroderma salvini* (CHSAL), *Chiroderma villosum* (CHVIL), *Choeroniscus godmani* (CHGOD), *Chrotopterus auritus* (CHAUR), *Desmodus rotundus*

(DEROT), *Diphylla ecaudata* (DIECA), *Glossophaga commissarisi* (GLCOM), *Glossophaga longirostris* (GLLON), *Glossophaga soricina* (GLSOR), *Leptonycteris yerbabuenae* (LEYER), *Lonchophylla mordax* (LOMOR), *Lophostoma brasiliense* (LOBRA), *Macrotus waterhousii* (MAWAT), *Micronycteris hirsuta* (MIHIR), *Micronycteris megalotis* (MIMEG), *Micronycteris microtis* (MIMIC), *Micronycteris minuta* (MIMIN), *Micronycteris sanborni* (MISAN), *Micronycteris schmidtorum* (MISCH), *Mimon bennettii* (MIBEN), *Mimon crenulatum* (MICRE), *Musonycteris harrisoni* (MUHAR), *Phylloderma stenops* (PHSTE), *Phyllostomus discolor* (PHDIS), *Phyllostomus elongatus* (PHELO), *Phyllostomus hastatus* (PHHAS), *Platyrrhinus helleri* (PLHEL), *Platyrrhinus lineatus* (PLLIN), *Platyrrhinus vittatus* (PLVIT), *Sphaeronycteris toxophyllum* (SPTOX), *Sturnira lilium* (STLIL), *Tonatia bidens* (TOBID), *Tonatia saurophila* (TOSAU), *Trachops cirrhosus* (TRCIR), *Trinycteris nicefori* (TRNIC), *Uroderma bilobatum* (URBIL), *Uroderma magnirostrum* (URMAG), *Vampyrum spectrum* (VASPE).

Figure 1

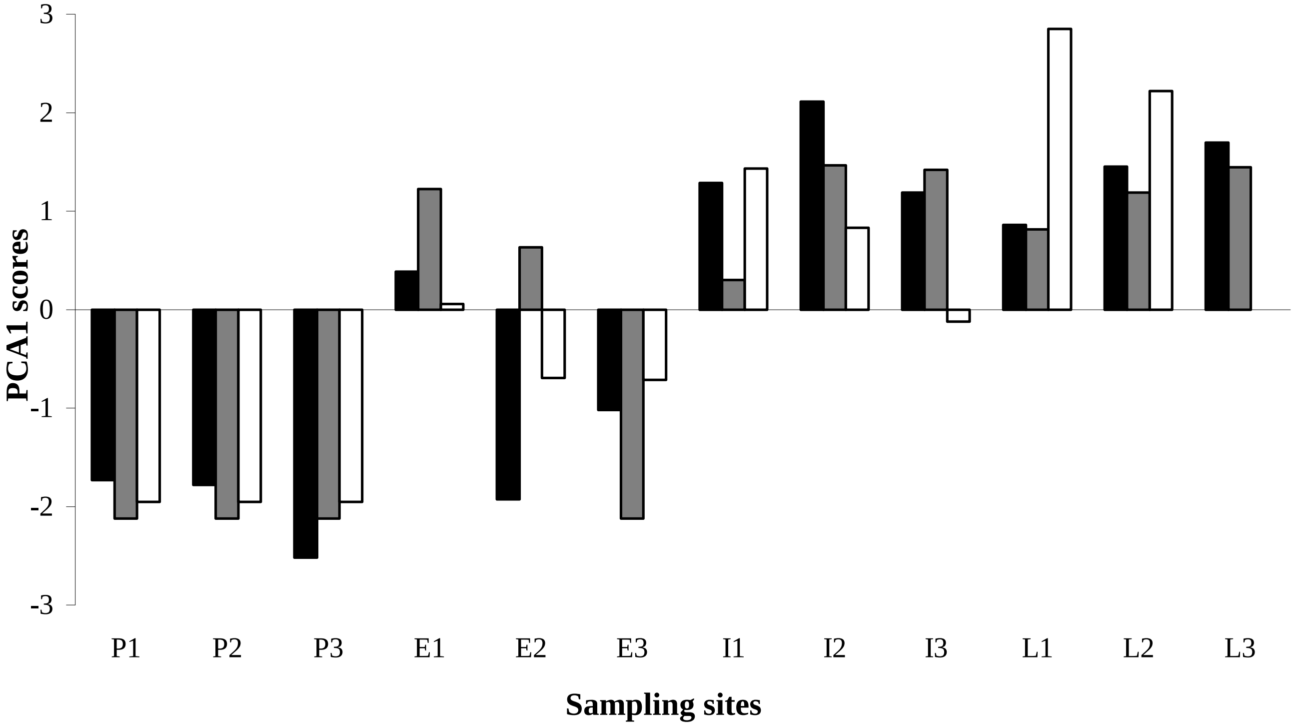

3
2
1
0
-1
-2
-3
PCA1 scores
P1
P2
P3
E1
E2
E3
I1
I2
I3
L1
L2
L3
Sampling sites

Figure 2

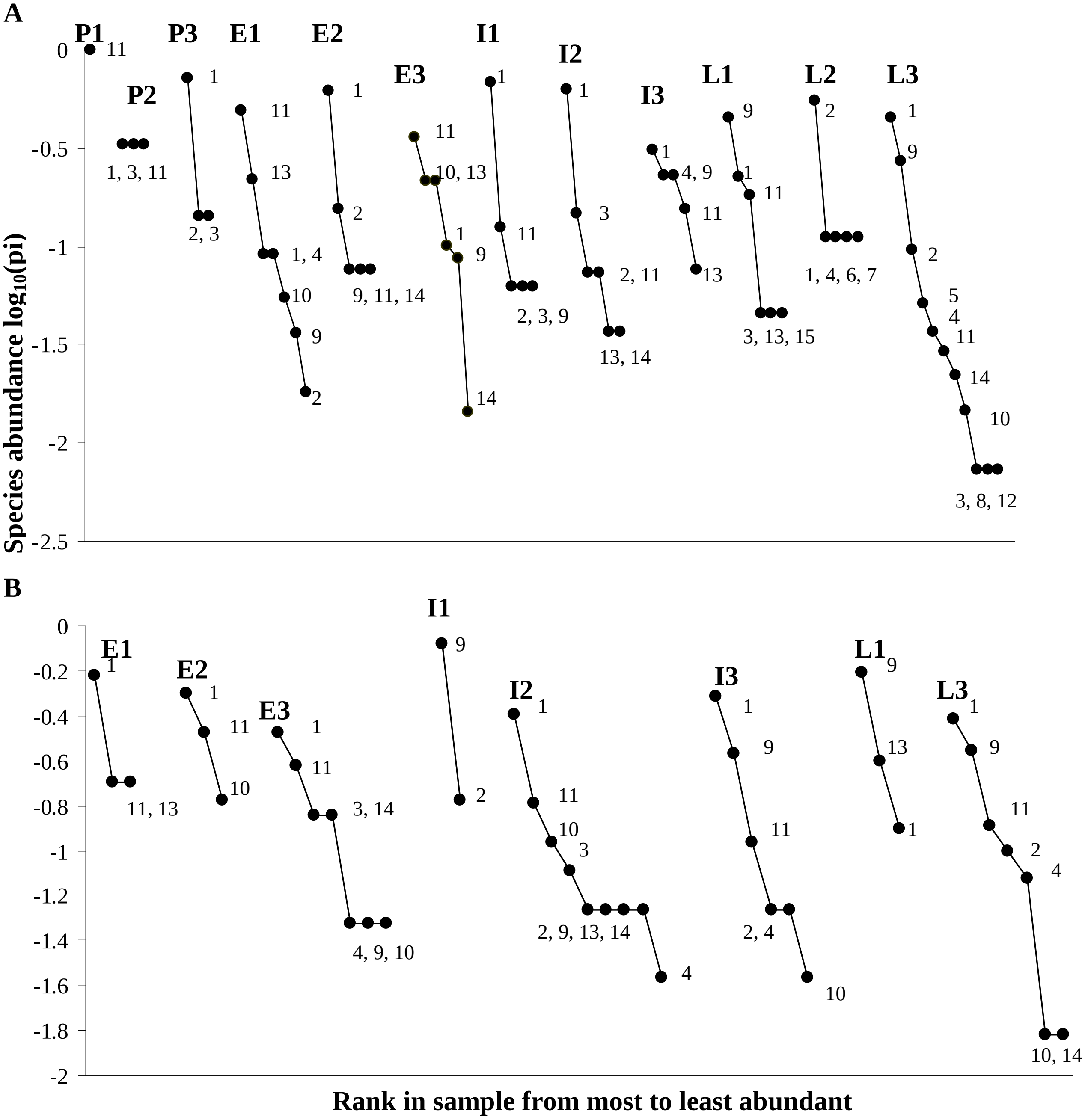
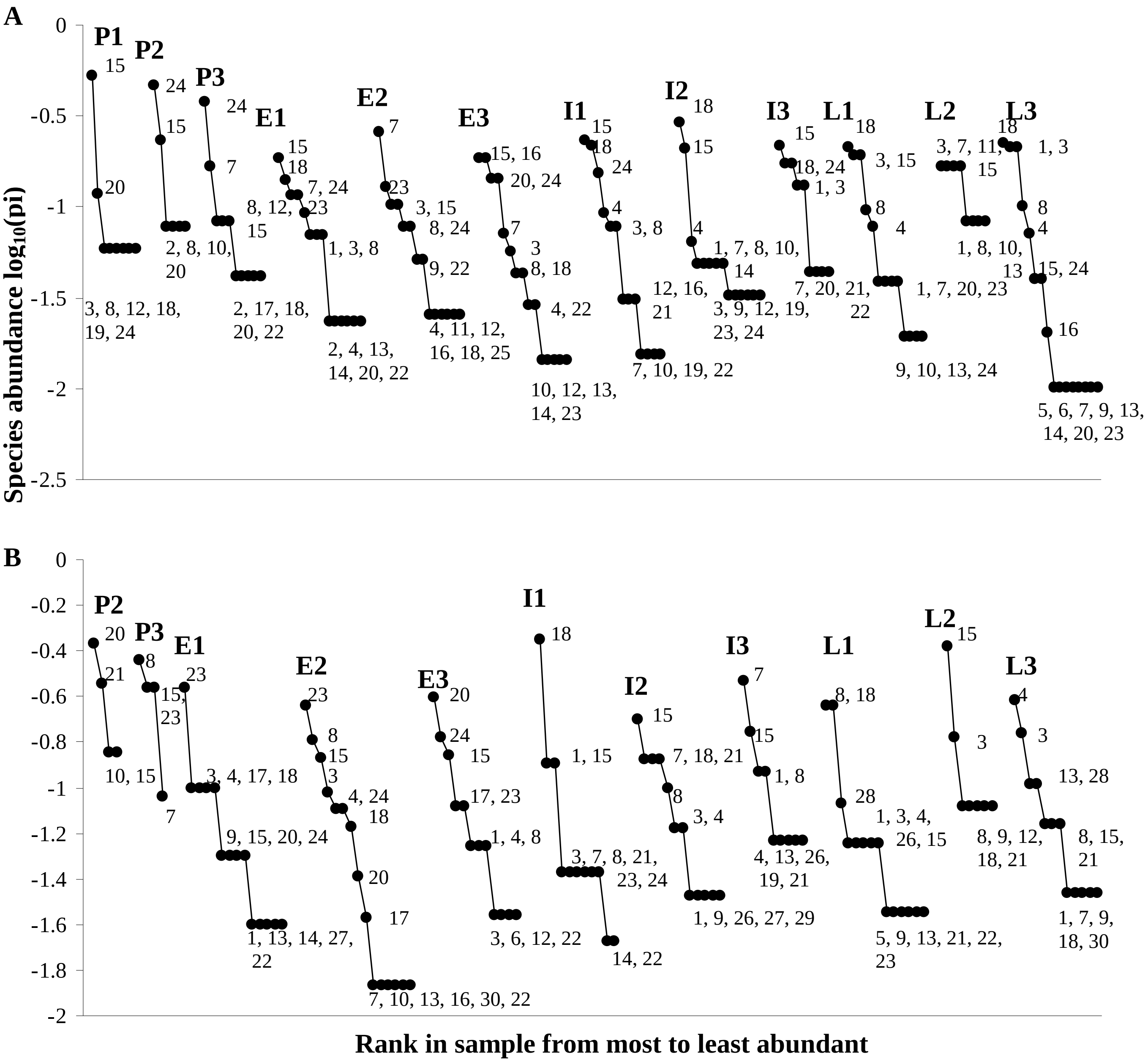

A
P1
P2
P3
E1
E2
E3
I1
I2
I3
L1
L2
L3
0
-0.5
-1
-1.5
-2
-2.5
Species abundance $\log_{10}(pi)$
11
1, 3, 11
1
2, 3
11
13
1, 4
10
9
2
1
2
9, 11, 14
11
10, 13
1
9
14
1
11
2, 3, 9
1
3
2, 11
13, 14
1
4, 9
11
13
9
1
11
3, 13, 15
2
1, 4, 6, 7
1
9
2
5
4
11
14
10
3, 8, 12
B
E1
E2
E3
I1
I2
I3
L1
L3
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
-1.6
-1.8
-2
1
11, 13
1
11
10
1
11
3, 14
4, 9, 10
9
2
1
11
10
3
2, 9, 13, 14
4
1
9
11
2, 4
10
9
13
1
1
9
11
2
4
10, 14
Rank in sample from most to least abundant

Figure 3



A
Species abundance log10(pi)
0
-0.5
-1
-1.5
-2
-2.5
P1
15
20
3, 8, 12, 18, 19, 24
P2
24
15
2, 8, 10, 20
P3
24
7
2, 17, 18, 20, 22
E1
15
18
7, 24
23
8, 12, 15
1, 3, 8
2, 4, 13, 14, 20, 22
E2
7
23
3, 15
8, 24
9, 22
4, 11, 12, 16, 18, 25
E3
15, 16
20, 24
7
3
8, 18
4, 22
10, 12, 13, 14, 23
I1
15
18
24
4
3, 8
12, 16, 21
7, 10, 19, 22
I2
18
15
4
1, 7, 8, 10, 14
3, 9, 12, 19, 23, 24
I3
15
18, 24
1, 3
7, 20, 21, 22
L1
18
3, 15
8
4
9, 10, 13, 24
L2
3, 7, 11, 15
1, 8, 10, 13
1, 7, 20, 23
L3
18
1, 3
8
4
15, 24
16
5, 6, 7, 9, 13, 14, 20, 23
B
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
-1.6
-1.8
-2
P2
20
21
10, 15
P3
8
15, 23
7
E1
23
3, 4, 17, 18
9, 15, 20, 24
1, 13, 14, 27, 22
E2
23
8
15
3
4, 24
18
20
17
7, 10, 13, 16, 30, 22
E3
20
24
15
17, 23
1, 4, 8
3, 6, 12, 22
I1
18
1, 15
3, 7, 8, 21, 23, 24
14, 22
I2
15
7, 18, 21
8
3, 4
1, 9, 26, 27, 29
I3
7
15
1, 8
4, 13, 26, 19, 21
L1
8, 18
28
1, 3, 4, 26, 15
5, 9, 13, 21, 22, 23
L2
15
3
8, 9, 12, 18, 21
L3
4
3
13, 28
8, 15, 21
1, 7, 9, 18, 30
Rank in sample from most to least abundant

Figure 4

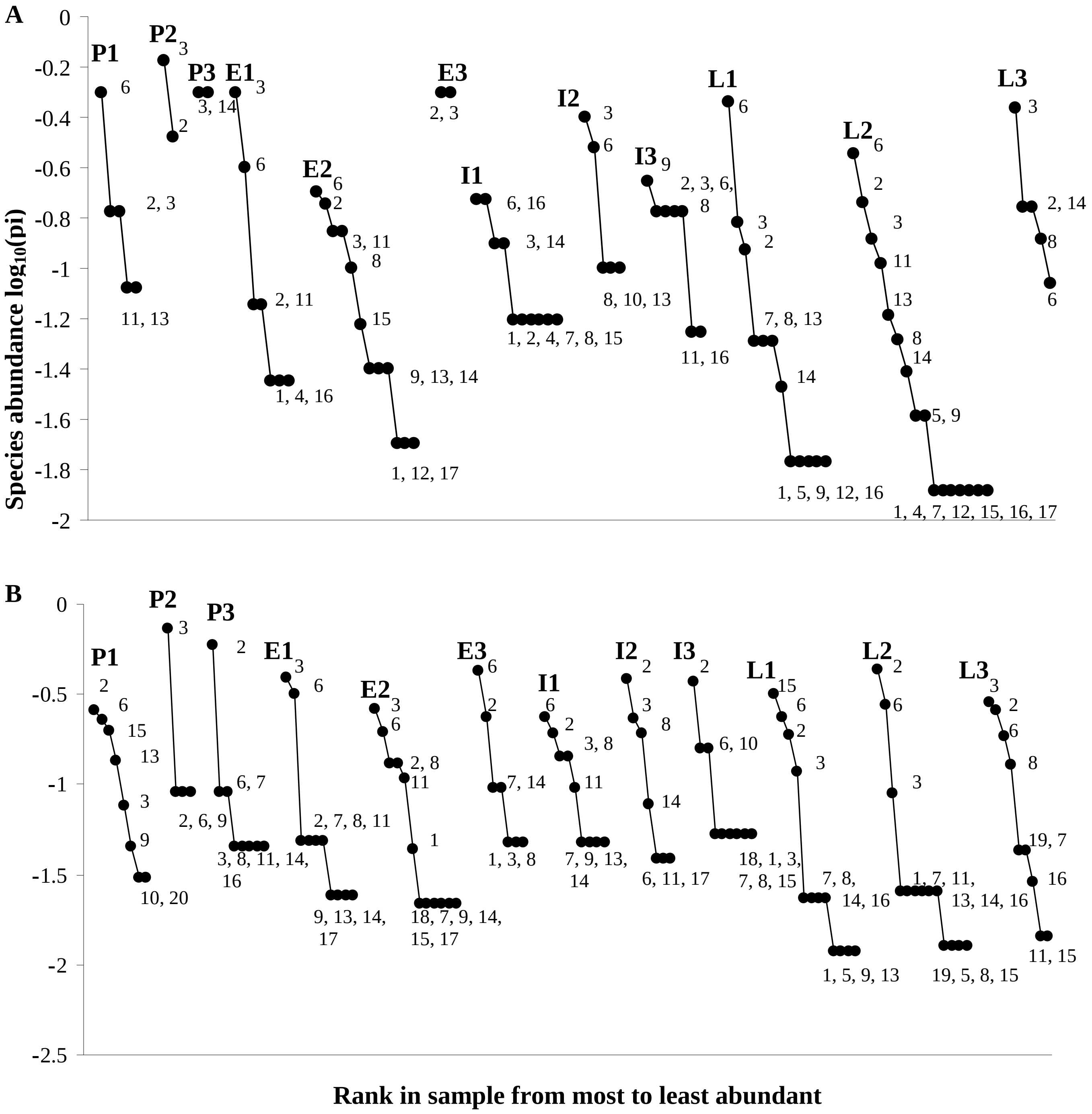

A
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
-1.6
-1.8
-2
Species abundance $\log_{10}$(pi)
P1
6
2, 3
11, 13
P2
3
2
P3
3, 14
E1
3
6
2, 11
1, 4, 16
E2
6
2
3, 11
8
15
9, 13, 14
1, 12, 17
E3
2, 3
I1
6, 16
3, 14
1, 2, 4, 7, 8, 15
I2
3
6
8, 10, 13
I3
9
2, 3, 6,
8
11, 16
L1
6
3
2
7, 8, 13
14
1, 5, 9, 12, 16
L2
6
2
3
11
13
8
14
5, 9
1, 4, 7, 12, 15, 16, 17
L3
3
2, 14
8
6
B
0
-0.5
-1
-1.5
-2
-2.5
P1
2
6
15
13
3
9
10, 20
P2
3
2, 6, 9
P3
2
6, 7
3, 8, 11, 14,
16
E1
3
6
2, 7, 8, 11
9, 13, 14,
17
E2
3
6
2, 8
11
1
18, 7, 9, 14,
15, 17
E3
6
2
7, 14
1, 3, 8
I1
6
2
3, 8
11
7, 9, 13,
14
I2
2
3
8
14
6, 11, 17
I3
2
6, 10
18, 1, 3,
7, 8, 15
L1
15
6
2
3
7, 8,
14, 16
1, 5, 9, 13
L2
2
6
3
1, 7, 11,
13, 14, 16
19, 5, 8, 15
L3
3
2
6
8
19, 7
16
11, 15
Rank in sample from most to least abundant

Figure 5

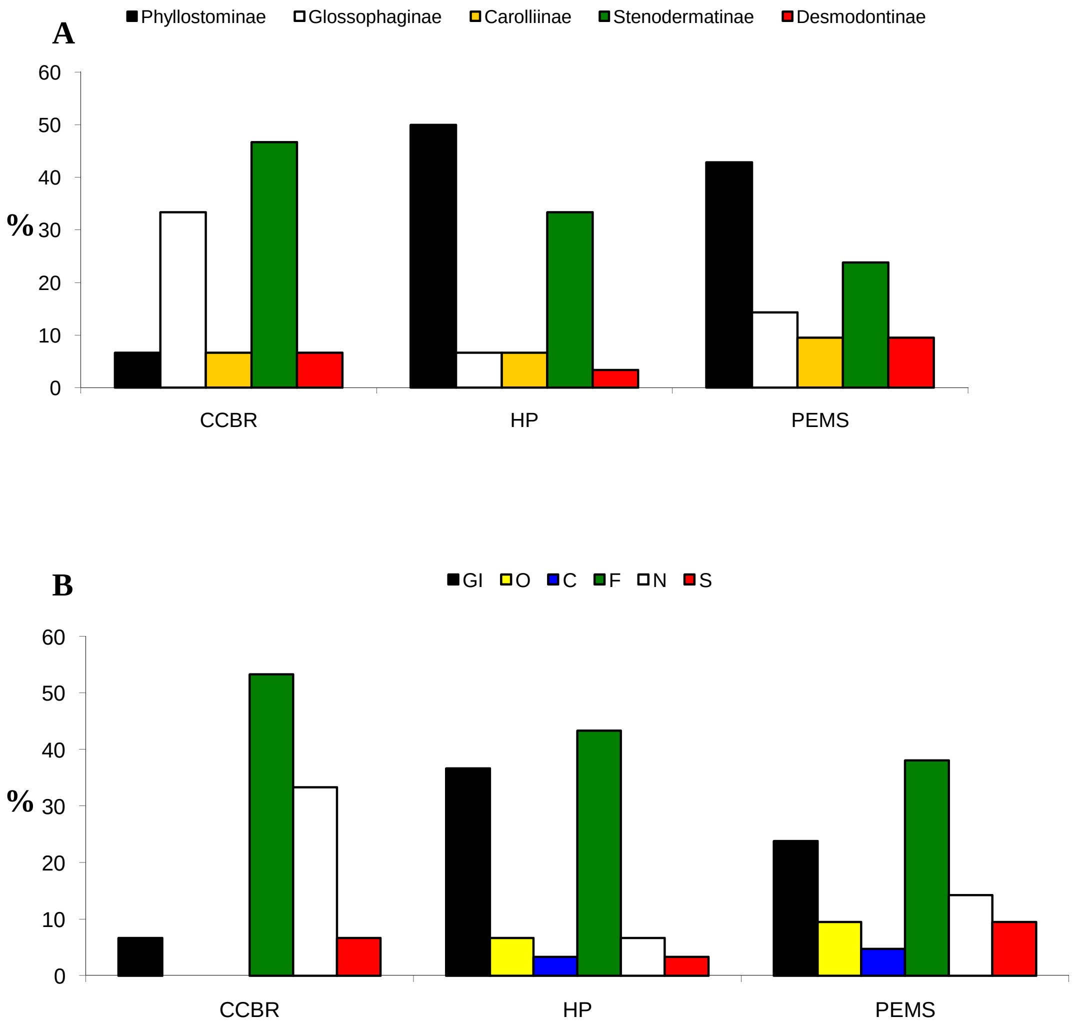

A
■ Phyllostominae
□ Glossophaginae
■ Carolliinae
■ Stenodermatinae
■ Desmodontinae
%
0
10
20
30
40
50
60
CCBR
HP
PEMS
B
■ GI
■ O
■ C
■ F
□ N
■ S
%
0
10
20
30
40
50
60
CCBR
HP
PEMS

