



El Colegio de la Frontera Sur

Respuesta de murciélagos insectívoros aéreos a variables físico-ambientales a nivel local y escala de paisaje en la región Lagos de Montebello, Chiapas, México

TESIS

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por

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Capítulo I

1. Introducción

1.1. Modelos teóricos para el estudio de los paisajes: punto de partida para su representación

Los modelos son representaciones abstractas de un sistema, simplificaciones de la realidad que permiten hacer predicciones (Turner et al. 2001); en otras palabras, explican un fenómeno de forma simplificada. Tienen como finalidad proveer un marco teórico para explorar causalidades ecológicas a través de datos empíricos (Fischer y Lindenmayer 2007). De esta forma, son instrumentos que ayudan a definir problemas de manera más precisa y conceptos de forma más clara, que permiten generar hipótesis como guía, así como los medios para ponerlas a prueba (Turner et al. 2001).

En el siglo XIX el estudio de los ecosistemas condujo al naturalista Alexander von Humboldt a observaciones como la siguiente: áreas más grandes contienen mayor cantidad de especies (Seip y Wenstøp 2006). Esta generalización, posteriormente desarrollada en lo que conocemos como la función de relación especies-área y que representa la descripción de uno de los patrones más consistentes en ecología (Arrhenius 1921; Gleason 1922; Bennett y Saunders 2010), fue fundamental para el surgimiento de teorías que derivaron en modelos en la actualidad vigentes para el estudio de poblaciones animales en ambientes modificados por el humano.

El concepto de relación especies-área, condujo en 1967 al desarrollo de la Teoría de Biogeografía de Islas (TBI) por parte de MacArthur y Wilson (MacArthur y Wilson 1967; Turner et al. 2001). Esta simple y elegante teoría (también conocida como modelo de islas) relaciona el número de especies en una isla con su área y grado de aislamiento, mediante predicciones sobre las tasas de colonización (inmigración) y extinción: las islas que son relativamente pequeñas y/o aisladas experimentan una disminución en sus tasas de inmigración, alojan poblaciones con probabilidades de extinción altas y, eventualmente, contendrán un número de especies menor (Bennett y Saunders 2010; Fischer y Lindenmayer 2007).

Para la perspectiva de la TBI, el contraste isla/mar es alto, por lo que es posible controlar los efectos atribuibles a la matriz (área predominante), que suelen ser confusos en ecosistemas terrestres de complejidad mayor (Forman 1995; Faria 2006). La TBI permitió estudiar en una analogía cómo en los continentes las

actividades humanas crean “islas” (fragmentos relativamente homogéneos), inmersos en un “mar” o matriz (Jules y Shahani 2003). De esta forma, se proveyó de un marco de referencia en ecosistemas terrestres (Bennett y Saunders 2010).

Posteriormente, el desarrollo de la ecología del paisaje contribuyó a formas de conceptualización nuevas, de tal forma que elementos como los corredores, que proveen conectividad sobre la matriz de fondo, se convirtieron en un paradigma influyente (Diamond 1975; Forman 1995; Bennett y Saunders 2010). Asimismo, se empieza a reconocer la importancia de la calidad de la matriz para el mantenimiento de la diversidad biológica y sus procesos metapoblacionales (Hanski 1999; Perfecto y Vandermeer 2002; Franklin y Lindenmayer 2009).

La teoría de metapoblaciones, definidas estas como “colecciones de subpoblaciones que ocupan un determinado porcentaje de hábitats adecuados en el paisaje”, surge con implicaciones evidentes, ya que una matriz poco permeable puede representar una barrera física para la movilidad de los organismos entre fragmentos, con consecuencias demográficas (Levins 1969; Vandermeer y Carvajal 2001). Las metapoblaciones se encuentran vinculadas entre sí por la inmigración y la emigración, y se mantienen por la dispersión desde hábitats fuente donde el éxito reproductivo sobrepasa la mortalidad, hacia hábitats sumidero donde de no existir inmigración periódica las condiciones de calidad menor favorecerían su desaparición (Pulliam 1988; Dunning et al. 2006).

Dos aspectos fundamentales sobre la crítica de la TBI son el paradigma fragmento/matriz y su visión blanco/negro (hábitat y no hábitat) desde una perspectiva humana (Franklin y Lindenmayer 2009). Entre los supuestos de esta teoría la matriz es homogénea y ecológicamente irrelevante (Jules y Shahani 2003; Vandermeer y Carvajal 2001). En este sentido, lo que es importante tener en cuenta es que la matriz puede representar un espacio homogéneo inhabitable, o bien un espacio heterogéneo (e.g. con distintos tipos de coberturas o usos del suelo) a través del cual los individuos pueden encontrar condiciones para moverse entre fragmentos del hábitat original (Perfecto y Vandermeer 2002).