Figure 6

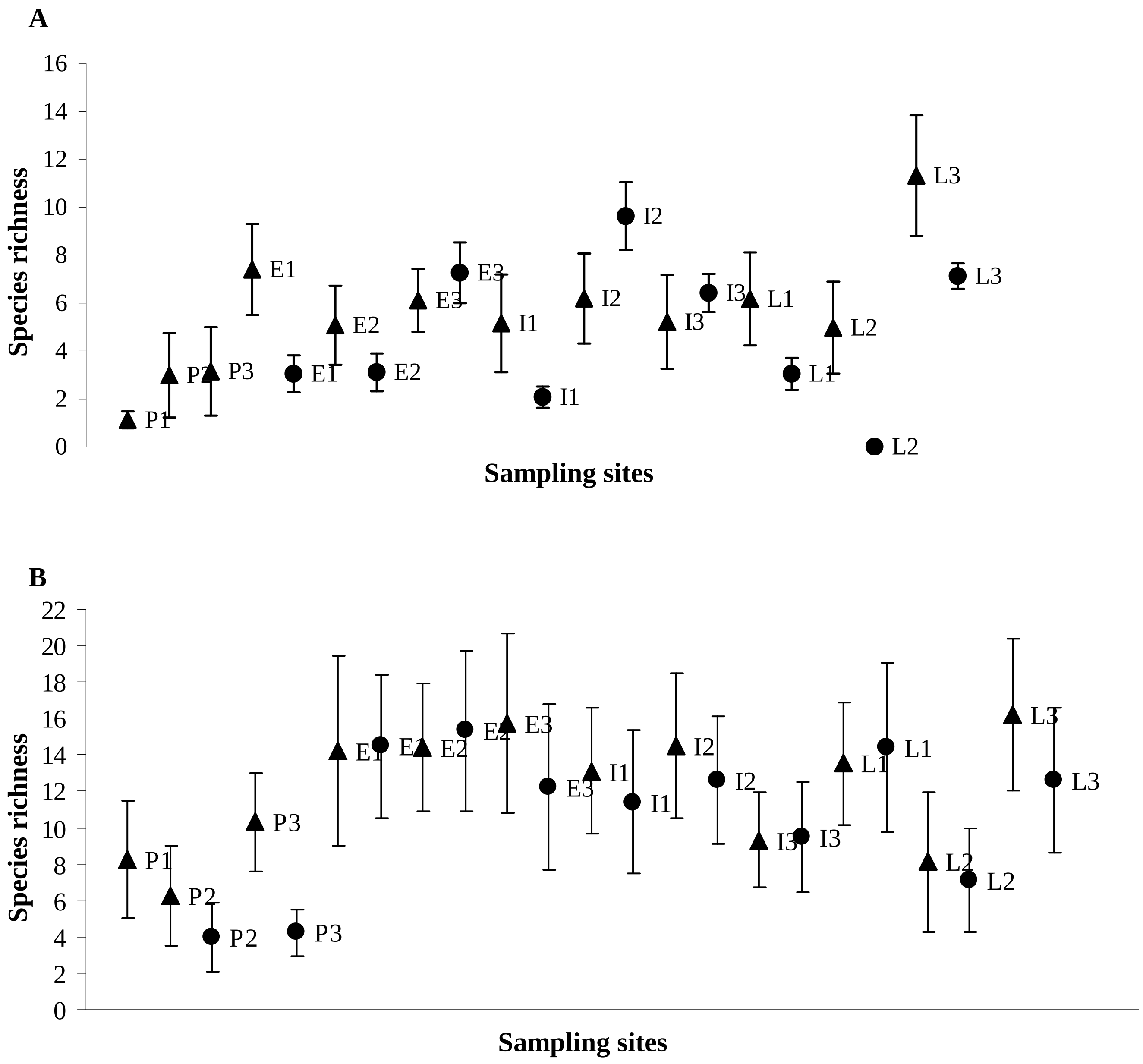

A
Species richness
16
14
12
10
8
6
4
2
0
P1
P2
P3
E1
E1
E2
E2
E3
E3
I1
I1
I2
I2
I3
I3
L1
L1
L2
L2
L3
L3
Sampling sites
B
Species richness
22
20
18
16
14
12
10
8
6
4
2
0
P1
P2
P2
P3
P3
E1
E1
E2
E2
E3
E3
I1
I1
I2
I2
I3
I3
L1
L1
L2
L2
L3
L3
Sampling sites

Figure 6 continued

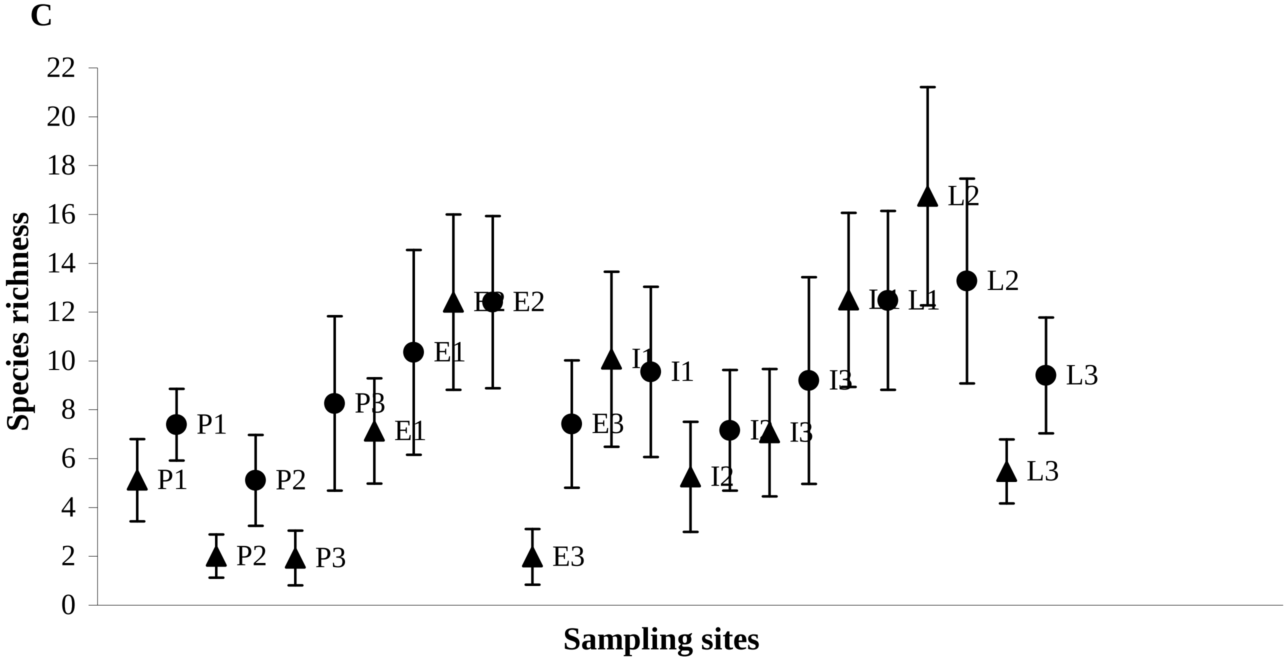


Figure 7

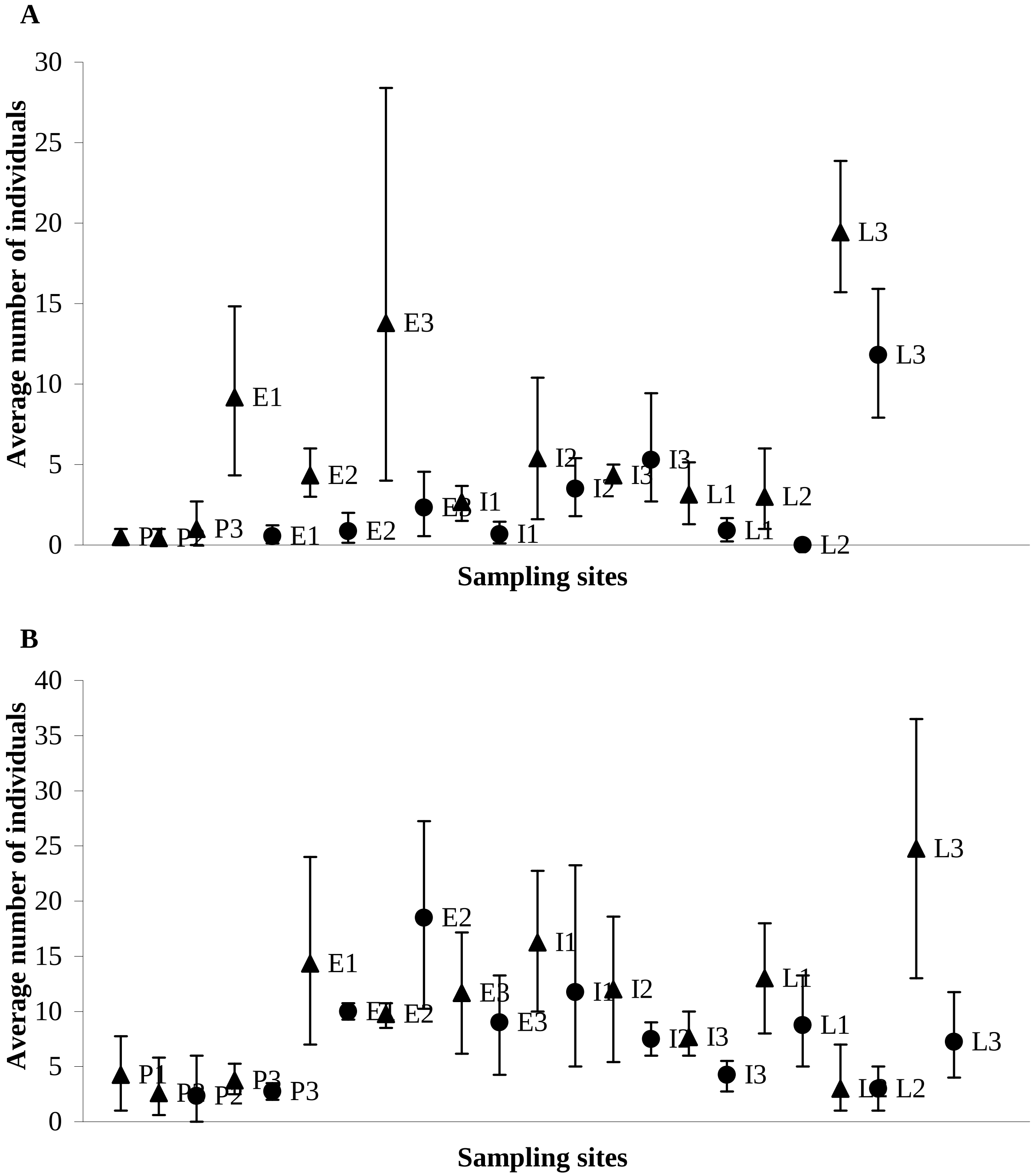

A
Average number of individuals
30
25
20
15
10
5
0
Sampling sites
P1
P2
P3
E1
E2
E3
I1
I2
I3
L1
L2
L3
P3
E1
E2
E3
I1
I2
I3
L1
L2
L3
B
Average number of individuals
40
35
30
25
20
15
10
5
0
Sampling sites
P1
P2
P3
P1
P2
P3
E1
E2
E3
E1
E2
E3
I1
I2
I3
I1
I2
I3
L1
L2
L3
L1
L2
L3

Figure 7 continued

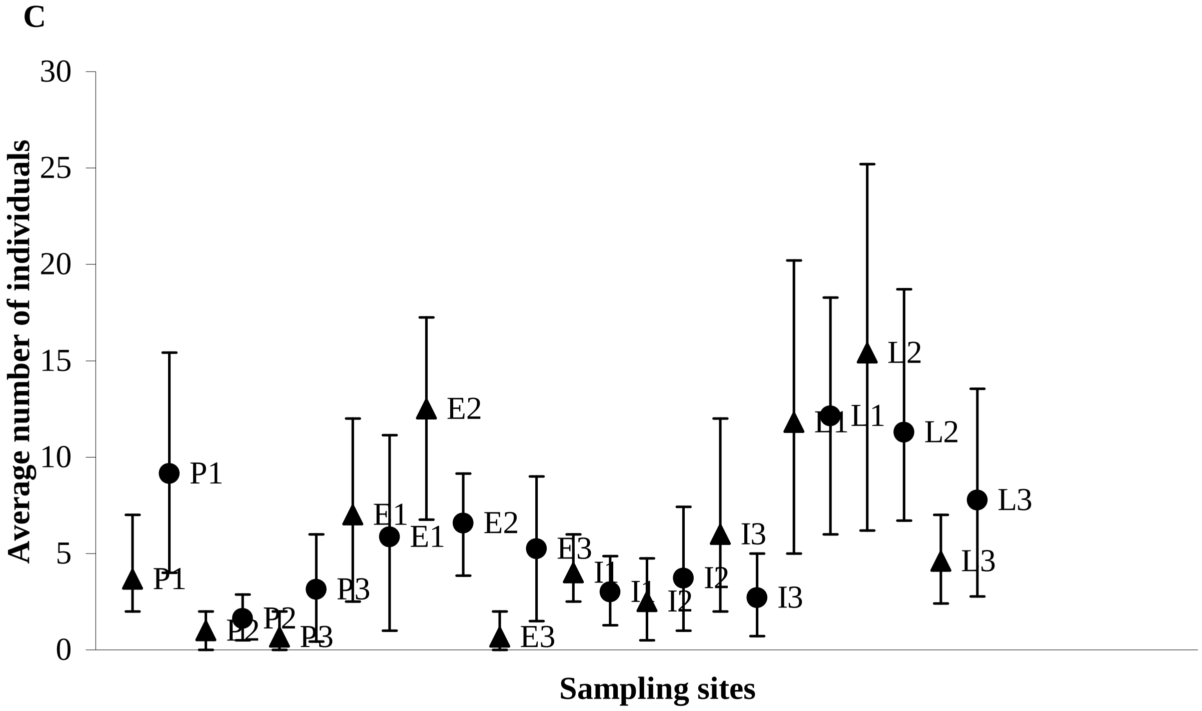
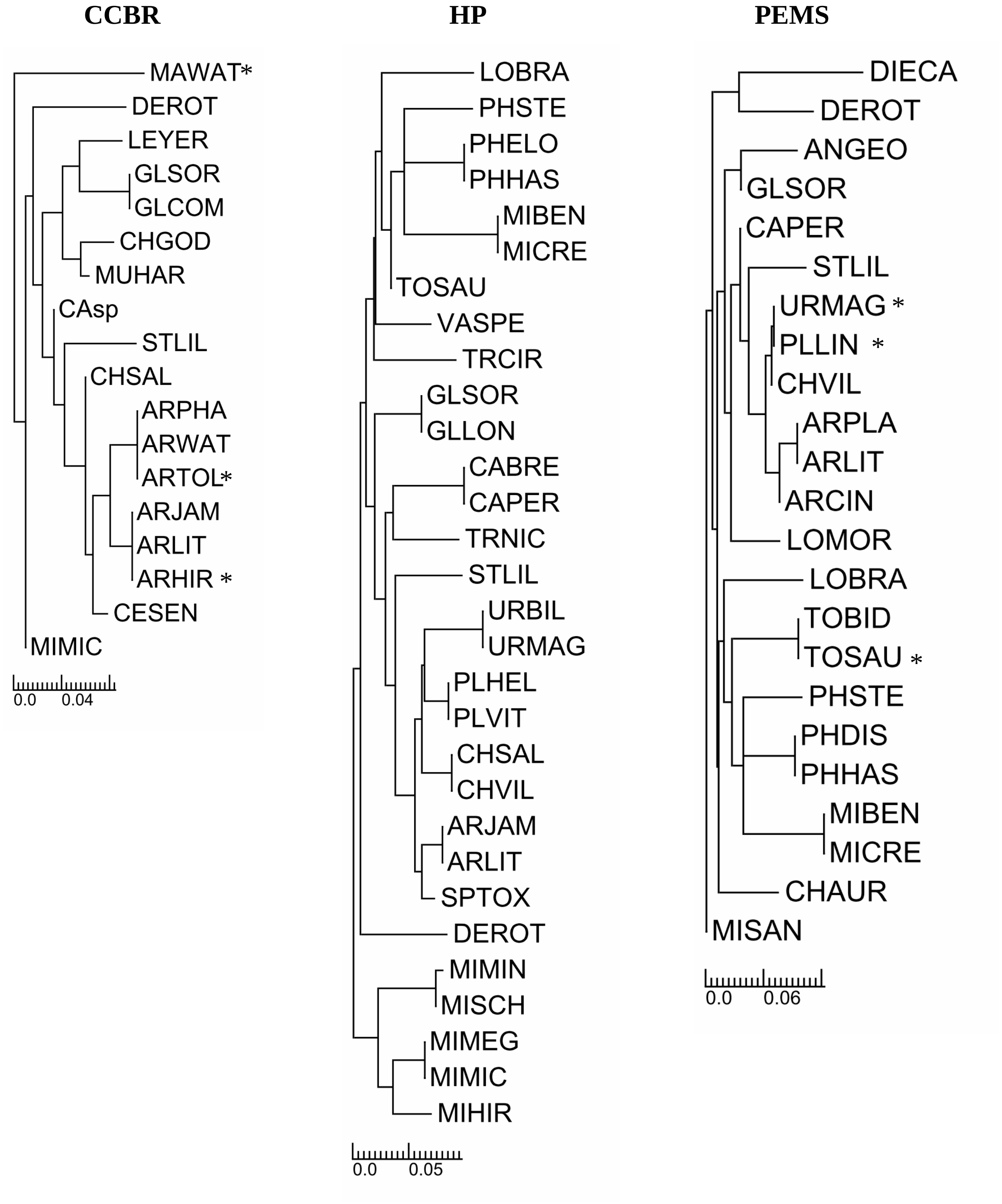


Figure 8


CCBR
MAWAT*
DEROT
LEYER
GLSOR
GLCOM
CHGOD
MUHAR
CAsp
STLIL
CHSAL
ARPHA
ARWAT
ARTOL*
ARJAM
ARLIT
ARHIR *
CESEN
MIMIC
0.0
0.04
HP
LOBRA
PHSTE
PHELO
PHHAS
MIBEN
MICRE
TOSAU
VASPE
TRCIR
GLSOR
GLLON
CABRE
CAPER
TRNIC
STLIL
URBIL
URMAG
PLHEL
PLVIT
CHSAL
CHVIL
ARJAM
ARLIT
SPTOX
DEROT
MIMIN
MISCH
MIMEG
MIMIC
MIHIR
0.0
0.05
PEMS
DIECA
DEROT
ANGEO
GLSOR
CAPER
STLIL
URMAG *
PLLIN *
CHVIL
ARPLA
ARLIT
ARCIN
LOMOR
LOBRA
TOBID
TOSAU *
PHSTE
PHDIS
PHHAS
MIBEN
MICRE
CHAUR
MISAN
0.0
0.06

APPENDIXES

Appendix 1. Non-metric multidimensional scaling ordinations (NMDS) of sampling sites, based on phyllostomid species identity and relative abundance for A: Chamela-Cuixmala Biosphere Reserve (CCBR) considering the rainy season (RS) captures, B: CCBR considering the dry season (DS), C: Hato Piñeiro (HP) considering the RS, D: HP considering the DS, E: Parque Estadual da Mata Seca (PEMS) considering the RS and F: PEMS considering the DS. Sampling sites representing different successional stages are: from P1 to P3= pastures, from E1 to E3= early stage, from I1 to I3= intermediate stage and from L1 to L3= late stage. The species codes for CCBR are as in Figure 2, for HP as in Figure 3 and for PEMS as in Figure 4. The stress-value of the ordinations appears on the top of the graphs.

Appendix 2. Average number of individuals captured per sampling night, per site and per season, representing the different guilds (N= nectarivores, F= frugivores, GI= gleaning insectivores, C= carnivores, S= sangivores and O= omnivores) at each study region. Regions and sampling sites are as in Appendix 1.

Appendix 3. Non-metric multidimensional scaling ordinations (NMDS) of sampling sites, based on guild's composition and relative abundance, for the three study regions at each season. Regions and sampling sites are as in Appendix 1. The stress-value of the ordinations appears on the top of the graphs.

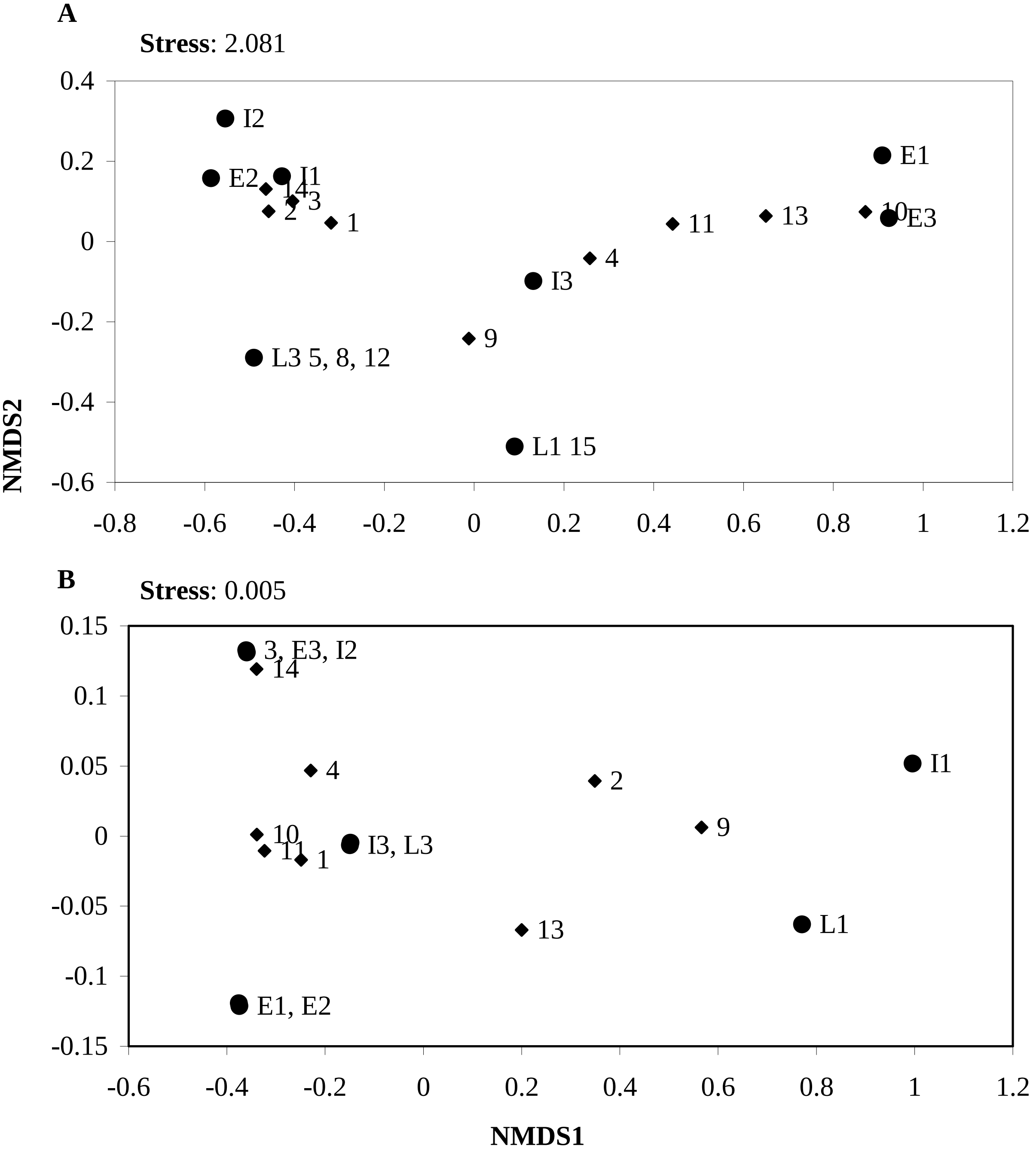
Appendix 4. Average values (and confidence intervals) of the response variables significantly differing among successional stages/seasons of the Chamela-Cuixmala Biosphere Reserve. Successional stages are: E= early, I= intermediate and L= late .The response variable at the population level is the average number of individuals of *G. soricina* (GLSOR) captured per night during the rainy season (RS); at the ensemble level the variable is the average number of nectarivores (N) captured per night during the RS; and at the assemblage level the response variables are: scores of the NMDS axes based on site dissimilarities of species (Species NMDS2, Species NMDS1) and guild composition (Guild NMDS2) during the RS and the dry season (DS).

Appendix 5. Average values (and confidence intervals) of the response variables significantly differing among successional stages/seasons in Hato Piñeiro. Successional stages are: E= early, I= intermediate and L= late .The response variables at the population level are: average number of individuals of *Uroderma bilobatum* (URBIL), *Uroderma magnirostrum* (URMAG), *Desmodus rotundus* (DEROT), and *Phyllostomus elongatus* (PHELO) captured per night during the rainy (RS) and dry season (DS). At the ensemble level the response variables are: average number of omnivores (O) and frugivores (F) captured per night during the RS and the DS.At the assemblage level the variables are the scores of axis 2 of the NMDS based on site dissimilarities of the assemblage's guild composition (during the RS), as well as estimated species richness (RS and DS) using the first-order jackknife estimator.

Appendix 6. Average values (and confidence intervals) of the response variables significantly differing among successional stages/seasons in Parque Estadual da Mata Seca. Successional stages are: E= early, I= intermediate and L= late. The response variable at the population level is the average number of individuals of *G. soricina* captured per night during the dry season (DS).At the ensemble level the response variable is the average number of nectarivores captured per night during the DS.

Appendix 7. Randomization test for the phylogenetic signal of phyllostomid trophic guilds.

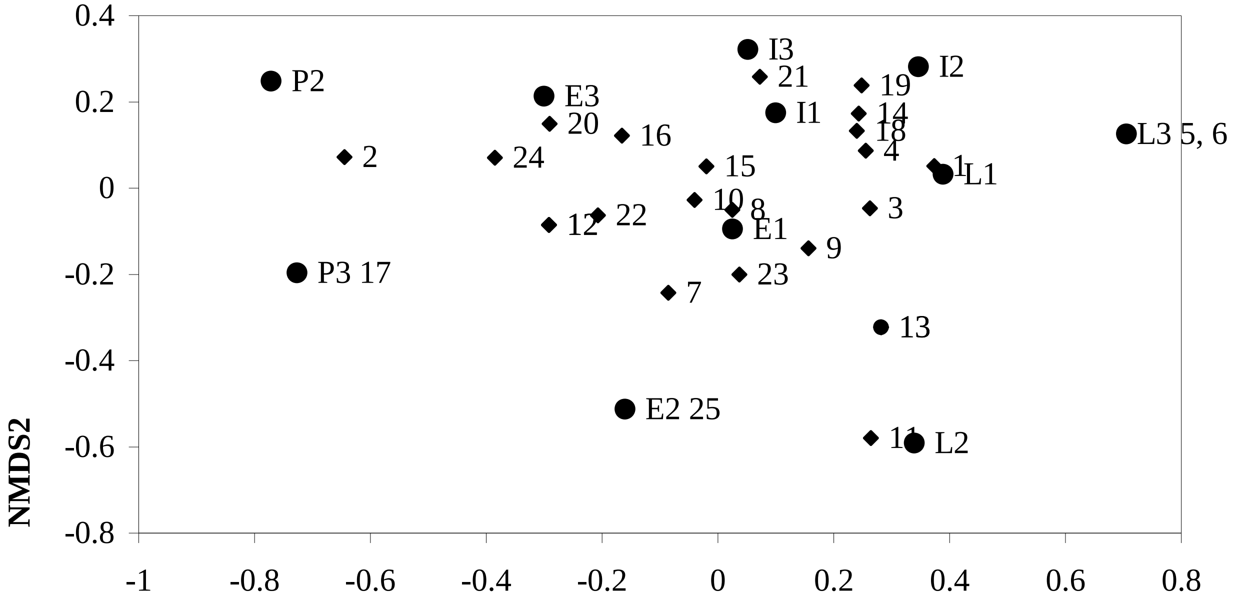
Appendix 1


A
Stress: 2.081
0.4
0.2
0
-0.2
-0.4
-0.6
NMDS2
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
1.2
I2
E2
I1
14
3
2
1
E1
10
E3
11
13
4
I3
9
L3 5, 8, 12
L1 15
B
Stress: 0.005
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
1.2
3, E3, I2
14
4
2
I1
9
10
11
1
I3, L3
13
L1
E1, E2
NMDS1

Appendix 1 continued

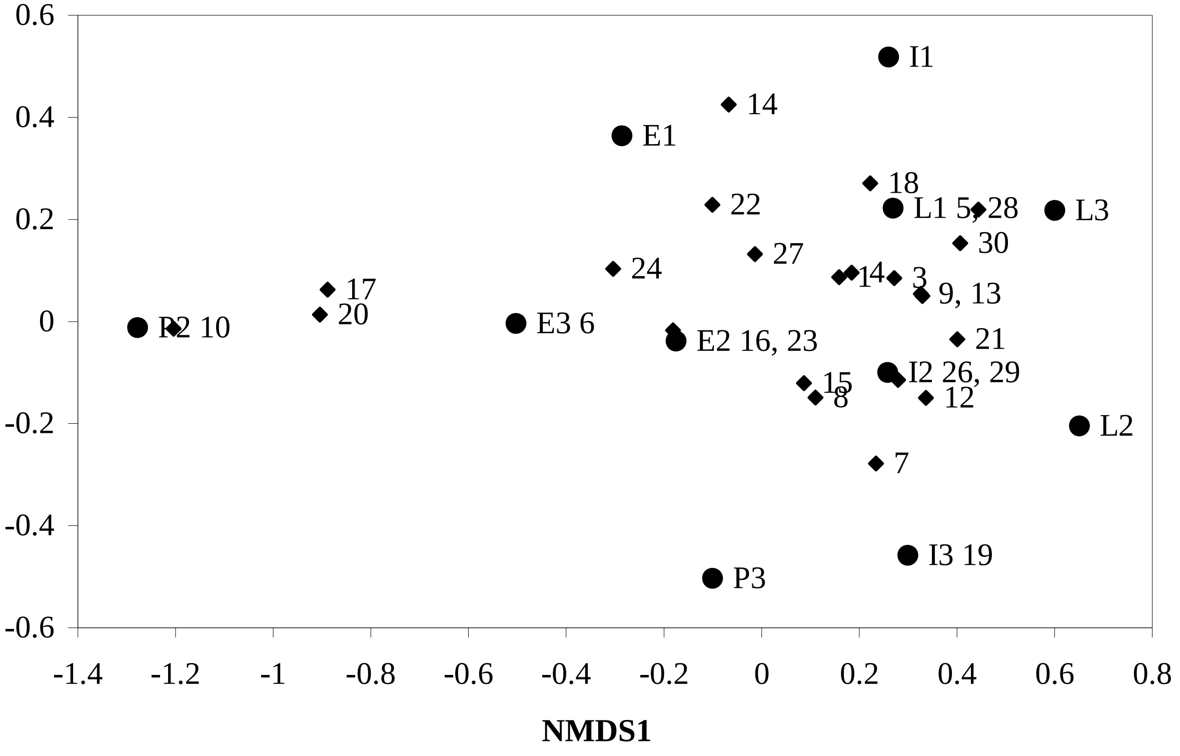
C

Stress: 10.858

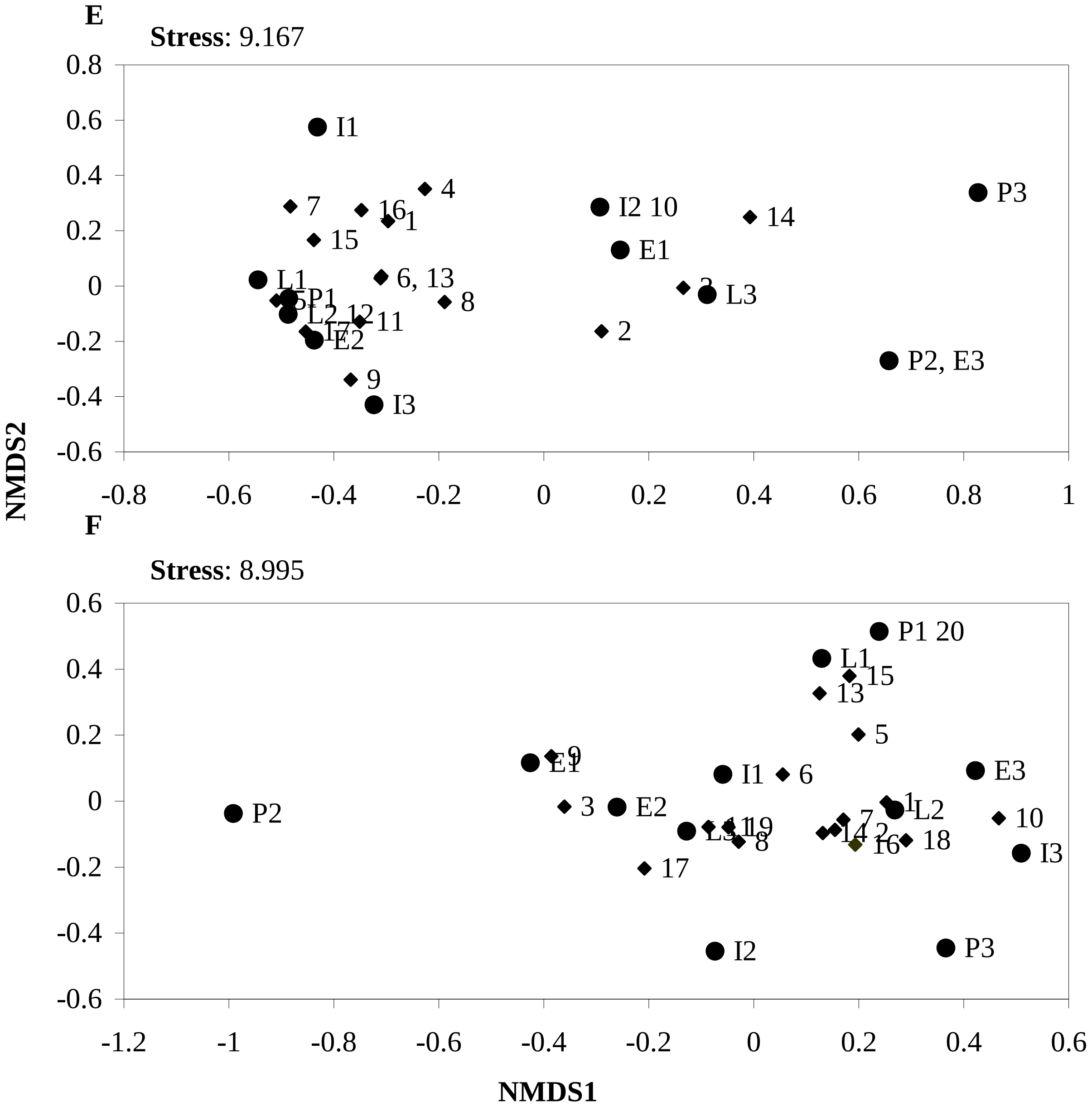


D

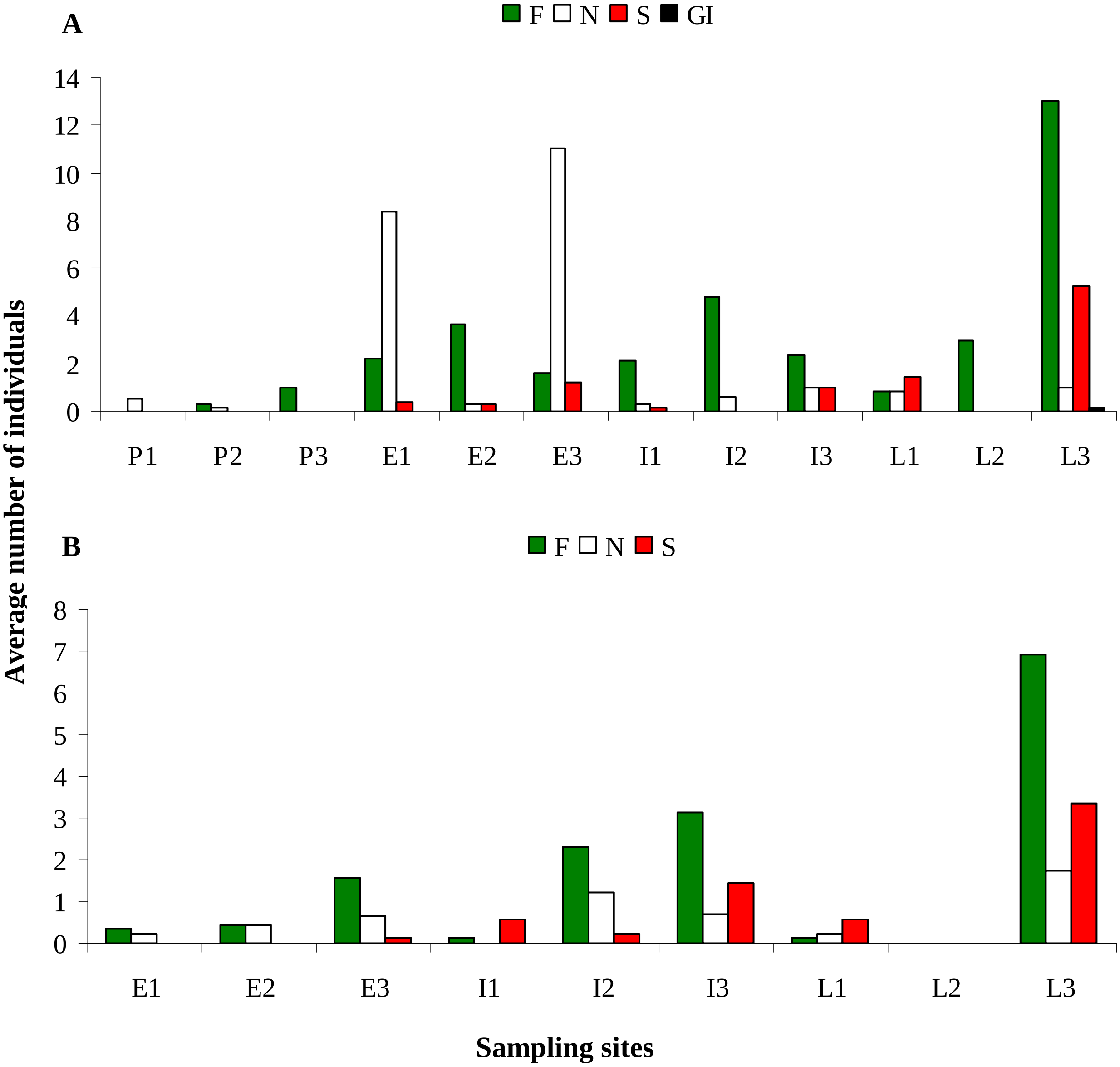
Stress: 13.187



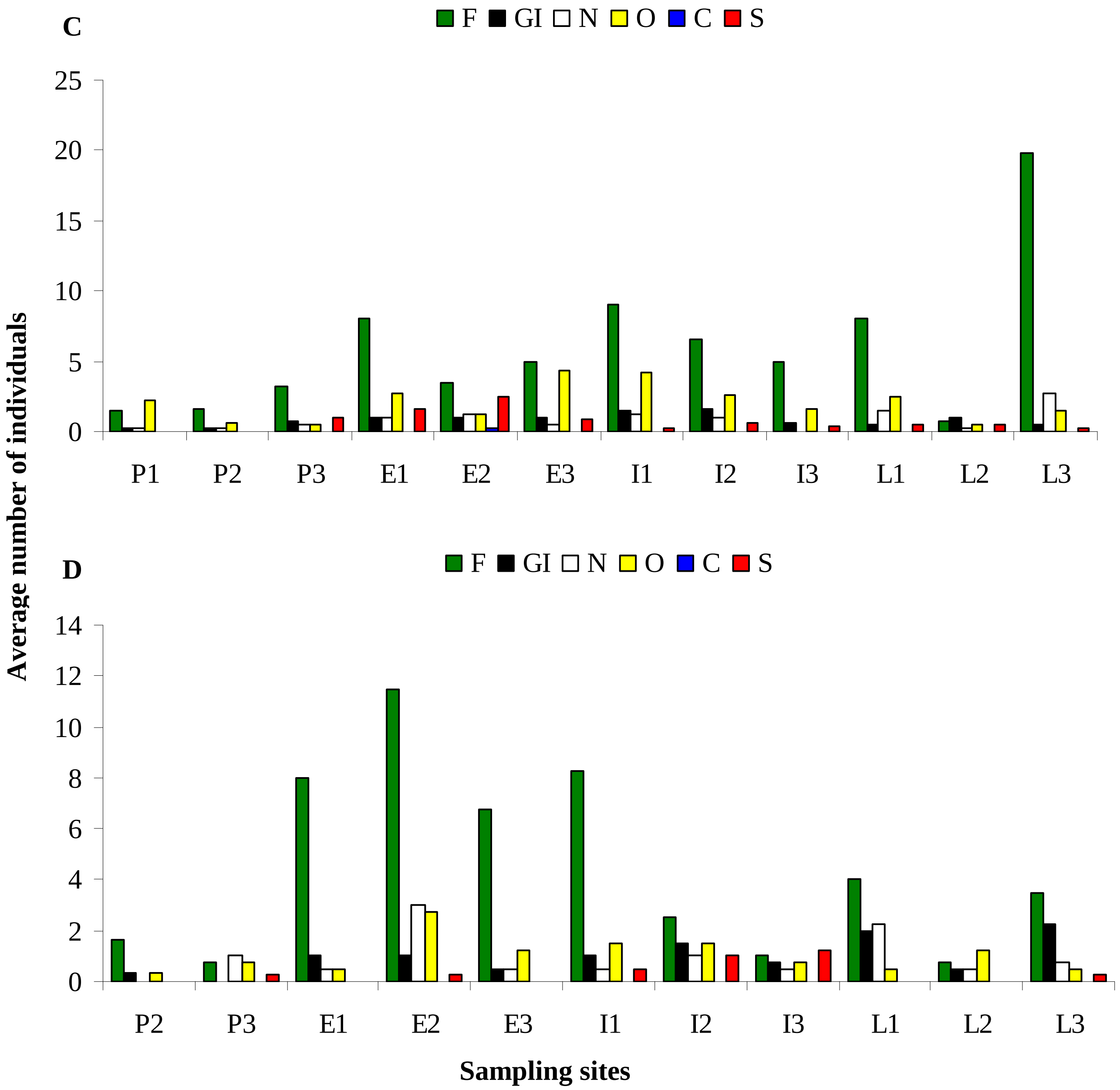
Appendix 1. continued



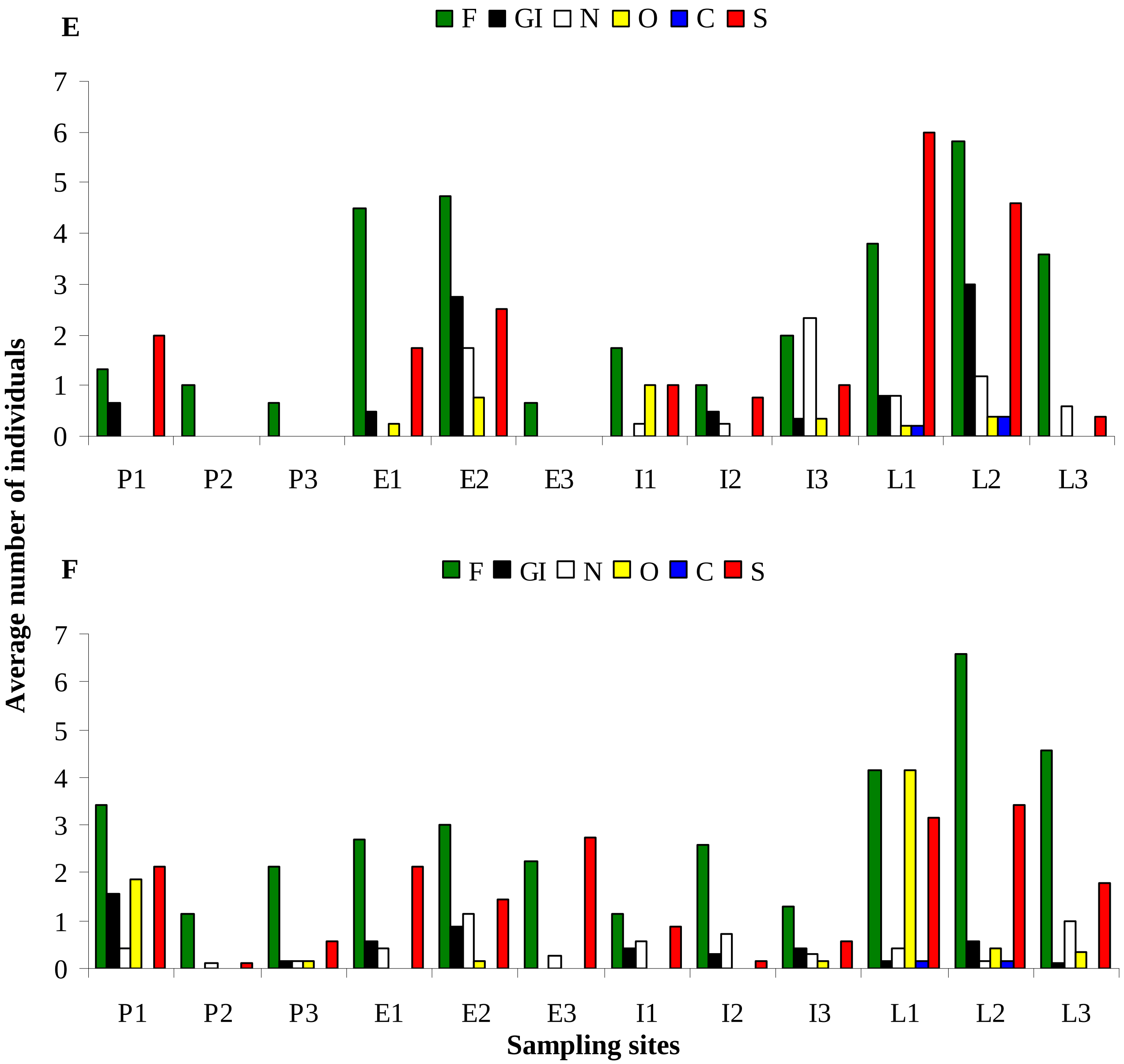
Appendix 2.


A
F
N
S
GI
14
12
10
8
6
4
2
0
P1
P2
P3
E1
E2
E3
I1
I2
I3
L1
L2
L3
B
F
N
S
8
7
6
5
4
3
2
1
0
E1
E2
E3
I1
I2
I3
L1
L2
L3
Average number of individuals
Sampling sites

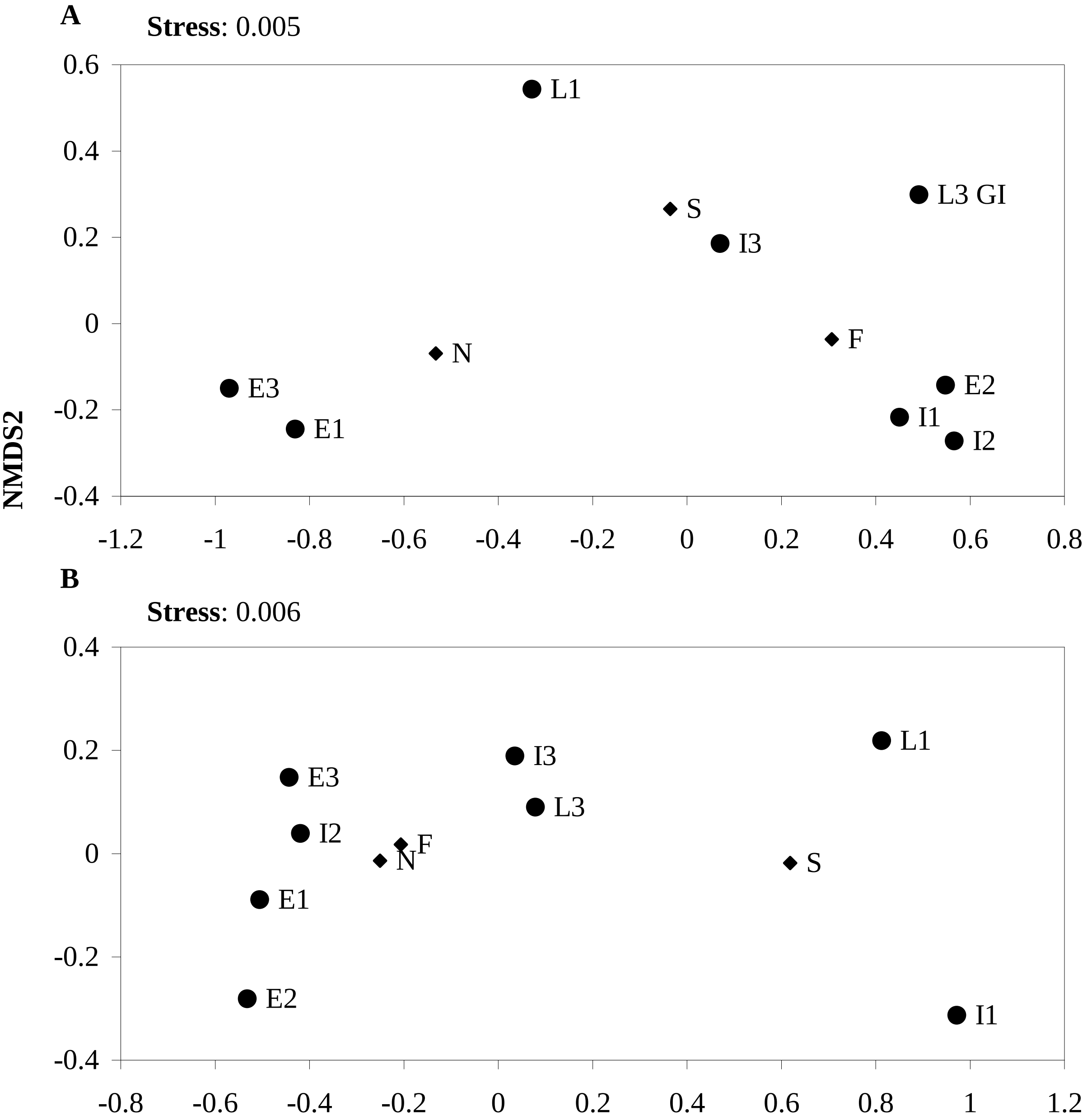
Appendix 2 continued



Appendix 2 continued

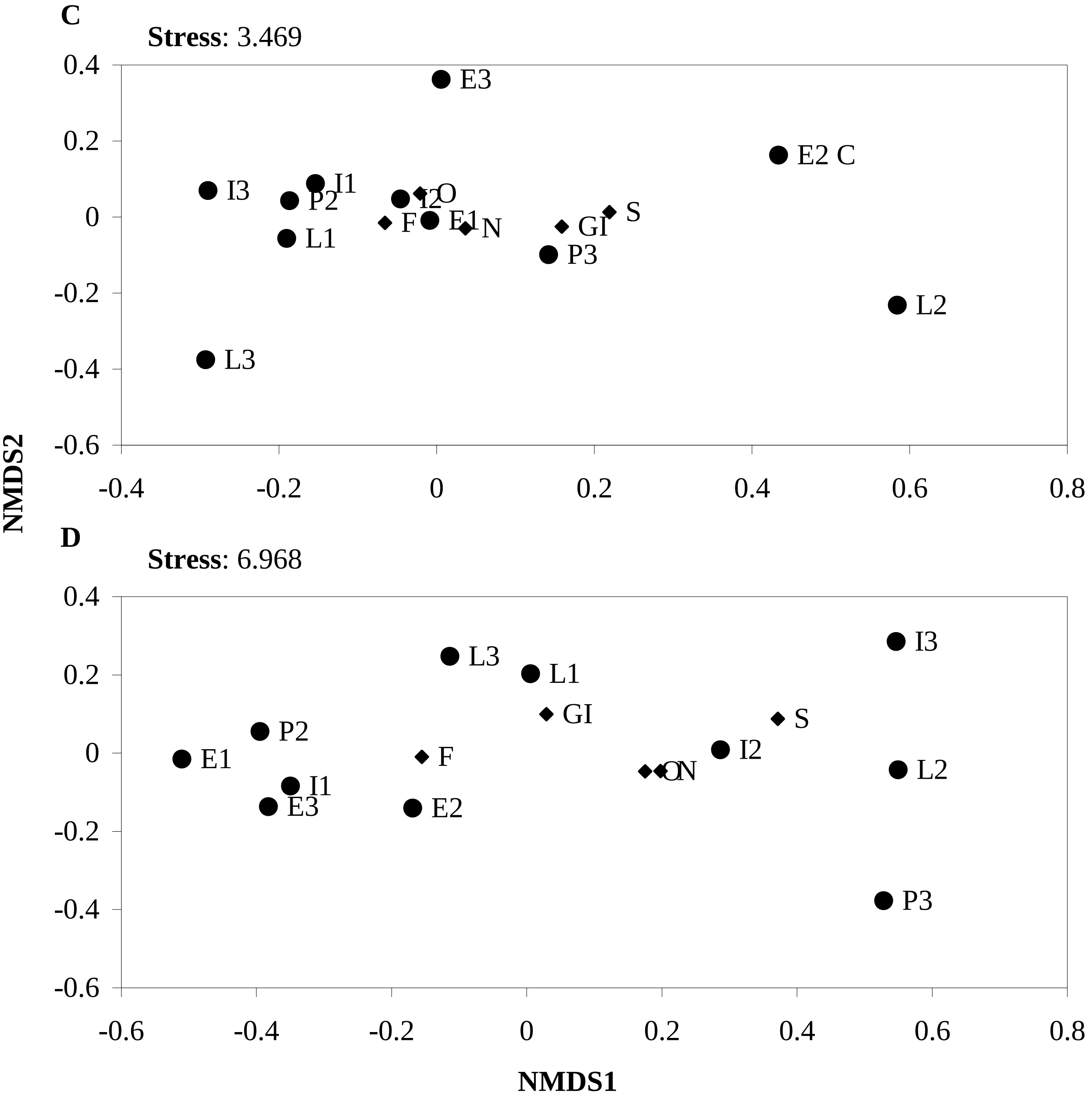


Appendix 3



A
Stress: 0.005
NMDS2
0.6
0.4
0.2
0
-0.2
-0.4
-1.2
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
L1
S
I3
L3 GI
N
F
E3
E1
E2
I1
I2
B
Stress: 0.006
0.4
0.2
0
-0.2
-0.4
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
1.2
I3
L1
E3
L3
I2
F
N
S
E1
E2
I1