De forma alternativa surge un grupo de modelos denominados de continuidad, los cuales conceptualizan los paisajes con base en el precepto de la vegetación como un continuo, en contraposición a elementos discretos (Fischer y Lindenmayer 2006; Manning et al. 2004). El modelo más recurrido es el de paisaje variegado, que reconoce cambios graduales (gradientes) en la cobertura de la vegetación y calidad

de los hábitats (Lindenmayer y Burgman 2005; MacIntire y Barrett 1992) y enfatiza la variedad de formas que los organismos perciben y responden al ambiente (Manning et al. 2004). Sin embargo, la demanda de herramientas analíticas sofisticadas y la falta de datos empíricos apoyando su marco conceptual, han tenido como consecuencia que estos modelos tengan un desarrollo lento (Fischer et al. 2004; Price et al. 2009). Asimismo, los denominados modelos de paisaje neutral y demografía del paisaje proveen un marco de referencia. El primero, se enfoca en el contraste con mapas aleatorizados caracterizados por la ausencia de factores de organización o estructuración de patrones (Gardner et al. 1987; Turner et al. 2001). En ecología del paisaje, el planteamiento de hipótesis nulas no es frecuente debido al número de variables que afectan los sistemas ecológicos (sistemas complejos), así como la falta de manipulación experimental y/o replicación verdadera que validen las comparaciones (Hurlbert 1984; Turner et al. 2001); sin embargo, los modelos neutrales permiten revelar diferencias en magnitud y significancia comparando con los paisajes observados (Turner et al. 2001). El segundo, se enfoca en el estudio de las propiedades demográficas de las poblaciones y sus determinantes en múltiples escalas, y en como las relaciones entre poblaciones y sus determinantes en una escala particular tienen influencia en el resultado demográfico en otras escalas (Gurevitch et al. 2016).

En contraste, la TBI derivó en una serie de modelos clásicos que incluyen el de anidamiento de especies, que predice que todas las especies en un sistema deberían ocurrir en el fragmento más grande y que los fragmentos más pequeños contienen subconjuntos compuestos de las especies generalistas (Patterson y Atmar 1986; Lindenmayer y Burgman 2005) y el de parche-matriz-corredor, que se basa en la identificación de elementos discretos en el paisaje (Forman 1995). Estos modelos siguen siendo fundamento para los estudios sobre los efectos de la modificación de los paisajes en la biodiversidad y son apropiados en paisajes de contraste alto (Manning et al. 2004; Fischer et al. 2006).

1.2. Los cambios temporales y espaciales en el paisaje: patrones y procesos subyacentes que afectan a las especies

La degradación, pérdida y fragmentación de los hábitats en un ecosistema se consideran transformaciones de distinta severidad (Groom y Vynne 2006; Manning et al. 2004; Bennett y Saunders 2010). La degradación generalmente se refiere a los

impactos temporales que afectan a muchas, pero no todas las especies, y no implican la pérdida total de hábitat para todas las especies; más bien, representa una reducción en la capacidad de un ecosistema para mantener subconjuntos de especies (Groom y Vynne 2006).

En contraste, la pérdida de hábitat se refiere a impactos severos a través de los cuales todas o casi todas las especies son afectadas negativamente y los hábitats ya no son capaces de mantener más que una fracción de sus funciones y especies originales (Groom y Vynne 2006). La pérdida de hábitat usualmente está correlacionada con la fragmentación (Fahrig 2003). Esta última puede definirse como la transformación de un hábitat de gran tamaño en numerosos fragmentos de área menor, aislados por una matriz distinta al hábitat original (Forman 1995), ya sea de forma natural o inducida por las actividades humanas. Cuando la fragmentación del hábitat ocurre, surgen tres cambios interrelacionados (Bennett y Saunders 2010): 1) la reducción de la cantidad total de vegetación; 2) la subdivisión de la vegetación remanente; y 3) la introducción y reemplazo por nuevos usos del suelo. Estos cambios están fuertemente relacionados, de tal forma que es complicado separar el efecto relativo de uno del otro (Fahrig 2003; Bennett y Saunders 2010), por lo que suelen ser referidos conjuntamente como “cambios en el paisaje” (Bennett y Saunders 2010). Una forma de contextualizar los cambios es precisamente en el “paisaje” (Fahrig 2003), que se puede interpretar como la “ventana espacial” que representa el escenario en el que las poblaciones se desarrollan y exhiben respuestas a cambios en el ambiente, cuya extensión depende de la percepción de la especie a la distribución de los recursos.