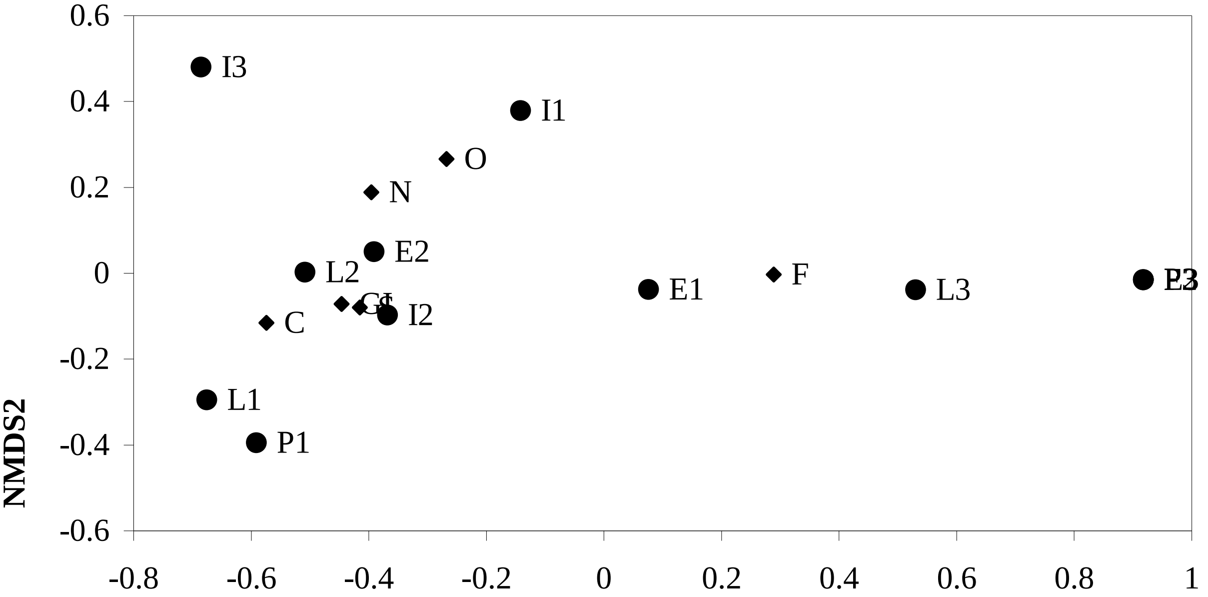
Appendix 3 continued



Appendix 3 continued

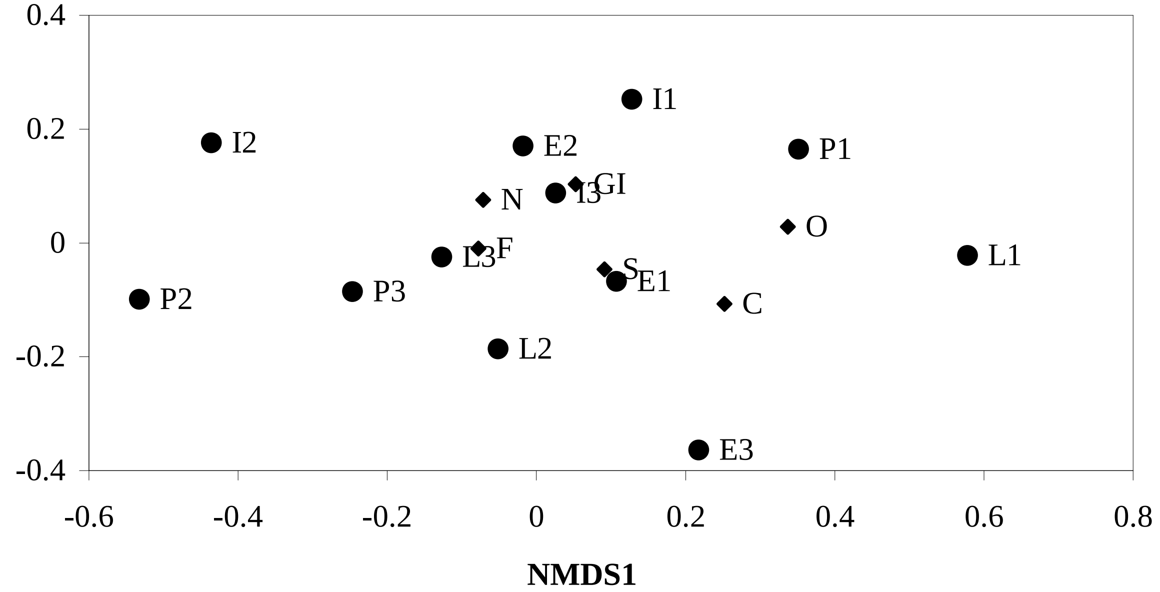
E

Stress: 5.208

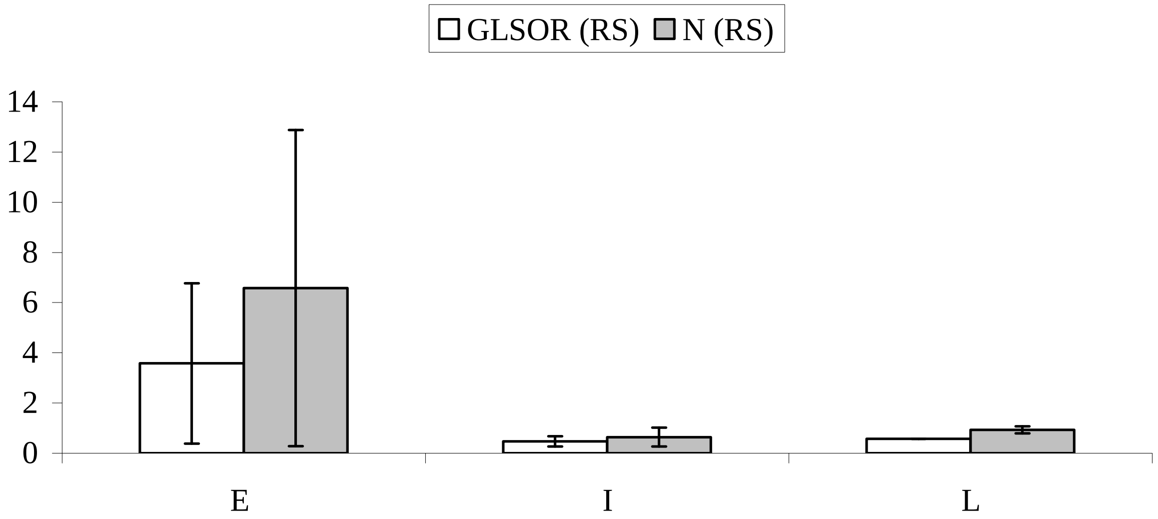


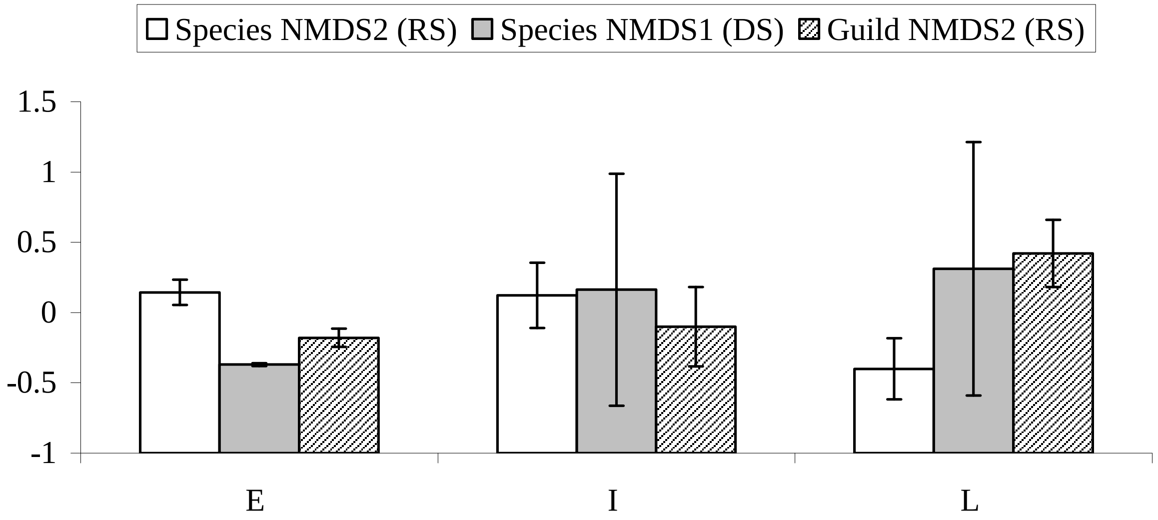
F

Stress: 8.313

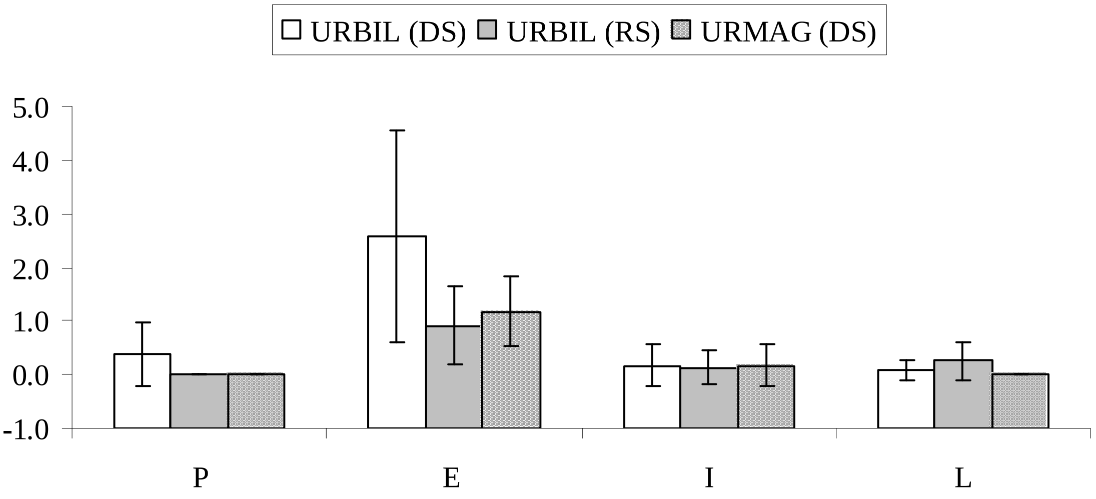


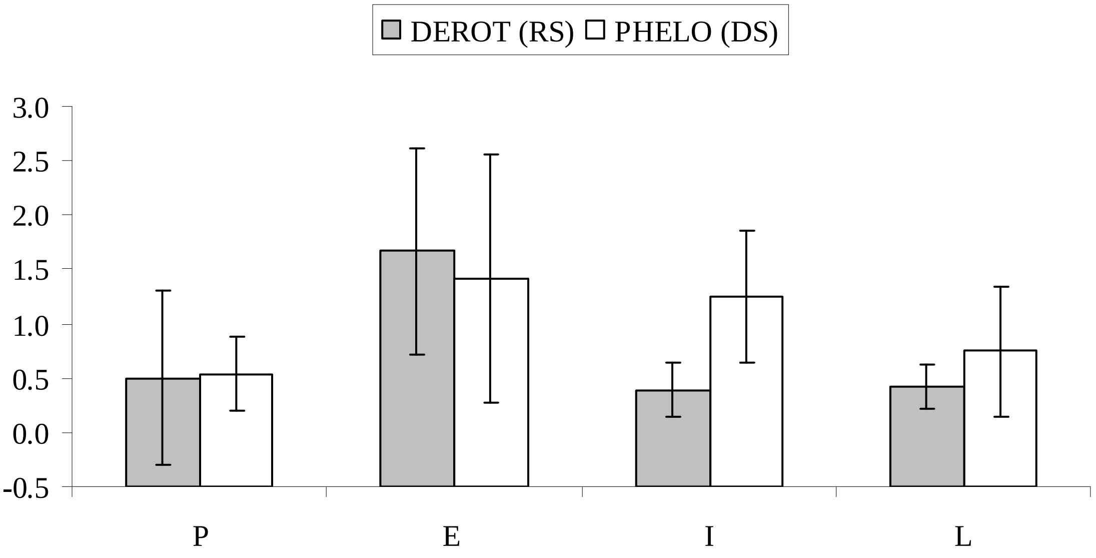
Appendix 4

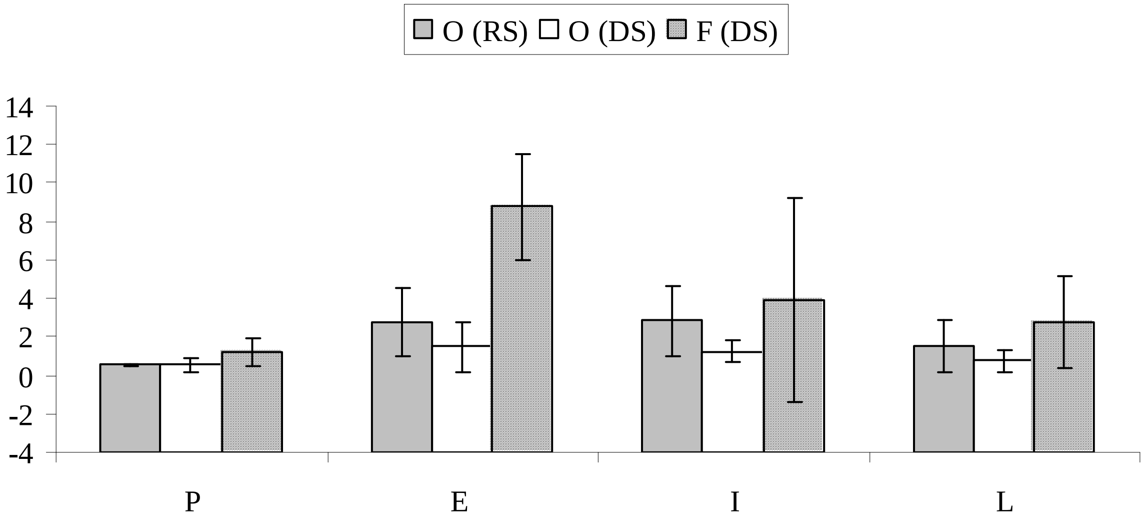

☐ GLSOR (RS)
▨ N (RS)
14
12
10
8
6
4
2
0
E
I
L


☐ Species NMDS2 (RS)
▨ Species NMDS1 (DS)
▨ Guild NMDS2 (RS)
1.5
1
0.5
0
-0.5
-1
E
I
L

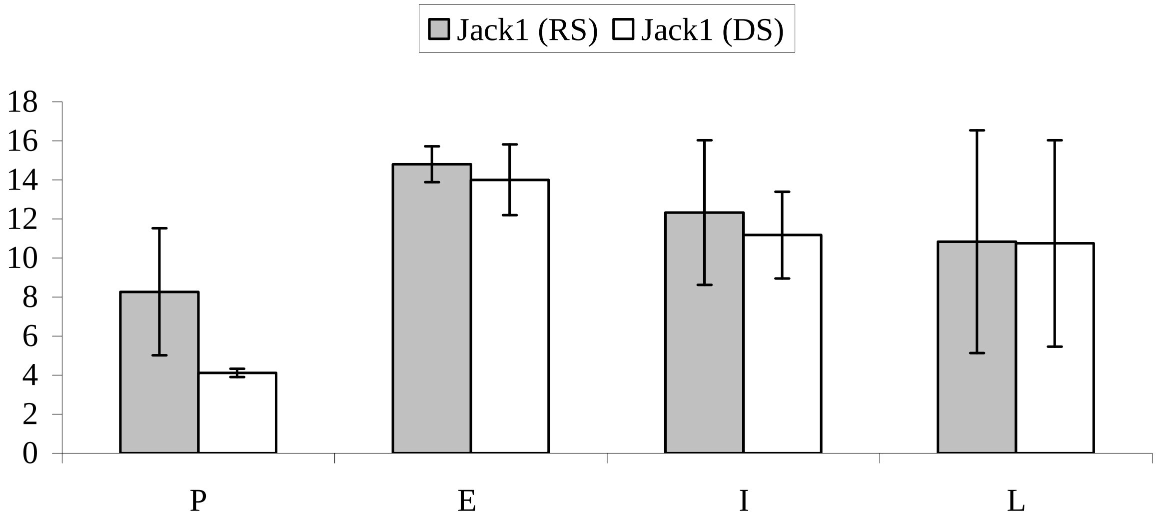
Appendix 5

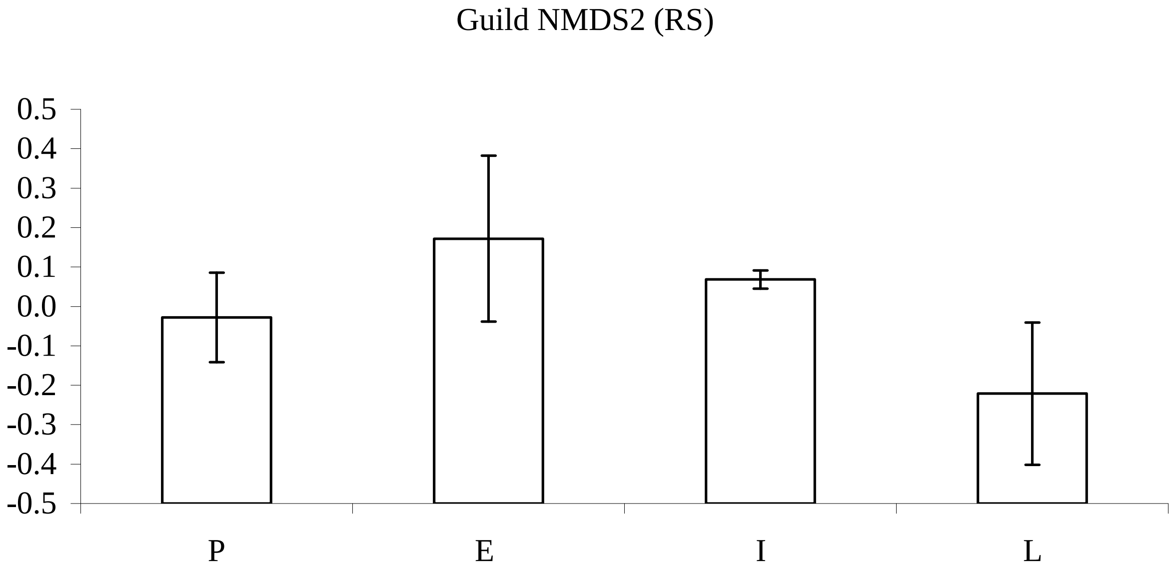

☐ URBIL (DS)
▨ URBIL (RS)
▨ URMAG (DS)
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
P
E
I
L


▨ DEROT (RS)
☐ PHELO (DS)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
P
E
I
L

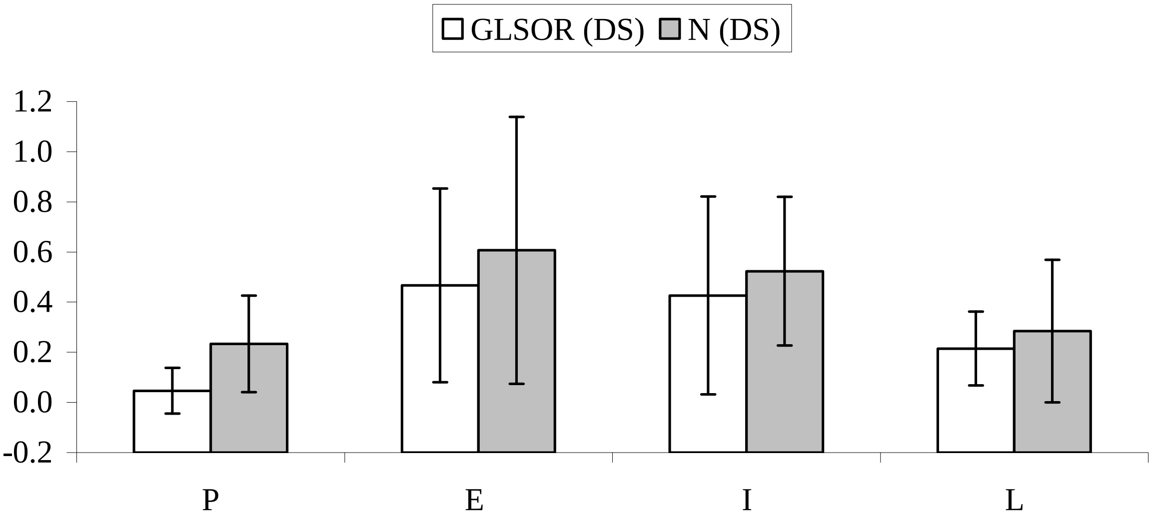

▨ O (RS)
☐ O (DS)
▨ F (DS)
14
12
10
8
6
4
2
0
-2
-4
P
E
I
L

Appendix 5 continued




Guild NMDS2 (RS)

Appendix 6



Appendix 7

In order to test for To determine if a phylogenetic signal (i.e. closely related taxa being functionally more similar to one another than to distantly related taxa) on trophic guilds we performed the randomization test suggested by Blomberg et al. (2003) on the phylogenetic “supertrees” (Figure 8) of the three study regions. In this way we evaluated whether a given tree better fits a set of data obtained through the random permutation of the original data (i.e. guild) across the tips of the original tree and consequently destroying any phylogenetic signal that may exist on the original tree. The baseline for this analysis was the variance of phylogenetically independent contrasts (Blomberg et al. 2003). The comparison of the real variance of contrasts versus the distribution of the variance of contrasts obtained through randomization, determines if the observed phylogenetic signal is statistically significant. A significantly lower variance of contrasts of the real data compared to the permuted data is evidence of a phylogenetic signal. A higher variance of contrasts of the real data compared to the permuted data indicates that the resemblance of relatives (i.e. taxonomically related species) is actually lower than expected, which is termed “antisignal” by Bloomerg et al (2003). The statistical test was based on 1,000 randomizations. All statistical analyses were performed in the R package “Picante” (Kembel et al. 2010, R Development Core Team 2010).

Results are presented in the following table where the p-values and Z-scores of the observed vs random variance of the phylogenetically independent contrasts are shown. Significant p-values are in bold.

Region	**p-value**	**Z-score**
CCBR	**0.007**	-1.468
HP	**0.001**	-2.613
PEMS	**0.002**	-1.388

These results are an evidence of phylogenetic signal on trophic guilds as, in the three regions; we found a significantly lower variance of contrasts on the real data that on the permuted data (negative Z-score).

CAPÍTULO 4

Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary dry forest

RESUMEN

Los bosques neotropicales están siendo reemplazados de forma creciente por un mosaico de parches de vegetación que representan diferentes estadios sucesionales, campos agrícolas y pastizales. Por este motivo, la identificación de los factores que definen la distribución y desempeño de los taxa en los paisajes transformados por la actividad humana esta ganando importancia, espacialmente para aquellos taxa que juegan un papel crítico en el funcionamiento de los ecosistemas. Entre los murciélagos filostómidos se encuentran representados la mayoría de los gremios tróficos identificados entre los murciélagos neotropicales, incluyendo los nectarívoros y frugívoros que juegan un papel importante en procesos como la reproducción de las plantas y la regeneración de los bosques. En este estudio, evaluamos las relaciones causales entre la variación en la presencia y abundancia de los murciélagos filostómidos en diferentes estadios sucesionales de un bosque neotropical seco (a nivel de ensamblaje, ensamble y población), y las variaciones en los atributos del hábitat, tanto a nivel local (complejidad estructural de la vegetación) como a nivel de paisaje (porcentaje de cobertura del bosque, área promedio de los parches de vegetación y diversidad de parches de vegetación). Con este propósito, muestreamos, con redes de niebla, 12 sitios representando 4 diferentes estadios sucesionales definidos con base en la edad de abandono: pastizales (0 año), inicial (3-5 años), intermedio (8-12 años), y tardío (más de 50 años). Durante 142 noches de muestreo capturamos 606 filostómidos representando 15 especies, 11 géneros, 5 subfamilias y 4 gremios tróficos. El análisis del paisaje se llevó a cabo empleando dos escalas espaciales diferentes correspondientes a circunferencias de 500 y 1000 m centradas en los sitios de muestreo. En general, encontramos que tanto la variación en los atributos del hábitat a nivel local, como a nivel de paisaje, explican la variación en la presencia y abundancia de filostómidos a través de la secuencia sucesional, siendo su poder explicativo dependiente de la escala de análisis. Encontramos también una respuesta gremio específica a las variaciones en los atributos del paisaje, de tal modo que la variación en la abundancia de frugívoros estuvo principalmente explicada por variaciones en la cobertura de vegetación riparia, mientras que las variaciones en la abundancia de nectarívoros estuvo principalmente explicada por variaciones en la cobertura de bosque seco. Esto se debe, probablemente, a que en la vegetación riparia prevalecen los recursos chiropterocóricos, mientras que en el bosque seco prevalecen los recursos chiropterofílicos. De hecho, la variación en la cobertura de la vegetación riparia estuvo significativamente asociada con variaciones en la composición específica y abundancia de los ensamblajes de filostómidos, debido

posiblemente al predominio de las especies de frugívoros en estos ensamblajes. Concluimos que, en los paisajes transformados, la conservación de las áreas de vegetación riparia es crucial para la conservación de la diversidad de murciélagos y de los servicios ecológicos que brindan.

Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary dry forest

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Abstract

Neotropical forests are being increasingly replaced by a mosaic of patches of different successional stages, agricultural fields, and pastures lands. The identification of factors shaping taxa distribution and performance in human-transformed landscapes is gaining importance, especially for those taxa playing critical roles in ecosystem functioning. Phyllostomid bats comprise most of the foraging guilds found among Neotropical bats, including nectarivores and frugivores that play important roles in processes of plant reproduction and forest regeneration. Here, we evaluate the causal/explanatory relationships between variations in the occurrence of phyllostomid bat assemblages, ensembles and populations in different successional stages and variations in habitat attributes at local (vegetation structure complexity) and landscape levels (percentage of forest cover, mean patch area, and diversity of patch types) in a Neotropical dry forest. For this purpose, we mist-netted bats in 12 sites representing 4 different successional stages defined by their age of abandonment: pastures (0 yrs), early (3-5 yrs), intermediate (8-12 yrs) and late successional forests (>50 yrs). During 142 sampling nights we captured 606 phyllostomids representing 15 species, 11 genera, 5 subfamilies and 4 broad guilds. Landscape analysis was performed at two different scales: 500 and 1000 m circumferences around sampling sites. In general, we found that variation in local and landscape habitat attributes significantly explained the variation of phyllostomid occurrence across the chronosequence, with their explanatory power scale-dependent. We also found a guild-specific response to variation in landscape attributes, where variation of frugivore abundance was mainly explained by variation in the amount of riparian vegetation, whereas variation of nectarivore abundance was mainly explained by variation in the amount of dry forest vegetation. These results are explained by the prevalence of quiropterochorous resources in the riparian habitat and of quiropterophilic resources in the dry forest. In fact, the variation in the amount of riparian vegetation was significantly associated with the variation in phyllostomid assemblage abundance and species composition, probably because of the prevalence of frugivorous species in phyllostomid assemblages. We conclude that the preservation of the riparian vegetation is crucial for the conservation of bat diversity and their important ecological interactions in tropical dry forest transformed landscapes.

Key words

Phyllostomid bat assemblage, Tropical dry forest, Secondary forest, Succession, Landscape ecology.

Introduction

Tropical landscapes have been increasingly modified by human activities, altering their natural structure and the course of ecological processes. As a consequence of small (i.e. death of one or a few trees) and large scale (i.e. wind falls, landslides, volcanism, fire, periodic and long-lasting flooding) natural disturbances, combined with the ongoing successional process in disturbed areas (Lobova et al 2009, Whitmore 1991), tropical landscapes are composed of a mosaic of different successional stages. Natural patterns and processes have been modified by human activities principally because of changes in land-use (Gascon et al. 2004, Primack et al. 2001, Sala et al. 2000, Whitmore 1997). This has provoked the removal of a great portion of vegetative coverage, the formation of more and smaller vegetation patches, the increment of habitat edges, the introduction of exotic species, the alteration of abiotic components of the environment, and the reduction of vegetation capabilities to recover from disturbance, among others (Chazdon et al. 2007, Gaston et al. 2004, Hilty et al. 2006, Laurance and Bierregaard 1997, Maass 1995).

Cattle raising, agriculture and logging are among the land-use changes that have most severely modified Neotropical landscapes. These activities have provoked the replacement of natural vegetation by a mosaic of patches of different successional stages, agricultural fields, pasture lands and human settlements (Chazdon et al. 2007, Nepstad et al. 1999, Primack et al. 2001, Quesada & Stoner 2004, Quesada et al. 2009, Sanchez-Azofeifa et al 2005, Skole & Tucker 1993). Some authors predict that these transformed landscapes will be the predominant habitat available for wildlife in the near future (Hilty et al 2006, Quesada et al. 2009).

In this context, the identification of factors that shape taxa distribution and performance in human-transformed landscapes is gaining an increasing importance (Green et al. 2005, Harvey et al. 2006) as an invaluable baseline for the preservation and management of biodiversity (Daily 2001, Daily et al. 2001, Green et al., 2005, Harvey et al., 2006, Schroth et al., 2004). In order to maintain ecosystem structure, as well as the viability of key ecological processes, particular attention must be paid to taxa playing critical roles in ecosystem functioning (Cosson et al. 1999b, Jordán 2009). Maintaining such processes will help to preserve an important fraction of the biodiversity in contemporaneous ecosystems.

In the Neotropics, bats are considered an important component of biodiversity (single sites hosting up to 70 species, Aguirre et al. 2003), as well as a keystone group. Due to the dramatic ecological and evolutionary radiation of bats, they occupy virtually every trophic level, from primary to tertiary consumers (i.e. folivores, nectarivores, pollinivores, frugivores, insectivores, animalivores and sanguivores), interacting with a large spectrum of organisms and regulating complex ecological processes (Bernard and Fenton 2002, Estrada et al. 1993a, Fleming 1988, Hutson et al. 2001). Their importance in ecosystem functioning is determined by the ecological services they provide in seed dispersal, pollination, control of invertebrate and small vertebrate populations, and recycling and translocation of nutrients and energy in the ecosystem (Charles-Dominique 1986, Fleming 1982, 1988, Gorchov et al. 1993, Kalka et al. 2008, Muscarella and Fleming 2007, Valiente-Banuet et al. 2004, Whitaker 1993, Williams-Guillén et al. 2008). In the

Neotropics bats visit and presumably pollinate approximately 573 species and disperse seeds from 549 species (Geiselman et al. 2002 onward, Lovoba et al. 2009), maintaining plant diversity, connecting distant plant populations via pollen and seed movement, and promoting forest regeneration in degraded lands via seed dispersal. In fact, in some Neotropical regions, nearly half of the most abundant pioneer plant species are bat-dispersed (i.e. *Solanum*, *Cecropia*, *Piper*, *Vismia*, Charles-Dominique 1986). Additionally, insectivorous bats can significantly decrease herbivory levels in some Neotropical forests as they may consume up to 1.5 times their body weight in insects per night (Kalka et al. 2008).

1.1 Bats´ response to anthropogenic disturbance

The response of bats to anthropogenic disturbance in Neotropical regions has received increasing attention during the last twenty years. Nevertheless, it remains poorly understood as studies have reported contradictory results (Table 1 in Avila-Cabadilla et al. 2009). Some studies suggest that bats are more tolerant to habitat modification than other animals and they attribute this to: (1) their capacity to fly, crossing habitat boundaries and open areas (including physical barriers for other species), (2) their ability to exploit resources that are patchy in space and time, and (3) their capacity to shift their diets or adapt their behavior to resource availability (Bernard and Fenton 2002, 2003, 2007, Castro-Arellano et al. 2007, Castro-Luna et al. 2007, Estrada et al. 1994, Gorrensen and Willig 2004, Lumsden and Benneet 2005, Montiel et al 2006, Offerman et al. 1995, Turner 1996). In contrast to the above mentioned studies, others suggest that bats are sensitive to habitat loss or modification and to the resulting variation in habitat structure, food and shelter. Bats´ responses to habitat alteration have been detected at the assemblage and ensemble-level (i.e. change in species composition, reductions in diversity and abundance), at the population-level (i.e. reduction in abundance and strong deviations in the populations´ sex ratio; Brosset et al. 1996, Bianconi et al. 2004, Cosson et al. 1999a, b, Estrada and Coates-Estrada 2002, Fenton et al. 1992, Henry et al. 2007, Medellín et al. 2000, Medina et al. 2007, Meyer and Kalko 2008, Reis and Muller 1995, Schulze et al. 2000), and at the individual level (i.e. more stressed individuals in fragments as shown by Henry et al. 2007, or changes in foraging patterns as shown by Stoner et al. 2002 and Quesada et al. 2004 for nectarivores and by Medellín and Gaona 1999 for frugivores).

In spite of the variation in results from different studies, some tendencies of bats´ response to habitat modification have been identified. For example, rare species with specialized diets and habitats (Medellín et al. 2000), such as the gleaning insectivores and carnivores from the subfamily Phyllostominae, are more tightly associated with mature forest (Bernard and Fenton 2003, Brosset et al 1996, Castro-Arellano et al. 2007, Castro-Luna et al. 2007, Clarke et al. 2005a, b, Fenton et al. 1992, Kalko et al. 1999, Medellín et al. 2000, Ochoa 2000, Peter et al. 2006, Wilson et al. 1996). In the case of frugivores in tropical humid forest, bat abundance is higher in anthropogenic habitats than in mature forests, which is linked to an increase in the abundance of chiropterochorous plants in the former sites (Brosset et al. 1996, Clarke et al. 2005a, Faria 2006, Faria et al. 2006, Faria and Baumgarten 2007, Mancina et al. 2007, Medellin et al. 2000, Ochoa 2000, Peters et al. 2006, Reis et al. 2003, Wilson et al. 1996). Finally, species least affected by habitat modification are those with: (a) large geographic ranges, (b) large body sizes, (c) large home ranges, (d) generalist habitat requirements, and (e) high natural abundances (Avila-Cabadilla et al. 2009, Cosson et al. 1999a, b, Estrada et al. 1993a, Estrada and Coates-Estrada 2002, Montiel et al. 2006).

In order to clarify our understanding of bat responses to habitat disturbance studies are needed that move forward the dichotomous and qualitative description of habitat (i.e. fragmented vs. continuous forest, disturbed vs. undisturbed habitat) (Fahrig 2003, Klingbeil and Willig 2009); a quantitative characterization of habitat attributes will allow us to identify specific factors determining bat occurrence in areas with different disturbance levels. Additionally, we need studies that evaluate not only the effect of variation on local habitat attributes (i.e. tree density, canopy cover, and fragment shape and area), but also the spatial configuration and composition of the landscape at different focal scales (Cosson et al 1999b, Gorrense and Willig 2004, Klingbeil and Willig 2009, Meyer and Kalko 2008). Moreover, it is crucial that studies analyze bat responses at the population-level, identifying species-specific responses to variation in particular habitat attributes (Gorrensen & Willig 2004, Gorrensen et al. 2005, Klingbeil & Willig 2009, Willig et al. 2007). The exclusive use of diversity indexes and other grouping measurements preclude a good understanding of bat responses, as they integrate the reaction of species with different ecological requirements and, in some cases, are influenced by the behavior of the most abundant species. Lastly, studies should include regions with contrasting ecosystems, regional pools of species, and disturbance regimes; this will facilitate the identification of general patterns of bat responses to anthropogenic habitat modification and may be useful in predicting outcomes for a broader spectrum of anthropogenic landscapes (Bierregaard et al. 1997, Cosson et al 1999a).

1.2. Study Focus and objectives

We focus on phyllostomid bats because: (1) in the Neotropics this is the most diverse bat family (Hutson et al. 2001) in taxonomic (i.e. 151 species) and functional terms, containing most of the foraging guilds and all of the nectarivorous and frugivorous species; (2) their specialized requirements for food, roosting and habitat (i.e. Phyllostominae bats), make them useful indicators of habitat change (Fenton et al. 1992, Jones et al. 2009); and (3) they are easy to sample using mist nets.

We are interested in tropical dry forest (TDF) because it presents unique structural and functional features suggesting that current knowledge of bat responses to habitat disturbance, mostly coming from moist / rainforest cannot be extrapolated to assemblages inhabiting TDF (Avila-Cabadilla et al. 2009). Moreover, this ecosystem is widespread in the Neotropics, being present in most latitudinal gradients (approximate extension 519,597 km^2; Portillo-Quintero and Sánchez-Azofeifa 2010) and it hosts a high number of endemic species (Ceballos 1995, Gentry 1995). Additionally, this ecosystem is under severe anthropogenic pressure and has suffered a 66% reduction of its original area (Portillo-Quintero and Sánchez-Azofeifa 2010) and is poorly represented in natural protected regions (Miles et al. 2006, Portillo-Quintero and Sánchez-Azofeifa 2010).

The main objective of our study was to identify causal/explanatory relationships between changes in phyllostomid bat assemblages, ensembles and populations and the variation in habitat attributes at local and landscape levels in a TDF caused by the most common anthropogenic disturbances (agriculture and cattle raising; Chazdon et al. 2007). We also discuss the implications of our results for phyllostomid bat conservation in anthropogenic TDF landscapes.

To evaluate the possible factors determining the occurrence of phyllostomid bats in different successional stages we used a chronosequence approach as a baseline. Tropical dry forest and riparian forest (RF) served as focal habitat types for characterizing landscape attributes. We predict that variation in phyllostomid assemblage composition, which includes a significant portion of species tightly associated with mature forest (6 of 15 species in the study system, Avila-Cabadilla et al. 2009), will be explained by variations in vegetation structural complexity and by vegetation cover among successional stages. Moreover, because of their contrasting ecological requirements (i.e. food resources), we predict that nectarivore and frugivore abundance, analyzed at the ensemble and population-levels, will respond in a guild-specific way to changes in local and landscape habitat attributes (Klingbeil & Willig 2009). Specifically, we expect to find the highest frugivores abundance in sites with the highest cover of riparian vegetation, as the riparian hosts most of the chiropterochoric species of the region (Lott 1993, 2002, personal observation). We also expect to find the highest nectarivores abundance in sites with a reduced amount of dry forest, as the most abundant nectarivorous species in the region tend to occur in higher abundance in the early successional stages of the tropical dry forest (Avila-Cabadilla et al. 2009).

2. Methods

2.1 Study area and sampling sites

The present study was conducted in and surrounding the Chamela-Cuixmala Biosphere Reserve (CCBR, Fig. 1), located in the central western coast of Mexico in the state of Jalisco (19°22’-19°35’N, 104°56’-105°03’W). The CCBR has an extension of 13,200 ha and is covered by a well preserved TDF (Lott 2002) and some small areas of RF, among other vegetation types (Lott 1993, 2002). In this region, the precipitation regime follows a markedly seasonal pattern as most of the rainfall occurs during June-October. Average annual precipitation from 1977 to 2006, is 763 ± 258 (SD) mm (http://www.ibiologia.unam.mx/ ebchamela/index.html) and average annual temperature is 24.6°C. During the sampling years, average annual precipitation and the months that received rainfall were: 2004, 652 mm (June-October); 2005, 384 mm (July-August); and 2006, 387 mm (June-October, http://www. ibiologia.unam.mx/ebchamela/index.html).

We selected twelve sampling sites (Fig. 1) representing a TDF successional gradient (chronosequence) of four successional stages: 3 pastures (P, sites used by farmers until the beginning of the study), 3 early sites (E, sites of 3-5 years of abandonment at the beginning of the study), 3 intermediate sites (I, sites of 8-12 years of abandonment at the beginning of the study) and 3 late sites (L, sites of at least 50 years old). Sites were located on slopes of small hills (slope ranging from 15° to 25°), at a mean height of 223 m.a.s.l. North facing slopes were not used to avoid the higher heterogeneity of plant communities occurring on such slopes (Balvanera et al.

2002). All secondary sites were located around the CCBR limits (Fig. 1), at a distance ranging from 1000 to 5000 m, and were constituted by plots of 120 * 90 m embedded within a matrix of the same vegetation type and protected by fire breaks and fences for keeping cattle out. For more detailed information about the land use history of sampling sites, including photographs, see Avila-Cabadilla et al. (2009).

2.2 Bat sampling

Bats were mist netted following a standardized sampling unit consisting of a set of five mist nets—two 6 m, two 9 m and one 12 m long (all were 2.6 m high). One set of mist nets comprised a sampling area of 109m^2 each sampling night. The sampling unit was located within and surrounding each plot (120 x 90 m), crossing natural corridors representing flyways for bats. Distance among nets was not shorter than 30 m. Sampling was performed for 5 hours after sunset, a period of time that coincides with peak foraging time for most phyllostomid bats (Fenton and Kunz 1977), avoiding windy, rainy and full moon nights to reduce variation in capture success.

Different phyllostomid species may be unequally sampled by mist nets. Nevertheless, this fact has not been documented systematically and we assume that capture data adequately reflect the relative abundance of all phyllostomid species. We are also aware that our data may represent a biased portrait of the bat assemblages as we only sampled one vegetation stratum. Nonetheless, due to the low canopy height of TDFs (tree height ranging from 5 to 10 m, Durán et al. 2002) in comparison to moist/rain forest, we consider ground mist nets an accurate method reflecting the relative abundance of phyllostomids at our study site.

From June 2004 to August 2006, most sites were sampled every 46 ± 15 (SD) days. In pastures we reduced the number of sampling nights due to the paucity of captures. During each census period we randomized the order in which sites were sampled. We also avoided biases due to trap-shy behavior by sampling each site for only one night during a census period.

Nets were checked approximately every 30 min and captured bats were stored temporarily in cloth bags. Bats were identified at the species level based on the dichotomous keys of Medellín et al. (1997) and Timm and Laval (1998). Excluding juveniles and non healthy individuals, all bats were marked on their forearm using numbered aluminum bands. Individuals were released where they were originally captured. We collected and identified the seeds found in bats feces inside the cloth bags. Bats nomenclature follows Simmons (2005) and bat ensemble assignation follows Timm and Laval (1998): frugivores, nectarivores, gleaning insectivores and sanguivores.

2.3 Habitat attributes

2.3.1 Local scale

In 2004 we assessed in a quadrate of 50*20 m within each plot, the following vegetation attributes for woody plants with a diameter at breast height equal or higher than 2.5 cm: 1. Number of individuals (IP), 2. Species number (SP), 3. Total basal area (BA), and 4. Average leaf area index per plot (LAI). LAI is the projected green leaf area per unit of a horizontal plane (Fournier et al. 2003). This index is considered a useful indicator of biophysical characteristics of vegetation. It allows for discrimination of successional stages as its value increases toward sites with higher vegetation complexity (e.g., higher number of strata, woody species, basal area, etc, Kalácska et al. 2004). LAI was measured during the rainy season by using a LAI-2000 Plant Canopy Analyzer (LI-COR, USA). Detailed information on how measurements were recorded in each successional stage can be found in Nassar et al. 2008.

To obtain a continuous synthetic variable summarizing sampling site variation in vegetation parameters we performed a principal component analysis (PCA) of all the variables described above. Axes 1 and 2 of the PCA explained, 83% and 11% of the variation, respectively, (Appendix 1). Therefore, axis 1 scores were used as a new variable reflecting the structural complexity of each site. This new variable was used as an explanatory variable for evaluating bat responses to local scale variation in the habitat. The four vegetation parameters considered in the PCA were positively correlated with axis 1 and their eigenvector values were: IP (0.48), SP (0.52), BA (0.52) and LAI (0.48). Based on this, we can assume that axis 1 represents a successional gradient where the sites with higher structural complexity (late and intermediate stages) present higher scores.

2.3.2 Landscape scale

2.3.2.1 Image classification

The estimation of landscape metrics used as explanatory variables in the study were based on a classified image comprised of 4 ASTER, cloud free, satellite images, acquired for the Pacific coast of Mexico on December 28, 2005. This date is the most appropriate for the study as it represents an intermediate moment along the bat sampling period and corresponds to the dry season, when the highest differentiation between pastures, TDF and RF occurs (Kalacska et al. 2005, Sanchez-Azofeifa et al. 2009). TDF and RF are the focal vegetation types for our study. The four ASTER images were georeferenced to a map produced by Sanchez-Azofeifa et al. (2009) on WGS84_UTM Zone 13 North. No atmospheric correction was applied to the images.

For image classification, we employed the first three bands of the ASTER sensor (green, red and near infrared), as well as two other bands produced by the calculation of two indices: the normalized difference vegetation index (NDVI) and single ratio (SR). These indexes are useful for the discrimination of successional stages of TDF (Arroyo-Mora et al. 2005, Hartter et al. 2008). Nominal spatial resolution of all bands is 15 m.

Image classification was based on a hierarchical classification analysis, where groups of pixels were classified sequentially. During this process, we employed two algorithms for defining the group of pixels—an unsupervised classification and a supervised classification (ERDAS Imagine v.9.2). The unsupervised classification was employed for the definition of the following classes: RF (including both gallery forest located along large rivers and gallery forest located along temporary creeks), mangroves, oak forest, seasonal growing field (i.e. corn, tomato, hot pepper and watermelon), long term growing field (i.e. mango, papaya, coconut and citrus), bare soil (including dirt and paved roads) and water. The supervised classification was employed for the definition of dry forest initial successional stages (dry forest pastures and early successional stages) and dry forest advanced successional stages (dry forest intermediate and late successional stages, DF).

Supervised classification was based on selected training areas spanning 200 pixels per class. Information on training areas was collected during the 2004-2005 field work. The unsupervised classification was performed using as reference the high resolution imagery available on Google Earth (http://earth.google.com), as well as the classified image presented by Sanchez-Azofeifa et al. (2009). Finally, in order to eliminate the "noisy" results produced by wrongly classified pixels we used the neighborhood function available in ERDAS Imagine v.9.2 (Leica Geosystems, Georgia, USA). During this operation each pixel is analyzed and recoded, if necessary, based on the number and location of the pixels in the neighborhood.

For image validation we used 50 reference points per class collected in the field and on Google Earth (http://earth.google.com), which is considered an adequate number of reference points for the extension of our image and our number of classes (Congalton 1991). The final accuracy of the classified image was estimated as 0.86 and 0.84 by the overall accuracy and Tau coefficient statistics, respectively. Analyses were performed with the software Image Analysis, Ver 1.01, and Accuracy, Ver. 1.0, created by T. de Camino-Beck at the Center for Earth Observation Sciences (CEOS), University of Alberta. Detailed information about statistical calculations can be found in Congalton (1991) and Ma and Redmond (1995).

2.3.2.2 Explanatory variables at the landscape scale

Landscape metrics considered were measured at two different focal scales defined within two nested concentric circles of 500 and 1000 m radius and centered on the centroid of the mist net distributions for each sampling site (Fig. 1). The focal scales we selected allowed us to encompass the expected home range of small and medium size phyllostomids inhabiting the region (i.e. *Glossophaga soricina*: 500 m radius, Lemke 1984; *G. commissarisi*: 151 m radius, Medina et al. 2007; *Sturnira lilium*: 636 m radius, Fenton et al. 2000). Moreover, the focal scales selected allowed us to minimize spatial overlap among neighboring circles, avoiding spatial autocorrelation and to compare our results with other studies, since 500 and 1000 m focal scales have been used by previous studies (Gorrensen and Willig 2004, Klingbeil and Willig 2009, Meyer and Kalko 2008). Nevertheless, sampling sites E1, I3 and L1 were not considered in the 1000 m radius analysis to minimize spatial overlap among neighboring circles (Fig. 1).

Landscape metrics used as explanatory variables were selected based on metrics found in other studies to be associated with the occurrence or abundance of phyllostomids, as well as an appropriate number of explanatory variables for statistical analysis. We aimed to avoid saturated models without explanatory power (Crawley 2007). The three variables selected were percentage of forest cover, mean patch area, and diversity of patch types. Percentage of forest cover was defined as the sum of the areas (m^2) of all patches of a given type, divided by the total area of the plot (circle) and multiplied by 100 (to obtain percentages). Mean patch area was defined as the sum of the areas (m^2) of all patches of a given type, divided by the number of patches of such type. Diversity of patch types was defined as the probability that any two cells selected at random would represent different patch types (Simpson’s diversity index). All coverage classes considered in the image classification were used in the determination of the diversity of patch types. Conversely, percentage of forest cover and mean patch area were estimated separately for the DF and RF classes, as these are the focal classes selected to evaluate the response of phyllostomids to variation in landscape attributes.

Calculations of landscape metrics were performed using Fragstat v.3.3 (McGarigal et al. 2002). Previous raster files corresponding to the 500 and 1000 m radius images were transformed to txt files in ArcMap v.9.2. These txt files were the input files for Fragstat.

Two explanatory variables not normally distributed were transformed: mean patch area of DF at 500 and 1000 m radius (log-transformed) and mean patch area of RF at 500 m radius (square root-transformed). To assess separately the influence of mean patch area and the influence of the percentage of forest cover (as these metrics are correlated, Fahrig 2003, Gorrensen & Willig 2004), in all subsequent analyses we substituted the estimated values of mean patch area by the residual values of the regression between these variables. This allowed us to eliminate the linear effects of the association between the two metrics.

2.4 Analysis

2.4.1 Bat sampling completeness

The completeness of the bat survey was evaluated by calculating, for all sampling sites, the percentage of species that were sampled relative to the estimated species richness. For estimation of species richness we employed the first and second order jackknife indices. These indexes deal properly with small sample sizes (< 100 individuals per site), producing a low biased estimation of species richness (Colwell and Coddington 1994). Consistency of these indices of species richness estimation was evaluated by analyzing a graph of the indices values (axis y) versus the number of samplings (axis x) as suggested by Colwell and Coddington (1994). Ninety percent of completeness was considered an appropriate level of sampling efficiency (Moreno and Halffter 2001).

2.4.2 Spatial autocorrelation

Ecological data are often spatially autocorrelated, meaning that, for a given pair of sites, assemblage structure and composition are more similar than expected for randomly associated pairs of observations. This lack of independence between a pair of assemblages violates the main assumptions of standard statistical analyses, being prone to a high type-I error (Legendre and Legendre 1998). To evaluate if our dataset presents some degree of spatial structure, we generated two kinds of matrices, an ecological distance matrix and a geographical distance matrix. For the construction of the ecological distance matrix, reflecting the dissimilarities between sampling sites in terms of structure and composition of bat assemblages, we used the Bray-Curtis coefficient. For the construction of the geographical distance matrix we used the Euclidian distance between sampling sites. Finally, we used a Mantel test, based on the Spearman rank correlation coefficients, for quantifying the association between the two generated matrices. Significance level ($\alpha = 0.05$) for testing if the real correlation could equal zero was calculated based on 999 permutations. A non-significant relationship between the two generated matrices indicates non-significant spatial structure in the dataset.

2.4.3 Population, ensemble and assemblage parameters as response variables

The response of phyllostomids to habitat variation at local and landscape scales was evaluated at the population, ensemble and assemblage-level. In all cases we used the mean number of individuals captured at each sampling site as an indicator of the abundance. At the population-level, only the species represented by 25 individuals or more (7 species) were considered in the analysis. At the ensemble and assemblage-level, we also considered, as a response variable, the species density (number of species per sampling night), which was rarified at 8 sampling nights. Rarefaction allowed us to compare indices, as it eliminates biases related to differences in sampling effort used for the estimation of indices (Gotelli and Colwell 2001). The site P1 was excluded from the analysis of species density due to its low number of sampling nights.

Dissimilarities between sampling sites in terms of species identity and abundance were quantified using the Bray-Curtis coefficient (Magurran 2004). This coefficient assigns the same maximum distance to all sites not sharing any species and is one of the preferred techniques for analyzing differences in species composition (Kindt and Coe 2005). However, the final value of this coefficient is more influenced by the species with the largest difference in abundance, provoking that a value obtained from a dataset dominated by a few species, mainly will be reflecting differences for those species (Kindt and Coe 2005). To avoid this bias, the matrix of sampling sites by species abundance was standardized using the square-root. All phyllostomids, including the rare ones (whose occurrence is restricted to the late stage), were considered in the analysis.

The distance matrix produced was used as an input matrix for a non-metric multidimensional scaling ordination (NMDS), which maps the observed assemblage’s dissimilarities in term of species composition. This iterative method of ordination has the advantage of properly handling nonlinear species response of any shape (Oksanen 2010) and has a good performance even when beta diversity is high (McCune & Grace 2002). It is one of the preferred ordination methods for analyzing community data (McCune & Grace 2002). The scores of the resulting axis were employed as a response variable to evaluate the relationship between the variation in assemblage species composition and the variation in the habitat attributes.

2.4.4 Phyllostomid response to variation in habitat attributes

We evaluated the relationship between the phyllostomid response and all the explanatory variables, at the 500 and 1000 m radius scales, using generalized linear models (GLMs). The NMDS scores and the rarified species density at the ensemble and assemblage-level were modeled using a gaussian error distribution with the identity link function, as this is the error distribution that best describes the structure of the data. The abundance data at the population, ensemble and assemblage-level were modeled using a Poisson error distribution with the log link function.

In order to identify the explanatory variables most likely to causally influence the response variables at the two analyzed scales, we performed a hierarchical partitioning analysis (HPA approach) (Chevan & Sutherland 1991). In this analysis, all possible GLMs combining the explanatory variables, are jointly considered and the increase in model fit (measured by the log-likelihood) generated by certain variables, is estimated by averaging its influence over all models in which that variable appears (Chevan & Sutherland 1991, Mac Nally 2000). At the end, we obtained a measure of the independent effect of each explanatory variable over the response variable. This procedure alleviates problems of multicollinearity between the explanatory variables. Multicollinearity problems can not be properly handled by statistical sequential methods (i.e. stepwise selection), as they would tend to select spurious models due to a high type-I error (Mac Nally 2000). Significance ($\alpha = 0.05$) of relationships between explanatory and response variables was evaluated by the randomization test suggested by Mac Nally (2002).

In order to validate the robustness of the HPA outcomes (Mac Nally 2000), we compared them to the outcomes of an information-theoretical approach to model selection (Akaike's information criterion: AIC approach, Akaike 1973). This approach allows us to select the most plausible models from a set of models. In our case, the set of models considered for every response variable, at each scale, included the null model (without explanatory power) and six other models considering each explanatory variable independently. As selection of the best model using the AIC is not based on acceptance or rejection of null models, it avoids complications with type-I error in sequential searching protocols (Mac Nally 2000). We used the version of AIC corrected for small sample size (AIC_c). Then, we compared the models using Δ_i, which is the difference of AIC_c between a given model and the best (lowest AIC_c) model. We also calculated the AIC weights (w_i) for each model. The w_i represents the weight of the evidence that a certain model is the best model given the data and the set of candidate models (Burnham and Anderson 2002). The 95% confidence set of the best models was defined by summing the w_i, from the largest to the smallest, until the sum is ≥ 0.95 (Burnham and Anderson 2002). Only models with an AIC_c lower than the null model were considered to define the 95% confidence set of plausible models.

Finally, based on the results of both statistical approaches (HPA and AIC), we classified the relationships between every explanatory variable and the corresponding response variables as: (1) robust: when a significant relationship was found according to the randomization test (HPA), and when the explanatory variable was selected as part of the most plausible models (AIC approximation), (2) those denoting a tendency: when the explanatory variables were among the ones explaining the greatest portion of the variation in the response variable and they were selected as part of the most plausible models (AIC approach), although no significant relationship was observed (HPA approach), and (3) no relationship: when the explanatory variables were not among the ones explaining the greatest portion of the variation in the response variable (HPA approach), and/or they were not selected as part of the most plausible models (AIC approach).

All the statistical analyses were performed in R (R Development Core Team 2009). We used the vegan package (Oksanen et al. 2010) for the mantel test and the Bray-Curtis coefficient calculation as well as the MASS package (Venables and Ripley 2002) for the NMDS ordination.

We also employed the hier.part package (Walsh and Mac Nally 2008) for the hierarchical partitioning analysis.

3. Results

3.1 Captured bat species, bat sampling completeness and spatial autocorrelation test

One hundred and forty-two sampling nights resulted in the capture of 606 phyllostomid individuals representing 15 species, 11 genera, 5 subfamilies and 4 broad guilds (Table 1). For the mean number of captured individuals per species see Table 1. The most abundant species were *Artibeus jamaicensis*, *G. soricina* and *Desmodus rotundus* and the broad guilds best represented in terms of species richness were frugivores and nectarivores.

Sampling effort was considered sufficient to properly characterize phyllostomid assemblages occurring in each sampling site. Completeness reaches 90% in all cases, ranging from 90 (i.e. P1, E2) to 96% (i.e. I2, I3). We found no evidence of spatial structure in our dataset. Ecological and Euclidian distance matrices were not significantly correlated (r = -0.05, p = 0.59).

The species of seeds collected from bats feces are listed in the appendix 4**.**

3.2 Phyllostomid response to variation in habitat attributes

Results of the two statistical approaches used can be consulted in Appendix 2 (HPA approach) and Appendix 3 (AIC approach), and explanatory variables that are most likely to causally influence the response variables, as obtained through the contrast of results from both statistical approaches are shown in Table 2. In most cases results from the HPA and AIC approach were similar. Nevertheless, in some cases, results obtained from each statistical approach were different. For example, the percentage of RF and the mean area of RF patches, at the 1000 m scale, were selected by the AIC approach as part of the most plausible models explaining variation of *G. soricina* abundance (Appendix 3), whereas according to the HPA approach (Appendix 2), these variables were not associated with variation of *G. soricina* abundance. Another example is that, at the 500 m scale, variation in *D. rotundus* abundance was associated (significantly) with the complexity of vegetation structure by the HPA approach (Appendix 2), whereas the AIC approach did not select this parameter among the variables explaining *D. rotundus* abundance variation (Appendix 3).

We also observed that phyllostomid response to variation in habitat attributes was scale-dependent, since variation in some explanatory variables was associated with variation in some response variables at just one of the two analyzed scales (Table 2).These results were obtained at both the population and assemblage-level.

3.2.1 Population-level

Species represented by 25 or more individuals (3 frugivores, 3 nectarivores and 1 sanguivore) showed a mean number of captured individuals ranging from 0.14 (*Artibeus phaeotis*) to 1.26 (*A. jamaicensis*) (Table 1).

Summarizing the results obtained through both statistical approaches, we found that variation in abundance of the three nectarivorous species was not robustly associated with the variation of any explanatory variable at the two focal scales (Table 2). Nevertheless, abundance tended to be negatively associated, at the two scales, with variation in the mean area of DF patches. We also identified a tendency for a positive association between *G. soricina* abundance and the diversity of land cover types (Table 2). On the other hand, while *G. soricina* only responded to changes in habitat attributes at the 500 m focal scale, *Leptonycteris yerbabuenae* only responded to such changes at the 1000 m focal scale.

Most of the variation in abundance of frugivorous species was positively associated with variations in percentage of RF (all species) and complexity of vegetation structure (*A. jamaicensis* and *A. phaeotis*). We also detected, at the 1000 m focal scale, that the mean area of DF patches tended to be associated with the abundance of both frugivores, *A. jamaicensis* (negative association) and *Artibeus lituratus* (positive association) (Table 2).

The abundance of the sanguivorous species, *D. rotundus*, was positively associated with variations in the percentage of RF (at the 500m focal scale) and the mean area of RF patches (at the 1000m focal scale) (Table 2).

3.2.2 Ensemble-level

Similar to the trends found at the population-level, the average number of nectarivorous individuals captured during each sampling, tended to be negatively associated, at the two scales, with variations in the mean area of DF patches. No explanatory variable was associated with the variation in the number of nectarivorous species rarified at 8 samples. Nevertheless, the variation in the number of frugivorous species rarified at 8 samples, was positively associated with variations in the complexity of vegetation structure. In contrast, the abundance of frugivores was tightly and positively associated with the percentage of RF estimated at the two scales.

3.2.3 Assemblage-level

The NMDS ordination (*stress* = 8.20 and correlation based on stress: $R^2 = 0.99$) is shown in Figure 2. Only two axes were considered because additional dimensions did not substantially lower the stress value. A successional gradient is represented along axis 2. In general, phyllostomid assemblages occurring in pastures tended to present higher scores and those occurring in late stages tended to present lower scores. Axis 1 did not show a clear gradient.

The gradient of vegetation structure complexity found along the successional gradient of PCA axis 1(Appendix 1) significantly explains at the 500 m scale, assemblage dissimilarities represented by NMDS axis 2 (Fig. 2, Table 2). Variation in assemblage species composition represented by NMDS axis 2, also was negatively associated, at the two scales, with the percentage of RF (Table 2). None of the considered explanatory variables were associated with variation represented by NMDS axis 1.

Phyllostomid abundance was also significantly associated with the percentage of RF (at the 500 m scale) and with the mean area of RF patches. No explanatory variables were associated with the variation in the number of phyllostomid species rarified at 8 samples.

4. Discussion

4.1 Bat response at population and ensemble-level

As expected, we found a guild-specific response to changes in local and landscape habitat attributes. At both the population and ensemble-level, nectarivore abundance tended to be negatively associated with the mean area of DF patches, while its species density was not associated with any of the considered explanatory variables. Frugivore abundance was tightly and positively associated with the percentage of RF while its species density and some species abundances were explained by the variation in the vegetation structural complexity. Similar to frugivores, the abundance of the unique sanguivorous species present in the region was positively associated with the amount of RF. Similar results (guild-specific bat response) have been found by Klingbeil and Willig (2009) in Amazonian rainforest, where frugivore abundance responded more to changes in landscape composition than to changes in landscape configuration, while gleaning animalivorous bats responded more to changes in landscape configuration. The guild-specific response of bats to variation in habitat attributes is likely due to the contrasting ecological requirements among bats of different ensembles.

The lack of relationship between nectarivore species density and the considered habitat attributes probably occurs because three of the five nectarivores reported in this study are ubiquitous. These species (*G. soricina*, *G. commissarisi* and *L. yerbabuenae*) were present in most of the sampling sites and successional stages with the exception of pastures, where only 3 individuals of *G. soricina* were captured (Avila-Cabadilla et al. 2009). On the other hand, the two species most susceptible to variation in habitat attributes (*C. godmani* and *M. harrisoni*), were strictly associated with the less disturbed areas (Avila-Cabadilla et al. 2009), being scarcely represented (one individual) in two of the three sites representing the late successional stage (Table 2 on Avila-Cabadilla et al. 2009).

The negative association between nectarivore abundance, at the population and ensemble-level, and the mean area of DF patches, could be attributable to the fact that the three most abundant nectarivores (*G. soricina*, *G. commissarisi* and *L. yerbabuenae*) are not dependent on large DF patches. All three nectarivorous species occur at an elevated abundance in the early successional stage, characterized by the presence of shrubs and some non-native grasses (Avila-Cabadilla et al. 2009). In fact, *Acacia farnesiana* and *Cordia alliodora*, highly abundant trees in secondary vegetation (i.e. early stage, P. Balvanera et al. unpublished data), have been previously reported as chiropterophilic species (Alvarez and González-Quintero 1970, Alvarez and Sanchez-Casa 1997, Tellez and Ortega 1999). *Glossophaga soricina*, *G. commissarisi* and *L. yerbabuenae* are well adapted to inhabit regions where vegetation has a simple structure, mostly dry areas (Arita and Santos del Prado 1999) like deserts, arid grasslands, scrublands, oak forests and lowland tropical and subtropical dry forests (Alvarez et al. 1991, Arita 1991, Cole & Wilson 2006, Webster and Jones 1993). Moreover, they are well adapted to exploit trophic resources (i.e. plants of the family Cactaceae and Asparageceae: genus *Agave*) available in these areas (Geiselman et al. 2002 onward, Valiente-Banuet et al. 1996). Nevertheless, in our study area, the abundance of these species suffered a drastic reduction in pastures, where non-native grasses predominate (Avila-Cabadilla et al. 2009) affecting the reproductive success of remnant chiropterophilic trees (Quesada et al. 2003).

In the case of *L. yerbabuenae,* which can fly up to 5 h and cover distances of up to100 km per night, the long commuting flights are a basic component of its foraging ecology (Horner et al. 1998). This high commuting capacity allows it to easily travel and exploit resources available in the anthropogenic landscape. This migratory species (Cockrum 1991), whose diet consist mainly of nectar and pollen and occasionally is supplemented with fruit (Cole and Wilson 2006), reaches its peak of abundance and reproductive activity in the region during the peak of flower resources (Stoner et al. 2003).

In contrast to *L. yerbabueanae, Glossophaga* spp. have relatively small home ranges and they do not cover much distance during foraging bouts (Lemke 1984, Medina *et al* 2007). Moreover, *Glossophaga* spp. is a generalist nectarivore with a high plasticity in terms of dietary behavior, complementing their nectar and pollen diet with fruit and insects. For *G. soricina* Herrera et al. (2001) found that most of the year in Chamela, insects are more important as a source of protein (51-75% of proteins) than plants. Both species are able to roost in a variety of places including: caves, trees, rock crevices, and man-made structures such as mines and abandoned buildings (Alvarez et al. 1991, Heithaus et al. 1975, Rodrigues et al 2007, Webster and Jones 1993). The high ecological plasticity of these two species allows them to exploit a variety of habitats in the disturbed landscape. This capability appears to be higher in *G. soricina*, the unique species positively responding to an increase in diversity of land cover types (Table 2).

In fact, a trend has been identified in nectarivores` response to habitat disturbance in Neotropical moist and rain forest—when they present generalist feeding and habitat preferences and feed primarily on early-successional chiropterocorous species (i.e. *Cecropia, Piper, Solanum*) and chiropterophilic plants associated with modified habitats (i.e. *Parkia pendula* abundant in cabrucas sites, *Manilkara zapota* abundant in cocoa plantations) (Estrada et al 1993a, Faria and Baumgarten 2007), they appear to be unaffected or exhibit greater abundances in disturbed habitats (i.e. areas subject to selective logging, banana, cacao and coffee agroforestry, cornfields, forest gaps, forest edges and secondary vegetation) than in undisturbed sites (Castro-Arellano et al. 2007, Castro-Luna et al. 2007, Clarke et al. 2005b, Brosset et al. 1996, Estrada et al. 1993a, Fenton et al. 1992, Harvey and González 2007, Mancina et al. 2007, Medellín et al. 2000, Meyer and Kalko 2008, Peters et al. 2006). This is the case for several species including *G. soricina, G. commissarisi*, *Lonchophylla robusta*, *Monophyllus redmani* and *Phyllonycteris poeyi.*

In contrast to the nectarivores' response, the frugivorous species` density, as well as the abundance of some frugivorous bats (*A. jamaicensis* and *A. phaeotis*) increased toward the more advanced successional stages, which present the highest structural complexity of vegetation (Appendix 1, Table 2). These positive associations can be explained by an increase in the diversity and amount of resources (i.e. food and shelter) as a consequence of the increase in the complexity of vegetation structure. Indeed, in pastures, the sites with the simplest vegetation structure, only three species of frugivores occurred (*A. jamaicensis*, *A. watsoni*, and *A. lituratus*) while in late successional stages, 8 species occurred, three of them (*Carollia sp*., *Centurio senex* and *Chiroderma salvini*) exclusively found in mature forest (Avila-Cabadilla et al. 2009). Many of the frugivorous species we found are flexible in their roosting requirements using foliage, hollow trees, tunnels, caves and abandoned buildings (Avila-Flores et al. 2004, Ceballos and Miranda 2000, Fenton et al. 2000, Ortíz-Ramírez et al. 2006). However, in the study region, almost all bat species depend, to a large extent, on roosts found exclusively in vegetation. This is probably due to the few caves and tunnels found in the area— just two sea caves, one on Don Panchito Island, and the other in Piratas Beach. Nevertheless, the cave on Don Panchito Island is mainly used by *L.*

yerbabuenae, which occupies almost the entire cave during its mating period (October to January); only a few moormopid species such as *Pteronotus parnellii*, *P. davyi*, *P. personatus* and *Mormoops megalophylla* can sometimes be found in the cave at this time (Stoner et al. 2003). Moreover, in the Neotropics the loss of trees due to grazing and agricultural practices can negatively influence frugivorous bat abundance by affecting their ability to locate suitable roosting sites, as they preferentially roost in hollow trees found in mature forest or in advanced successional stages (Fleming 1988, Evelyn and Stiles 2003, Ortíz-Ramírez et al. 2006).

Only one study (Vargas et al. 2009) directly evaluated the relationship between vegetation complexity and the diversity and abundance of chiropterochorous plants in the Neotropics. In this study, the authors found that the most complex habitat did not harbor the greatest diversity, fruit mass and fruit density of chiropterochorous plants. However, this study was performed in a moister environment (Calakmul, Mexico) and compared different types of forest (i.e. tropical subhumid and semi-deciduos forest). In our case, several of the chiropterochoric resources most important for frugivorous bats in the region (Appendix 4) belong to the Cactaceae and Moraceae families, which mainly occur in the more advanced successional stages (P. Balvanera et al. unpublished data) while the early successional forests show the simplest vegetation structure and are dominated by anemochorous and autochorous plants which do not constitute food resources for frugivorous bats (Vieira and Scariot 2006). This contrasts with the patterns found in tropical humid and rain forest, where chiropterochorous species such as *Cecropia* spp., *Piper* spp., *Solanum* spp., and *Vismia* spp., are dominant in the early stages of succession (Brosset et al. 1996, Fleming 1988).

Several studies show *A. jamaicensis* to be one of the most abundant species in phyllostomid bat assemblages while *A. phaeotis* represents an intermediate level of abundance (Castro-Luna et al 2007, Mancina et al. 2007, Medellín et al. 2000, Meyer and Kalko 2008). These species are both conspicuous in modified landscapes as they occur in a diverse array of habitat types. In moist and rain forests, Castro-Luna et al. (2007), Mancina et al. (2007) and Medellín et al. (2000) captured more specimens of *A. jamaicensis* in habitats or successional stages exhibiting the highest vegetation complexity. In contrast, similar numbers of s *A. phaeotis* were captured in habitats differing in vegetation structure, suggesting no response of this species to changes in this vegetation attribute (Castro-Luna et al. 2007, Medellín et al. 2000). In our case, the positive association between *A. jamaicensi*s and *A. phaeotis* abundance and the degree of complexity of dry forest vegetation structure can be explained by a greater availability of chiropterochoreous fruits in sites with higher complexity. This, in addition to the potential greater availability of roosts in such sites, is the most likely explanation for this result.

Among the seeds best represented in the feces of both species collected during the census period, we found *Ficus cotinifolia*, a species mostly associated with more advanced TDF successional stages (P. Balvanera, et al. unpublished data). Almost all of the other seeds found (for *A. jamaicensis*: *Ficus obtusifolia*, for *A. phaeotis*: *Piper arboretum*, for both species: *F. pertusa* and *F. insipida*), correspond to species of RF (see Appendix 4), which possibly explains the positive association detected between the abundance of these bat species and the percentage of RF (Table 2). *Artibeus jamaicensis* in particular, shows a high trophic plasticity as it complements its diet with others sources of food like nectar, pollen and insects (Ortega and Castro-Arellano 2001). This, added to its high capability of covering long distances in a single night (8 ± 2 km, Morrison 1978), could allow this species to exploit resources available in areas with an intermediate level of disturbance (early and intermediate stages). These facts could also explain the negative association found, at the 1000 m scale, between *A. jamaicensis* abundance and the mean area of DF patches. Only a few individuals of this species were captured in pastures (Avila-Cabadilla et al. 2009).

The abundance of the other frugivore analyzed (*A. lituratus*), as well as the overall abundance of frugivorous bats, also was positively related to the percentage of RF. This strong association likely occurs because most of the plant species used by frugivorous bats in the region occur almost exclusively in RF (Fig. 3B, Appendix 4). This is the case for Moraceae (4 species) and Piperaceae (2 species), which are preferred, respectively, by the two most specious genera, *Artibeus* and *Carollia* (based on data collected from feces in our study and from Lobova et al. 2009). Although several chiropterochorous Cactaceae occur in the dry forest, we did not find cactus seeds in any of our fecal samples, suggesting that Cactaceae are not among the most important species used by frugivorous bats in this area.

Artibeus lituratus is a large canopy frugivore able to forage in open spaces of the upper canopy while utilizing creek corridors and tree fall gaps (Lobova et al. 2009). It is tightly associated with pristine forest and humid environments, although it has been reported in dry areas, including the Brazilean Caatinga, as well as in small urban areas (Zortéa 2007). Despite the large list of species (approximately 146 fruit species) consumed by this bat, in addition to supplementing its´ diet with nectar, pollen and insects), in several regions this species appears to be selective for the fruits it consumes (Lobova et al. 2009). In our study, *A. lituratus* was one of the species occasionally found in pastures (only one individual was captured). Nevertheless, its abundance is higher in areas showing the highest percentage of RF and the highest mean area of DF patches (Table 2). This suggests a high association of this species with large continuous forest and humid areas where their main food species are found (*Ficus insipida* and *F. pertusa;* Appendix 4). Several captured individuals of *A. lituratus* were previously identified as *A. intermedius* (Table 2 on Avila-Cabadilla et al. 2009), but re-classified as *A. lituratus* based on Redondo et al. (2008) and Hoofer et al. (2008).

We found a marked difference between the nectarivore and frugivore ensembles in relation to their response to variations in landscape compositional attributes regarding the two types of vegetation cover. Variations in nectarivore abundance tended to be associated with variation in landscape attributes concerning DF while variation in frugivore abundance was tightly associated to variation in landscape attributes concerning RF. This guild-specific response could be a consequence of the differences between dry and riparian forest in terms of the availability of resources for both guilds (Fig. 3). Although dry and riparian forest host an equal number of chiropterochorous plant families and species (8 families, 12 species), the plants preferentially used by most of the frugivorous species (Moraceae, Piperaceae) are almost exclusively found in riparian forest (Lobova et al. 2009). On the other hand, most chiropterophilic species (23 species from 9 families), as well as the chiropterochorous Cactaceae species, occur in the dry forest, constituting an important food resource for nectarivorous bats (seeds from fecal samples, Stoner et al. 2003, Lobova et al. 2009). Only 8 chiropterophilic species, representing 6 plant families, occur in the RF. Consequently, in the region, dry forest hosts more plant species that constitute resources for nectarivores than riparian forest, while riparian forest hosts the plant species principally consumed by frugivores (Fig. 3). Similar tendencies were reported in this same region, albeit comparing bat assemblages occurring in only one dry and one riparian forest. Chavez and Ceballos (2001) found that nectarivores were best represented in the dry forest vegetation, where two of the three captured species (*L. yerbabuenae*, *M. harrisoni*) were exclusively found. With respect to frugivorous bats, two of the three most abundant species (*A. lituratus*, *A. jamaicensis*) occurred at higher abundance in riparian forest, while the other frugivorous species (*A. phaeotis*) was more abundant in the dry forest.

The abundance of the sanguivorous guild represented by the unique species *D. rotundus* was positively associated with the percentage of RF (at the 500 m scale) and the mean area of RF patches (at the 1000m scale). We propose three non-exclusive explanations for this result. First, *D. rotundus* uses the RF for roosting and/or as stepping stones when searching for food in the vegetation matrix where cattle occur. This mechanism previously was suggested by Estrada and Coates-Estrada (2002) for explaining how this species uses forested areas when searching for food in pasture-dominated landscapes. Moreover, according to Lord (1988) and Taddei et al. (1991) riparian areas present higher abundances of *D. rotundus* because of the higher roost availability in this habitat. According to Novaes et al. (2010), the frequency of vampires feeding on cattle is best explained by distance to forest fragments, being higher in areas closer to fragments.

A second possible explanation for the positive association between vampires and RF may be because there is a higher availability of the sanguivores native food sources (mammals) in these habitats. Riparian forests contain important resources for the maintenance and connectivity of the home ranges of medium and large-sized mammals (Núñez et al. 2000, Sanchez-Azofeifa et al. 2009, Saunders et al. 1991, Valenzuela and Ceballos 2000). Moreover, some mammal species concentrate their activities in RF during the dry season when most resources are limited in the region (Sanchez-Azofeifa et al. 2009).

Finally, the last explanation may come from the fact that in the Chamela-Cuixmala region RF also hosts a higher source of non-native food for sanguivorous bats (i.e. cattle, personal observation). Riparian forest, *sensu* the present study, occurs on the alluvial terraces along the channels of ephemeral and permanent streams. As these areas constitute the most important source of water for cattle in the dry forest mosaic of vegetation, farmers concentrate cattle in these areas; this concentration reaches a maximum during the dry season (Pers. Obs). Novaes et al. (2010) found that bat attacks on cattle were more frequent in areas with higher cattle density as cattle constitute an important attractant for sanguivores.

In general, *D. rotundu*s is well adapted to habitat modifications (Bonaccorso 1979, Lord 1988) because of its plasticity in selecting places for roosting (i.e. hollow trees, caves, tunnels, abandoned mines and human buildings) and because introduced domestic mammals (i.e. bovine and equine) constitute a great source of food (Ceballos and Miranda 2000, Greenhall et al. 1983, Oliveira et al. 2009). For this reason, this species has been considered as a good indicator of habitat disturbance, being abundant in modified sites (Medellín et al. 2000). Nevertheless, *D. rotundus* behavior in a tropical moist forest chronosequence, exhibited no pattern with respect to the degree of succession (Castro-Luna et al. 2007).

4.2 Bat response at assemblage-level

As expected, a portion of the variation among phyllostomid bat assemblages, in terms of species composition and structure (NMDS axis 2, Fig. 2), was tightly associated with variations in vegetation structural complexity and riparian vegetation cover. Phyllostomid abundance was significantly associated with the percentage of RF (at 500 m scale) and with the mean area of RF patches (at 1000 m scale). These results integrate the results obtained at the species and ensemble-level.

The association between the variation in assemblage species composition and structure, and the variation in vegetation structural complexity has several potential explanations. First, a group of species may be found exclusively in sites with a determined vegetation structure. This is the case for rare species (represented by one individual) and some species with an intermediate level of abundance (*Micronycteris microtis*, *Musonycteris harrisoni*, *Choeroniscus godmani*, *Carollia* sp., *Centurio senex*, *Chiroderma salvini*), which are strictly associated with late successional stages (Table 2 and Fig. 2 on Avila-Cabadilla et al. 2009). In fact, *M. microtis*, *M. harrisoni*, *C. godmani and C. senex* already have been identified as forest dwelling species (Alvarez and

Sanchez-Casas 1997, Estrada et al. 1993a, Fenton et al. 1992, Schulze et al. 2000, Stoner et al. 2002). Another explanation may be that variation of some species abundance is tightly associated with variation in vegetation structure. This is the case for some of the most abundant frugivorous species, which in spite of the fact that they are found in a variety of sites with different vegetation structure, their abundance varies greatly among these. As discussed above, these responses could follow variations in availability of roosting sites and/or food for the species sensitive to these changes.

The positive association between the variation in the amount of RF and the variation in assemblage species composition and structure could be mainly a consequence of the frugivore response, as they constitute the best represented ensemble in terms of species richness and number of captured individuals. The abundance of the three most common frugivores as well as the abundance of all frugivores, tends to increase towards sites with greater RF, possibly because of the previously discussed increase in food availability in these habitats.

4.3 Importance of considering different scales and statistical approximations

In accordance with previous studies (Gorrensen & Willig 2004, Gorrensen et al. 2005, Klingbeil and Willig 2009, Meyer and Kalko 2008), our results showed that bat responses to habitat modification are scale-dependent. Such dependence can be due to the species-specific degree of mobility, habitat requirements and life-history characteristics (Klingbeil and Willig 2009). These results indicate that the spatial scale must be taken into account when determining habitat attributes whose variation defines bat response in a transformed landscape. A single scale approach may be inadequate for understanding bat response to habitat modifications. Thus, ecological models used as a baseline for bat conservation must consider a multi-spatial scale approach when modeling associations between bat responses and variations in landscape attributes. As most of the studies evaluating bat response to habitat modification have been performed at a single landscape scale (Meyer and Kalko 2008), this suggested approach should be taken into account.

Larger scales than the ones considered in our study were found to be relevant for phyllostomids in other studies (Gorrensen & Willig 2004, Gorrensen et al. 2005, Klingbeil and Willig 2009, Meyer and Kalko 2008). In some of them, larger scales showed a greater number of bat responses to landscape characteristics than smaller scales. In our study, restrictions on the availability of sampling sites with the required conditions precluded the consideration of larger spatial scales in the analysis. Nevertheless, even at the 500 m scale, variations in landscape attributes were associated with variations in phyllostomid abundance. This may result from the prevalence of small-sized bats in the analyzed assemblages.

The two statistical approaches we employed have been used recently for identifying habitat attributes whose variation may explain bat response to habitat modifications (Klingbeil and Willig 2009, Meyer and Kalko 2008). Analysis applying both approaches to the same dataset can, on certain occasions, result in different outcomes (as in the present study). Therefore, it is necessary to compare outcomes resulting from different statistical approximations in order to identify the most relevant associations among bat responses and variation in habitat attributes.

4.4 Implications for phyllostomid bat conservation

In accordance with some previous studies (Brosset et al. 1996, Cosson et al 1999a, b, Fenton et al. 1992, Gorrensen and Willig 2004, Klingbeil and Willig 2009, Medellín et al. 2000), our results reflect phyllostomid bat sensitivity to habitat loss or modification, in the form of species and guild-specific responses to variation in habitat attributes at both local and landscape scales. Specifically, bat response to habitat modification was largely determined by variation in local (vegetation) and landscape attributes.

In TDF, large expanses of continuous mature forest have been substituted by a mosaic of fragments representing different successional stages, pasture lands and agricultural fields (Quesada and Stoner 2004, Sanchez-Azofeifa et al. 2005). The long-term successful conservation of phyllostomids under this scenario can only be achieved if TDF management plans incorporate a landscape perspective adopting the vision that conservation of context is as important as conservation of content. Furthermore, appropriate policies must be implemented to eliminate unsustainable land use practices guaranteeing the maintenance of most of the original biodiversity.

In order to preserve phyllostomid bat assemblages and the ecosystem services they provide, we suggest the following actions and policies must be enforced:

1. Land-use policies must focus on the maintenance of large areas of mature forest. The loss or significant reduction of TDF can provoke a decrease in the abundance or even the local extinction of some phyllostomids. The most affected species will be the rare ones, the most tightly associated to well preserved forest due to their specialization in diet and habitat (Avila-Cabadilla et al. 2009). The presence of preserved forest in the region will favor the conservation not only of the rare species, but also of the abundant ones as they find in this forest an important source of resources.
2. The conservation and restoration of RF must be prioritized in dry forest landscapes. RF is scarcely represented (only 3.7% of land cover) and barely protected (only 2.0% is inside the Reserve) in the study region (Sanchez-Azofeifa et al. 2009). This habitat and its surrounding areas have been extensively affected by agricultural and cattle production as they represent the main source of water and fertile soils (Maass et al. 2005, Sanchez-Azofeifa et al. 2009). Bat abundance at the species, ensemble and assemblage-levels is negatively affected by reductions in the amount of RF as this habitat represents an important source of trophic resources for a great percentage of

phyllostomids inhabiting the region, especially for the frugivores (Fig. 3). The amount of RF can be even more critical for bat assemblages during the dry season, when availability of food is limited in TDF and most resources are concentrated in RF (Sanchez-Azofeifa et al. 2009); however, more studies evaluating this pattern are needed. In addition, RF can play an important role in the maintenance and connectivity of bats´ home ranges functioning as a vegetation corridor across the agricultural landscape, providing physical connectivity among isolated forests or acting as stepping stones (Estrada and Coates-Estrada 2001, Medina et al. 2007).

3. Land-use policies must focus on the reduction and shift of cattle raising, an environmentally destructive and inefficient practice in TDF (Maass 1995, Maass et al. 2005, Quesada and Stoner 2004) to alternative sources of economic gains. Phyllostomid bat assemblages occurring in pastures are depauperate in comparison to the ones occurring in more advanced successional stages. This indicates that a pasture-dominated landscape would cause a strong reduction in phyllostomid diversity. Although small scale habitat transformation may not preclude the free movement of bats across the vegetation matrix, large extensions of open areas can negatively affect their movement (Bernard & Fenton 2003, Gorchov et al. 1993, Klingbeil & Willig 2009). Thus, the threshold of minimum pasture size allowing bats to cross must be determined in order to contribute to designing “fauna-friendly” agricultural landscapes.

4. Policies must also consider the inclusion of secondary vegetation (Rendón-Carmona et al. 2009) in conservation areas/programs as suggested by the “Red de Areas Ejidales Protegidas” proposed by Sanchez-Azofeifa et al. (2009). A great portion of the phyllostomids in the study region occurs, and presumably exploit available resources in areas of secondary vegetation. In fact some species of nectarivores show a higher abundance in secondary vegetation compared to mature forest. Consequently, secondary vegetation must be considered as an important habitat for preserving bat diversity. Other studies have reported high bat species richness in moderately disturbed areas (i.e.

Bernard and Fenton 2002, 2003; Estrada et al., 1993a,b; Gorrensen and Willig 2004; Klingbeil and Willig 2009, Willig et al. 2007).

4.5 Study's relevance

This is the first study evaluating, at a landscape level, how variation in habitat attributes determines the occurrence of bats in a Neotropical dry forest landscape. Our study is also one of the few that compares local vs landscape level importance of habitat attributes in determining bat occurrence (Meyer & Kalko 2008) in different TDF successional stages (Castro-Luna et al. 2007). This approach is extremely important as the predominance of different successional stages is a recurrent feature of current Neotropical landscapes. Finally, our study shows how simplistic approximations, where fragments mostly representing one type of vegetation cover are considered as imbibed in a neutral matrix (real or not), will not allow us to understand the complex processes and mechanisms involved in the dynamics of biological communities and populations.

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TABLES

Table 1. Summary statistics (mean, standard deviation, and range) of phyllostomid species abundance (average number of individuals captured each night at each sampling site) and parameters at the ensemble and assemblage-level analyzed as response variables. Only taxa in bold were analyzed at the population level. n: number of sampling sites. SD: standard deviation. Ensemble (GI: gleaning insectivores, N: nectarivores , F: frugivores and S: sanguivores). Parameters at ensemble level: S_8(N) and S_8(F) –number of nectarivorous (N) and frugivorous (F) species rarified at 8 samples, Ab(N) and Ab(F) –average number of nectarivorous and frugivorous individuals captured each night at each sampling site. Parameters at assemblage level: SC_1 and SC_2 -scores of the first and second NMDS axis, reflecting sampling site dissimilarities according to the species composition of the phyllostomid assemblage, S_8(P) –number of phyllostomid (P) species rarified at 8 samples, and Ab(P) –average number of phyllostomid individuals captured each night at each sampling site.

	Ensemble	***n***	**Mean**	**SD**	**Range**
Population-level					
Micronycteri microtis	GI	12	0.00	0.02	0-0.06
Glossophaga soricina	N	12	0.62	0.68	0-2.00
Glossophaga commissarisi	N	12	0.17	0.32	0-1.14
Leptonycteris yerbabuenae	N	12	0.20	0.37	0-1.07
Choeroniscus godmani	N	12	0.00	0.02	0-0.06
Musonycteris harrisoni	N	12	0.01	0.02	0-0.06
Carollia sp.	F	12	0.03	0.11	0-0.39
Artibeus jamaicensis	F	12	1.26	1.72	0-6.22
Artibeus watsoni	F	12	0.09	0.14	0-0.47
Artibeus phaeotis	F	12	0.14	0.23	0-0.72
Artibeus lituratus	F	12	0.24	0.36	0-1.28
Sturnira lilium	F	12	0.07	0.12	0-0.29
Centurio senex	F	12	0.01	0.03	0-0.11
Chiroderma salvini	F	12	0.01	0.03	0-0.11
Desmodus rotundus	S	12	0.60	1.08	0-3.78

Table 1. continued

	Ensemble	***n***	**Mean**	**SD**	**Range**
Ensemble-level					
S_8(N)	N	11	1.65	1.06	0-2.98
Ab(N)	N	12	1.00	1.29	0-4.21
S_8(F)	F	11	2.65	1.18	1-5.14
Ab(F)	F	12	2.52	3.15	0.38-14.22
Assemblage-level					
SC_1		12	0	0.50	-0.99-0.58
SC_2		12	0	0.55	-0.75-1.17
S_8(P)		11	4.61	1.97	1.00-8.04
Ab(P)		12	3.46	3.89	0.38-14.22

Table 2. Summary of robust relationships and tendencies of association between response and explanatory variables, as obtained from comparing results of both statistical approaches (HPA and AIC). Response variables at population level: species abundance; at ensemble and assemblage levels variables are as in Table 1. Explanatory variables are as in Table 2.

		Type of relationships among variables	
Response variable	**Scale**	**Robust**	**Tendency**
Population level			
Nectarivore			
G. soricina	500		DF_{area}(-); Div
G. commissarisi	500		DF_{area}(-)
	1000		DF_{area}(-)
L. yerbabuenae	1000		DF_{area}(-)
Frugivore			
A. jamaicensis	500	V_{struct}	$RF_{\%}$
	1000		DF_{area}(-)
A. phaeotis	500		V_{struct}; $RF_{\%}$
	1000		$RF_{\%}$
A. lituratus	500	$RF_{\%}$	
	1000		DF_{area}; $RF_{\%}$
Sanguivore			
D. rotundus	500	$RF_{\%}$	
	1000		RF_{area}
Ensemble-level			
Nectarivore			
Ab(N)	500		DF_{area}(-)
	1000		DF_{area}(-)
Frugivore			
S_8(F)	500	V_{struct}	
	1000		V_{struct}
Ab(F)	500	$RF_{\%}$	
	1000	$RF_{\%}$	
Assemblage-level			
SC_2	500	V_{struct}(-); $RF_{\%}$(-)	
	1000		$RF_{\%}$(-)
Ab(P)	500	$RF_{\%}$	
	1000	RF_{area}	

FIGURES

Figure 1. Classified image of the study region showing the twelve sampling sites and the concentric circles of 500 and 1000 m radius delimited around each site for estimating the landscape attributes. Sampling sites E1, I3 and L1 were not considered in the analysis at the 1000 m scale in order to avoid a high degree of overlap with the analyzed areas of adjacent sites. The dark lines represent the limits of the Chamela-Cuixmala Biosphere Reserve. Only land cover types considered in the analyses are represented. Light gray represents intermediate and late stages of dry forest (DF) and dark gray represents the riparian forest (RF). Successional stages (P: pastures, E: early, I: intermediate and L: late).

Figure 2. NMDS ordination of sampling sites representing different successional stages, based on the identity and abundance of phyllostomid species occurring in these sites. The matrix used in the analysis was built using the Bray-Curtis index (Magurran 2004). Successional stages (P: pastures, E: early, I: intermediate and L: late). NMDS 1 and 2: axis 1 and 2 of the ordination.

Figure 3. Number of chiropterophilic (A) and chiropterochoric (B) species present in the dry and riparian forest (white and black bars respectively) of the Chamela region. The entire species' checklist and detailed information on how it was generated appear in Appendix 4.

Figure 1.

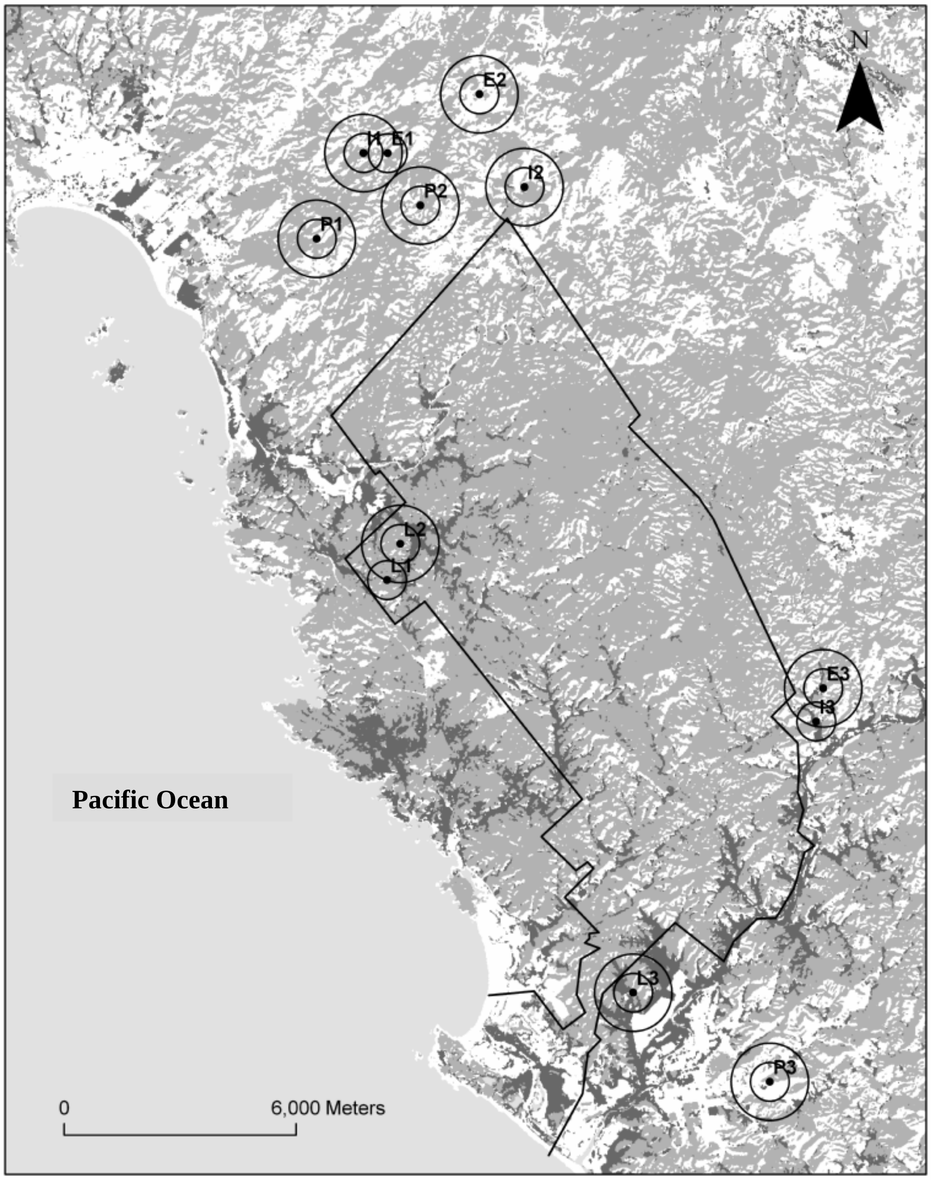


Figure 2.

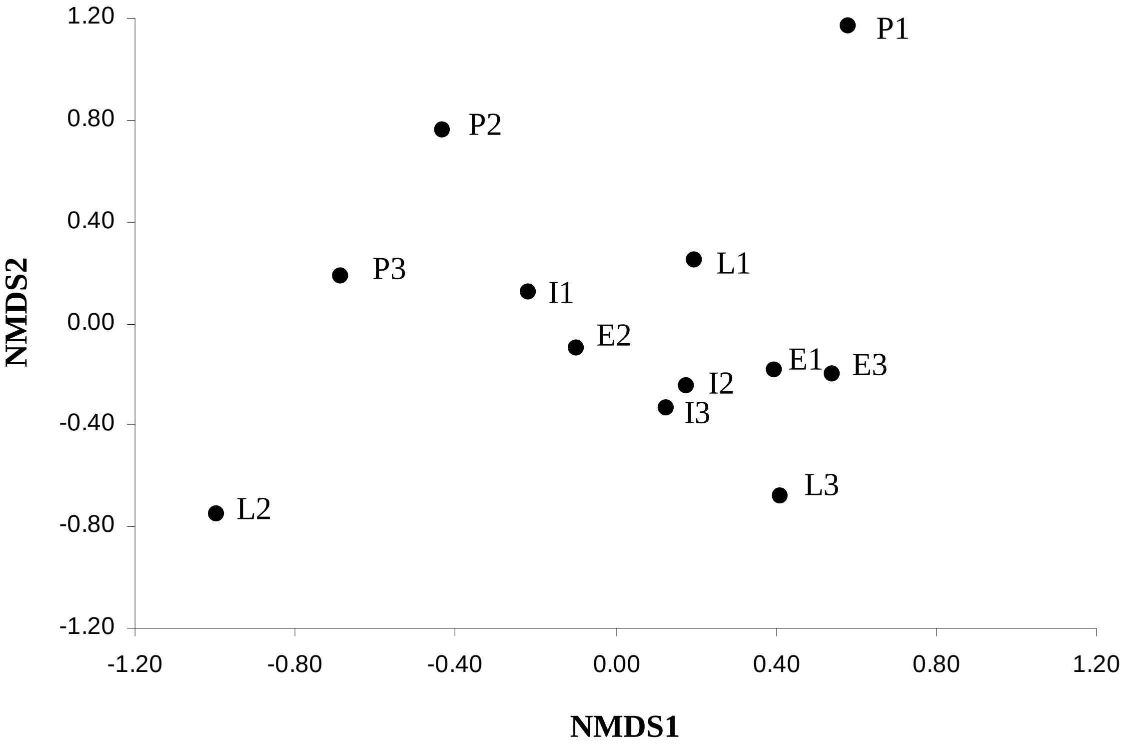
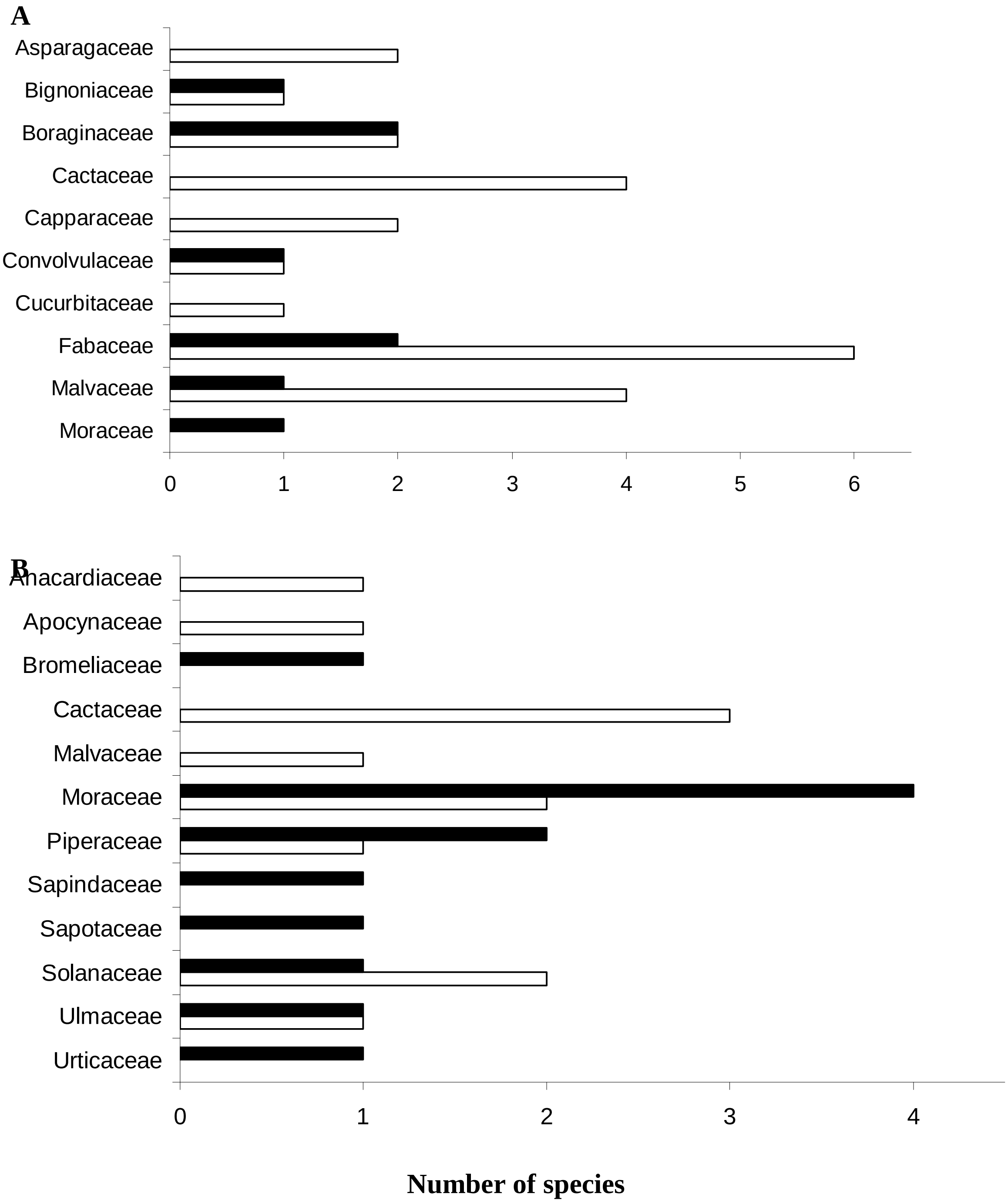

P1
P2
P3
I1
L1
E2
E1
E3
I2
I3
L3
L2
1.20
0.80
0.40
0.00
-0.40
-0.80
-1.20
-1.20
-0.80
-0.40
0.00
0.40
0.80
1.20
NMDS2
NMDS1

Figure 3.


A
Asparagaceae
Bignoniaceae
Boraginaceae
Cactaceae
Capparaceae
Convolvulaceae
Cucurbitaceae
Fabaceae
Malvaceae
Moraceae
0
1
2
3
4
5
6
B
Anacardiaceae
Apocynaceae
Bromeliaceae
Cactaceae
Malvaceae
Moraceae
Piperaceae
Sapindaceae
Sapotaceae
Solanaceae
Ulmaceae
Urticaceae
0
1
2
3
4
Number of species

APPENDIXES

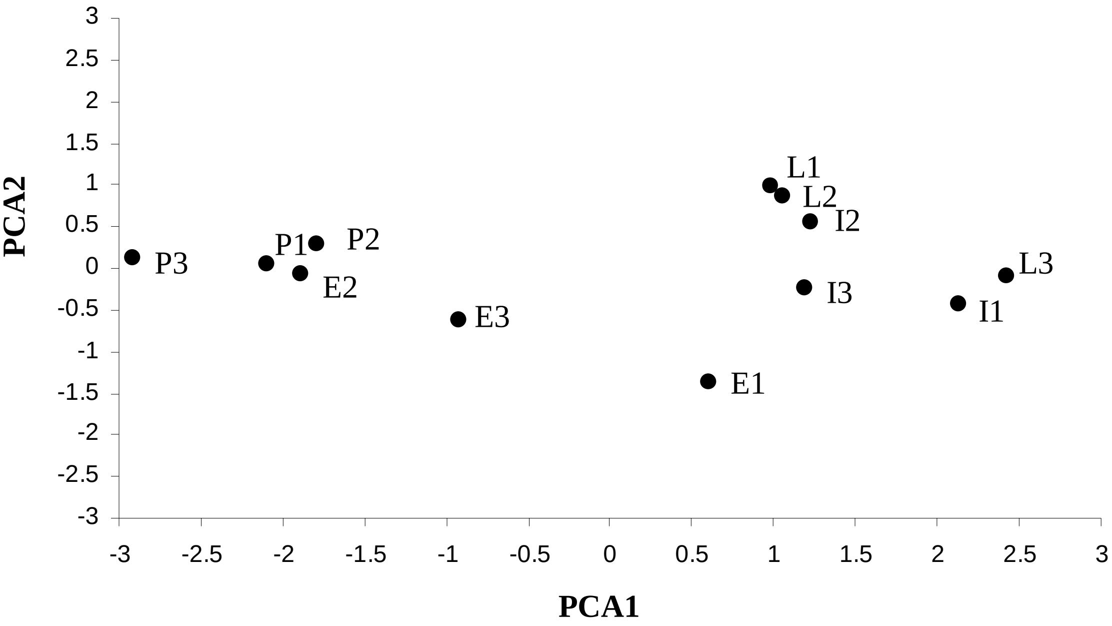
Appendix 1. Ordination of sampling sites representing different successional stages based on the structural attributes of their woody plant assemblages. Axis 1 (PCA1) represents 83% of the total variation in the dataset, while axis 2 represents 11%. Successional stages (P: pasture, E: early, I: intermediate and L: late).

Appendix 2. Percentage of variation of response variables, associated with the variation of each of the explanatory variables at the focal scales of 500 and 1000 m. Explanatory variables are V_{struct}: sampling site scores of PCA axis 1 reflecting the vegetation structure complexity of each site, $DF_{\%}$: percentage of dry forest cover, DF_{area}: mean area of dry forest patches, $RF_{\%}$: percentage of riparian forest cover, RF_{area}: mean area of riparian forest patches, and Div: Simpson's diversity index of land covers types. Sample size is shown by n. Significant relationships according to the randomization test appear in bold. Negative relationships among variables are shown in parentheses. R^2_{dev} is the fraction of the total deviance explained by a model considering all explanatory variables when the Poisson error distribution was used and R^2 when the normal error distribution was used. Response variables at the population level: species abundance; at the ensemble and assemblage levels variables are as in Table 1.

Appendix 3. Confidence set of plausible models (95%) explaining the variation in response variables at the 500 and 1000 m focal scales. *K*: number of estimated parameters, *logLik*: log-likelihood, AIC_c: sample-size adjusted Akaike information criterion, Δ_i*:* Akaike differences and w_i: Akaike weights. Response variables at the population level: species abundance; at ensemble and assemblage levels variables are as in Table 1. Explanatory variables are as in Table 2.

Appendix 4. Family and species of chiropterophilic and chiropterochoric plants occurring in the dry and riparian forest (DF and RF respectively) in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. The information was generated using the Neotropical bat/plant interactions database (Geiselman et al. 2002 onward) with the vascular plant checklist of Lott (2002). Only records at the species level were included in our list. We also considered the seeds collected and identified during our bat samplings (78 fecal samples from which 63 presented seeds), as well as information on *Stenocereus chrysocarpus, S. fricci and S. standleyi* gathered from Rojas-Martinez et al. (1999). Plant families follow the angiosperm phylogeny group classification (APG III 2009). Plant species names correspond to the nomenclature of Tropicos.org. Missouri Botanical Garden. 01 Apr 2010 (http://www.tropicos.org/).

Appendix 1.


PCA2
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
PCA1
P3
P1
P2
E2
E3
E1
L1
L2
I2
I3
L3
I1

Appendix 2.

				Explanatory variable					
Response variable	**Scale**	***n***	R^2_{dev}	**V_{struct}**	**$DF_{\%}$**	**DF_{area}**	**$RF_{\%}$**	**RF_{area}**	**Div**
Population-level									
Nectarivores									
G. soricina	500	12	0.17	7.34 (-)	8.79	40.65 (-)	7.94	5.19	30.09
	1000	9	0.70	4.75	6.97	35.09 (-)	10.11	30.23	12.85
G. commissarisi	500	12	0.50	15.19 (-)	2.80	49.79 (-)	11.18	6.45	14.59
	1000	9	1.00	16.23	12.81 (-)	48.40 (-)	6.28 (-)	7.97	8.30
L. yerbabuenae	500	12	0.10	5.73 (-)	34.23	9.82 (-)	4.55 (-)	1.17 (-)	44.50
	1000	9	1.00	2.03	1.56 (-)	11.23 (-)	2.37	4.36	1.43 (-)
Frugivores									
A. jamaicensis	500	12	0.86	**36.70**	14.58 (-)	6.74	28.08	2.43 (-)	11.47 (-)
	1000	9	1.00	20.24	13.64 (-)	20.58 (-)	9.42	17.86	18.26 (-)
A. phaeotis	500	12	0.79	29.67	11.98	5.03	25.76	2.72	24.84
	1000	9	1.00	17.37	8.85 (-)	18.94 (-)	23.35	16.17 (-)	15.32 (-)
A. lituratus	500	12	0.84	32.89	7.08 (-)	3.43	**36.96**	15.61	4.03 (-)
	1000	9	1.00	17.61	4.89 (-)	28.81	24.00	15.80 (-)	8.90 (-)
Sangivorous									
D. rotundus	500	12	0.88	**41.28**	3.85 (-)	3.31 (-)	**44.73**	3.31 (-)	3.52 (-)
	1000	9	1.00	18.93	7.62 (-)	21.42 (-)	13.73	23.87	14.43 (-)
Ensemble-level									
Nectarivores									
S_8(N)	500	11	0.30	14.74 (-)	2.72	43.14 (-)	5.33	32.83 (-)	1.24
	1000	8	0.94	14.43	12.74 (-)	20.18 (-)	12.81	28.01	11.83 (-)
Ab(N)	500	12	0.18	5.92 (-)	9.47	42.63 (-)	6.48	5.09	30.40
	1000	9	0.74	6.54	7.18	46.85 (-)	9.05	18.41	11.97
Frugivores									
S_8(F)	500	11	0.90	**26.06**	12.10 (-)	13.30 (-)	**24.43**	17.43	6.69 (-)
	1000	8	0.95	31.68	12.33 (-)	18.66 (-)	12.58	15.08	9.67 (-)
Ab(F)	500	12	0.75	23.41	2.30 (-)	2.47 (-)	**54.44**	14.74	2.64 (-)
	1000	9	1.00	20.73	6.27 (-)	18.99 (-)	**39.89**	7.79 (-)	6.34 (-)

Appendix 2. continued

				Explanatory variable					
Response variable	**Scale**	***n***	R^2_{dev}	**V$_{\text{struct}}$**	**DF$_{\%}$**	**DF$_{\text{area}}$**	**RF$_{\%}$**	**RF$_{\text{area}}$**	**Div**
Assemblage-level									
SC$_1$	500	12	0.26	5.02 (-)	15.53	35.37 (-)	3.74 (-)	36.48 (-)	3.87
	1000	9	0.64	2.98 (-)	9.52	18.22 (-)	7.31 (-)	50.46	11.50
SC$_2$	500	12	0.81	**37.47** (-)	19.91	2.07 (-)	**32.69** (-)	2.83 (-)	5.04
	1000	9	0.94	28.80 (-)	14.82	8.33	28.68 (-)	7.22	12.15
S$_8$(P)	500	11	0.60	28.65	12.21 (-)	10.51 (-)	36.18	8.57	3.84 (-)
	1000	8	0.98	21.09	15.40 (-)	16.05 (-)	23.37	9.31	14.79 (-)
Ab(P)	500	12	0.72	30.66	5.99 (-)	9.00 (-)	38.48	4.30	11.57
	1000	9	0.91	18.25	9.02 (-)	19.45 (-)	16.70	20.16	16.42 (-)

Appendix 3.

Response variable	**Scale**	**Model**	***K***	***logLik***	AIC_c	Δ_i	w_i
Population-level							
Nectarivore							
G. soricina	500	DF_{area}	2	-54.21	113.74	0.00	0.68
		Div	2	-56.16	117.66	3.91	0.10
	1000	$RF_{\%}$	2	-40.40	86.81	0.00	0.38
		RF_{area}	2	-40.78	87.55	0.74	0.26
G. commissarisi	500	DF_{area}	2	-26.78	58.90	0.00	0.72
	1000	DF_{area}	2	-23.08	52.15	0.00	0.65
L. yerbabuenae	1000	DF_{area}	2	-10.78	27.57	0.00	1.00
Frugivore							
A. jamaicensis	500	$RF_{\%}$	2	-76.10	157.53	0.00	0.90
		V_{struct}	2	-78.30	161.94	4.41	0.10
	1000	DF_{area}	2	-38.58	83.16	0.00	0.99
A. phaeotis	500	V_{struct}	2	-17.11	39.56	0.00	0.59
		$RF_{\%}$	2	-17.49	40.31	0.75	0.40
	1000	$RF_{\%}$	2	-8.18	22.36	0.00	1.00
A lituratus	500	$RF_{\%}$	2	-21.78	48.90	0.00	0.95
	1000	DF_{area}	2	-15.40	36.81	0.00	0.50
		$RF_{\%}$	2	-15.45	36.91	0.10	0.48
Sangivore							
D. rotundus	500	$RF_{\%}$	2	-37.55	80.43	0.00	1.00
	1000	RF_{area}	2	-18.31	42.62	0.00	0.91
Ensemble-level							
Nectarivore							
Ab(N)	500	DF_{area}	2	-91.95	189.24	0.00	0.95
	1000	DF_{area}	2	-74.45	154.90	0.00	0.46
		$RF_{\%}$	2	-74.70	155.40	0.50	0.36
Frugivore							
S_8(F)	500	V_{struct}	3	-14.06	37.55	0.00	0.40
	1000	V_{struct}	3	-7.14	26.29	0.00	0.80
Ab(F)	500	$RF_{\%}$	2	-19.29	43.91	0.00	1.00
	1000	$RF_{\%}$	2	-13.35	32.70	0.00	0.99
Assemblage-level							
SC_2	500	$RF_{\%}$	3	-5.97	17.93	0.00	0.51
		V_{struct}	3	-6.53	19.06	1.13	0.29
	1000	$RF_{\%}$	3	-4.49	19.79	0.00	0.54
Ab(P)	500	$RF_{\%}$	2	-133.37	272.08	0.00	1.00
	1000	RF_{area}	2	-104.52	215.03	0.00	0.99

Appendix 4.

FAMILY	**Chiropterophilic**		**Chiropterochoric**	
Species	**DF**	**RF**	**DF**	**RF**
Anacardiaceae				
Spondias purpurea			X	
Apocynaceae				
Stemmadenia donnell-smithii			X	
Asparagaceae				
Agave angustifolia	X			
Agave colimana	X			
Bignoniaceae				
Crescentia alata	X			
Cydista diversifolia		X		
Boraginaceae				
Cordia alliodora	X	X		
Cordia gerascanthus	X	X		
Bromeliaceae				
Aechmea bracteata				X
Cactaceae				
Pachycereus pecten-aboriginum	X			
Stenocereus chrysocarpus	X		X	
*Stenocereus fricii**	X		X	
Stenocereus standleyi	X		X	
Capparaceae				
Capparis flexuosa	X			
Crataeva tapia	X			
Convolvulaceae				
Ipomoea ampullacea		X		
Ipomoea wolcottiana	X			
Cucurbitaceae				
Cucurbita argyrosperma	X			
Fabaceae				
Acacia farnesiana	X			
Albizzia occidentalis	X	X		
Bauhinia pauletia	X			
Bauhinia ungulata	X			
Calliandra formosa	X			
Inga vera	X			
Mucuna sloanei		X		
Malvaceae				
Ceiba aesculifolia	X			
Ceiba grandiflora	X			
Ceiba pentandra		X		
Guazuma ulmifolia			X	
Helicteres baruensis	X			
Pseudobombax ellipticum	X			

Appendix 4. continued

Family **Species**	**Chiropterophilic**		**Chiropterochoric**	
	DF	**RF**	**DF**	**RF**
Moraceae				
Brosimum alicastrum		X		X
Chlorophora tinctoria			X	
*Ficus cotinifolia**			X	
*Ficus insipida**				X
*Ficus obtusifolia**				X
*Ficus pertusa**				X
Piperaceae				
*Piper arboreum**			X	X
Piper hispidum				X
Sapindaceae				
Sapindus saponaria				X
Sapotaceae				
Pouteria campechiana				X
Solanaceae				
Solanum erianthum			X	
Solanum hazenii			X	
Solanum diphyllum				X
Ulmaceae				
Celtis iguanaea				X
Trema micrantha			X	
Urticaceae				
Urera caracasana				X

* Seeds collected and identified from feces collected from bats captured during the present study.

CAPÍTULO 5

Discusión general

DISCUSIÓN GENERAL

Respuestas generales a la perturbación/sucesión

En general, se conocen algunas tendencias sobre la respuesta de los murciélagos neotrópicales a la modificación del hábitat. Por ejemplo, las especies raras con hábitos y dietas especializadas, como los insectívoros de sustrato y carnívoros de la subfamilia Phyllostominae, están más estrechamente asociadas al bosque maduro (Bernard y Fenton 2003, Brosset et al 1996, Castro-Arellano et al. 2007, Castro-Luna et al. 2007, Clarke et al. 2005a, b, Fenton et al. 1992, Kalko et al. 1999, Medellín et al. 2000, Ochoa 2000, Peter et al. 2006, Wilson et al. 1996). En el caso de los frugívoros, éstos suelen mostrar mayor abundancia en los paisajes transformados que en los bosques conservados, lo cual está ligado a que la abundancia de plantas quiropterocóricas aumenta en los paisajes transformados (Brosset et al. 1996, Clarke et al. 2005a, Faria 2006, Faria et al. 2006, Faria y Baumgarten 2007, Mancina et al. 2007, Medellin et al. 2000, Ochoa 2000, Peters et al. 2006, Reis et al. 2003, Wilson et al. 1996). Finalmente, las especies menos afectadas por la modificación del hábitat son aquellas que se distribuyen en un rango geográfico amplio, presentan un ámbito hogareño también amplio, tienen tallas grandes, son generalistas y muestran una abundancia natural alta (Cosson et al. 1999a, b, Estrada et al. 1993, Estrada y Coates-Estrada 2002, Montiel et al. 2006).

La respuesta de los filostómidos a la transformación del paisaje en el BTS, de acuerdo a nuestros resultados, concuerda con solo algunas de estas tendencias (reportadas mayormente para bosques húmedos y lluviosos), al tiempo que muestra ciertas particularidades. En el caso de la Reserva de la Biósfera Chamela-Cuixmala (RBCC) se detectó, por ejemplo, una notable reducción en la riqueza y abundancia de filostómidos hacia los pastizales, mientras que la mayor riqueza de especies fue detectada en el conjunto de sitios que representan el estadio más avanzado de la sucesión (Capítulo 2). Fue también en estos sitios donde se presentaron, de forma exclusiva, un gran porcentaje (67%) de las especies registradas en la RBCC, algunas de las cuales (*Centurio senex*, *Chiroderma salvini*, *Micronycteris microtis*, *Musonycteris harrisoni*) se consideran asociadas a las áreas más conservadas (Fenton et al. 1992, Estrada et al. 1993, Schulze et al. 2000, Stoner et al. 2002). Un rasgo notable en la respuesta de los filostómidos de esta región, fue el aumento significativo en la abundancia de nectarívoros hacia los estadios iniciales de la sucesión, lo cual se asoció con la gran abundancia de plantas quiropterofílicas en estos estadios (Capítulo 2), así como con la capacidad de los nectarívoros más abundantes de forrajear en áreas con poca vegetación (Capítulo 4). Contrario a lo reportado para áreas neotropicales más húmedas, los frugívoros no se presentaron en mayor abundancia en las áreas perturbadas debido a que en los estadios tempranos del BTS no abundan las plantas quiropterocóricas, como generalmente ocurre en los bosques húmedos y lluviosos (Fleming 1988, Charles-Dominique 1986, Lobota et al. 2009). En el BTS, los estadios tempranos están dominados por especies anemocóricas y autocóricas que no constituyen un recurso alimentario para los filostómidos (Vieira y Scariot 2006, Capítulo 2).

Ahora bien, además de estas tendencias generales, los resultados de la RBCC (Capítulo 2) evidenciaron una gran variación entre los ensamblajes de filostómidos que se presentan en los diferentes estadios sucesionales del BTS. Esta variación fue evidente no solo a nivel de ensamble (principalmente en frugívoros y nectarívoros), sino también a nivel de ensamblaje, en parámetros como la abundancia total de individuos y la densidad de especies. En la mayoría de los casos, de hecho, no se observaron diferencias significativas entre los estadios sucesionales debido a la gran variación que se presentó, no solo entre los sitios que representaban diferentes estadios sucesionales, sino también entre aquellos sitios que representaban un mismo estadio sucesional (Capítulo 2, figuras 4 y 5). La comparación de estos resultados con aquellos obtenidos en los BTS de Hato Piñeiro (HP), Venezuela y Parque Estadual da Mata Seca (PEMS), Brasil (Capítulo 3), muestra también un gran nivel de variación en la presencia y abundancia de los filostómidos a lo largo del gradiente sucesional, siendo ambos parámetros diferentes entre especies, gremios tróficos, estaciones y, de forma general, entre las tres regiones analizadas. De hecho, no se encontraron, a nivel de ensamblaje, ensamble o población, patrones concretos en la respuesta de los filostómidos a la alteración del hábitat entre las tres regiones. Esta gran variación indica la importancia de examinar cómo distintos factores, como la estacionalidad o los atributos del hábitat (tanto a nivel local como de paisaje), modulan la presencia y abundancia de los filostómidos en el BTS.

Estacionalidad

De manera general, los murciélagos del BTS enfrentan marcados cambios estacionales en las condiciones ambientales (*v. gr*. la estructura de la vegetación) y en la disponibilidad de alimento (*v. gr*. tipo y abundancia). Esto debido a que los BTS presentan patrones fenológicos y de productividad primaria altamente estacionales (Borchert 1994, Martínez-Yrizar et al. 1996, Kalacska et al. 2005). Los cambios en la estructura de la vegetación, por ejemplo, pueden impactar la actividad de varias especies neotropicales que son dependientes del bosque, la mayoría de ellos filostómidos que dependen de áreas cerradas para forrajear (Kalko et al. 1996, Cosson et al. 1999b). La estacionalidad en el régimen de precipitación afecta también la abundancia y diversidad de insectos (Wolda 1978, Frith y Frith 1985, Pescador-Rubio et al. 2002), por lo que los murciélagos insectívoros pueden experimentar cambios importantes en la disponibilidad de alimento entre estaciones. En el mismo sentido, una marcada estacionalidad en los patrones de floración y fructificación, provocaría variaciones estacionales importantes en la disponibilidad de recursos para los murciélagos nectarívoros y frugívoros (Frankie et al. 1974, Fleming 1988, Stoner 2005).

En el caso de nuestros sitios de estudio, Fernández-Hernández (2008) y Pezzini (2008) encontraron, para la RBCC y el PEMS respectivamente, diferencias muy marcadas entre los estadios sucesionales en relación a la estacionalidad, frecuencia y duración de la producción de hojas, flores y frutos. Así, la composición específica de los ensamblajes de plantas y sus patrones fenológicos particulares, podrían explicar las variaciones estacionales de la presencia y abundancia de los filostómidos en los diferentes estadios sucesionales del BTS.

Ahora bien, la naturaleza e intensidad de las variaciones estacionales que sufren los ensamblajes en los diferentes estadios sucesionales no fueron consistentes entre las tres regiones de estudio. Esto puede deberse, en parte, a las diferencias entre las regiones en relación al promedio anual de precipitación (HP = 1469 mm, PEMS = 818 mm, RBCC = 763 mm) y a atributos del paisaje como la presencia o ausencia de cuerpos de agua permanentes. En este sentido, la significativa reducción en riqueza y abundancia de filostómidos, que se evidenció hacia la época seca, en la mayoría de los sitios de muestreo de la RBCC, está probablemente relacionada con la ausencia de cuerpos de agua permanentes en esta área. Las lagunas y ríos presentes tanto en HP como en el PEMS, por otra parte, explicarían porque en estos sitios no se produjo una reducción tan dramática en la riqueza y abundancia de este grupo durante la época seca (Capítulo 3).

Los atributos del hábitat

Las variaciones en los atributos del hábitat tanto a nivel local (*v. gr*. composición florística, estructura de la vegetación), como a nivel del paisaje (*v. gr*. porcentaje de cobertura de diferentes tipos de vegetación, área promedio y riqueza de los parches de vegetación), definen de forma significativa la presencia y abundancia de los filostómidos (Capítulo 4). En HP, por ejemplo, la variación en la abundancia de los insectívoros de sustrato y de algunos frugívoros estuvo relacionada con las variaciones en la complejidad estructural de la vegetación, mientras que la mayor abundancia de frugívoros en el estadio inicial estuvo relacionada a la abundancia de especies quiropterocóricas en ese estadio (J. Nassar, datos no publicados). Por otra parte, en la RBCC y el PEMS, los frugívoros no incrementan su abundancia hacia los estadios iniciales porque estos estadios están dominados por especies anemocóricas y autocóricas que no representan un recurso trófico para ellos (para CCBR: P. Balvanera, G. Ibarra-Manríquez, A. Pérez-Jiménez y M. Martínez-Ramos, datos no publicados; para PEMS: M. M. Espírito-Santo, datos no publicados). Las diferencias en cuanto a la composición específica de los estadios iniciales entre las tres regiones podrían, a su vez, estar relacionadas con sus diferencias en el promedio anual de precipitación.

A nivel de paisaje, las variaciones en la cobertura de la vegetación resultan también determinantes. En la RBCC, por ejemplo, las variaciones en la abundancia de frugívoros y hematófagos estuvieron principalmente asociadas a variaciones en el porcentaje de cobertura de la vegetación riparia, mientras que las variaciones en la abundancia de nectarívoros estuvieron principalmente asociadas a variaciones en el porcentaje de cobertura del bosque seco. Esto estaría explicado por el predominio de especies quiropterocóricas en la vegetación riparia, para el caso de los frugívoros, y por el predominio de especies quiropterofílicas en el bosque seco, para el caso de los nectarívoros. En el caso de los hematófagos, su mayor abundancia hacia las áreas con mayor cobertura de vegetación riparia obedecería a factores como: 1) la concentración, en estas áreas, de mamíferos autóctonos e introducidos, 2) el uso preferencial de refugios propios de este tipo de vegetación y 3) la utilidad de estas áreas como corredores para desplazarse a través de la matriz de vegetación (Obs. per. Lord 1988, Taddei et al. 1991, Núñez et al. 2000, Valenzuela y Ceballos 2000, Sanchez-Azofeifa et al. 2009).

Por todo lo anterior, se puede decir que existe un gran nivel de especificidad en la respuesta de los murciélagos a la perturbación del BTS. Esta especificidad estaría definida, en gran medida, por los requerimientos ecológicos de las especies que conforman el pool regional de especies y por atributos particulares del hábitat tales como: 1) las condiciones climáticas particulares de cada región, 2) la composición, estructura y patrones fenológicos de los ensamblajes de plantas asociados a los diferentes estadios sucesionales y 3) los atributos particulares del paisaje (composición y conformación), mismos que estarían determinados por la naturaleza de la perturbación que los transformó (origen, escala, intensidad y duración).

El estudio de los paisajes tropicales transformados

Los paisajes tropicales actuales son altamente heterogéneos, no solo por la naturaleza de los sistemas tropicales en sí, sino también por las altas tasas de transformación a la que están expuestas como resultado de las actividades antropogénicas (Primack et al. 2001b, Miles et al. 2006, FAO 2009). Una alta heterogeneidad supone, en principio, dificultades en la búsqueda de patrones y en la capacidad de generar modelos de la dinámica de estos sistemas. Sin embargo, la alta variación inherente a estos paisajes debe ser considerada e incorporada a su estudio (*v. gr*. diseños experimentales, técnicas estadísticas), en aras de detectar respuestas cada vez más representativas de su realidad. En el caso de los murciélagos, por ejemplo, es sólo la consideración y estudio de varios factores a la vez (atributos del hábitat, estacionalidad, latitud, matriz de vegetación, etc.), lo que nos permitió vislumbrar no precisamente patrones en su respuesta, sino los factores que modulan estas respuestas y como la variación de estos factores dirige la dinámica del sistema.

La caracterización cuantitativa de los atributos del hábitat constituye un paso en este sentido al representar, de manera más precisa, la heterogeneidad inherente al paisaje (Klingbeil y

Willig 2009). Una caracterización meramente cualitativa del mismo, en contraparte, “enmascararía” la variación intra-categoría y no develaría la identidad de los factores que modulan la respuesta estudiada. Es el caso de la gran variación en complejidad estructural de la vegetación encontrada entre sitios de un mismo estadio sucesional; de no haber cuantificado esta complejidad en los diferentes sitios de estudio, no hubiese sido posible detectar su efecto en los filostómidos, ya que éste efecto era independiente del estadio.

Por otra parte, el estudio de los factores que modulan la respuesta de los animales a la perturbación, requiere, en muchos casos, de un análisis a escala de paisaje que nos permita vislumbrar como la composición y configuración del mismo determinan la presencia y abundancia de estos organismos. En el caso de organismos tan vágiles como los murciélagos, que pueden tener una movilidad de hasta 10 km por noche (Morrison 1978), es probable que la escala a la que realizamos la mayoría de los estudios sea muy pequeña para determinar adecuadamente sus patrones de presencia y abundancia.

La respuesta de los murciélagos en paisajes transformados: recomendaciones

El comportamiento de los filostómidos en los paisajes transformados del BTS indica claramente que las estrategias de conservación de este grupo y de sus servicios ecosistémicos en el BTS, requieren de la consideración tanto de la vegetación conservada como de la vegetación secundaria, ya que un gran porcentaje de estos murciélagos usan (e impactan) ambos tipos de vegetación. Especial interés se le debe prestar a la vegetación riparia, ya que ésta resulta determinante para la conservación de un gran número de especies de filostómidos que habitan en el BTS.

Ahora bien, con base en los resultados obtenidos en este estudio así como en las limitaciones detectadas en el transcurso del mismo, sugerimos que, en estudios posteriores, se priorice: 1) la identificación de los atributos del hábitat, tanto a nivel local como a nivel de paisaje (a grandes escalas), que puedan estar determinando la presencia y abundancia de los murciélagos en los diferentes parches de vegetación, 2) la evaluación de las fluctuaciones estacionales en la disponibilidad de recursos y en las condiciones ambientales, ya que éstas modulan las respuestas de los filostómidos y 3) la ampliación del rango de escenarios estudiados (incorporación de la heterogeneidad), desde el estudio de un mayor número de sitios por región, hasta la incorporación de diferentes regiones de estudio.

De manera general, la conjunción de resultados provenientes de diferentes regiones con diferentes ecosistemas, especies y regímenes de perturbación, facilitaría la identificación de patrones en la respuesta de los murciélagos a la transformación del hábitat y sería útil en la proyección de escenarios para un espectro más amplio de paisajes antropogénicos. Debido a la escasez de estudios abordando esta problemática en el BTS, esto aún no es posible para este ecosistema, pero dada la atención creciente que se ha vertido sobre él en los últimos años, confiamos en que la comunidad científica tome conciencia plena de la urgencia de conocer, tanto la respuesta de su biota a la perturbación, como su dinámica sucesional y de regeneración natural. Sobre todo, exhortamos a la comunidad científica a generar acciones de manejo y conservación que contrarresten los efectos de la transformación en nuestros paisajes tropicales.

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