El cambio en el paisaje puede conducir ya sea a la degradación, específicamente como gradientes en la calidad del hábitat, o bien a la subdivisión del hábitat (Lindenmayer y Burgman 2005). En la dimensión espacial, el cambio para paisajes hipotéticos con cobertura vegetal similar, puede darse de las siguientes formas (Bennett y Saunders 2010): 1) por el grado de subdivisión (muchos contra pocos fragmentos); 2) por la densidad de los hábitats (agregados contra dispersos); 3) por la forma de los fragmentos (formas simples contra complejas). El cambio también es un proceso dinámico y puede apreciarse como un patrón a través del tiempo en una secuencia como la siguiente (Fahrig 2003): 1) disminución en el tamaño de los fragmentos; 2) incremento en el aislamiento de fragmentos; 3) cambio en la forma de los fragmentos, con cambios en la proporción de hábitat de borde.

Por último, con los cambios en el paisaje se experimentan cambios en los procesos biológicos, ya que se alteran procesos biofísicos de forma acumulativa; por ejemplo, los fragmentos pequeños pueden experimentar “efectos de borde” más fuertes y el microclima en el límite de un fragmento/matriz de contraste alto puede variar mucho en incidencia de luz, humedad, temperatura del suelo y aire, y velocidad del viento, lo que a su vez tiene efecto en los ciclos de nutrientes y finalmente en la estructura y composición de la vegetación (Bennett y Saunders 2010).

Los cambios en el paisaje pueden afectar a las especies de forma variable y las respuestas pueden ser neutrales, positivas o negativas. La respuesta de las especies en un paisaje puede reflejarse como patrones y sus procesos subyacentes. Los patrones pueden presentarse en distintos niveles, por ejemplo (Turner et al. 2001; Bennett y Saunders 2010): 1) a nivel genético, con la fragmentación del hábitat puede disminuir la dispersión y la variabilidad genética entre los individuos puede decrecer por efecto de endogamia; 2) a nivel poblacional, con la disminución del tamaño del fragmento y su cambio de forma, el hábitat interior va perdiendo superficie y el número de individuos disminuye; 3) a nivel de comunidad, con la disminución del tamaño de los fragmentos se van perdiendo las especies raras, quedando únicamente subconjuntos de las especies generalistas, ya que se pierde variabilidad ambiental para organismos con distintos requerimientos y tolerancias. Un proceso subyacente puede ser exógeno (e.g. cambio en el hábitat), endógeno (e.g. cambio en conducta), determinístico o estocástico (Fischer y Lindenmayer 2007; Bennett y Saunders 2010). Finalmente, las causas de extinción poblacional pueden ser genéticas, demográficas y/o ambientales, deterministas como estocásticas, y el nivel de vulnerabilidad depende en gran medida de rasgos ecológicos como el grado de especialización, tolerancia a la perturbación, capacidad de movilidad, entre otros (Sodhi et al. 2009).

1.3. Los murciélagos como grupo de estudio: indicadores de perturbación en ambientes modificados

Los murciélagos son un grupo reconocido como indicadores de perturbación en el ambiente; estos organismos, se caracterizan por su abundancia alta y su representación ecológica, taxonómica y trófica (Fenton et al. 1992; Medellín et al. 2000). Estos mamíferos son apropiados para el estudio de los efectos de la transformación del ambiente por actividades humanas, ya que la mayoría de

especies se agrupan en colonias y forrajean desde un punto central para explotar recursos que se encuentran esparcidos espacialmente en el paisaje (Pinto & Keitt 2008; Rainho & Palmeirim 2011). Asimismo, su sensibilidad a la interrupción del hábitat puede ser evaluada con base en rasgos específicos, tales como abundancia, movilidad, entre otros (Meyer et al. 2008; García-García et al. 2014; Farneda et al. 2015).

En particular, los murciélagos insectívoros aéreos son de importancia debido al papel que tienen como controladores de insectos nocturnos que actúan como plagas agrícolas (e.g. Cleveland et al. 2006; Kunz et al. 2011), así como depredadores potenciales de vectores de enfermedades infecciosas no transmisibles (Reiskind et al. 2009). Dentro de este grupo, los murciélagos con sistema de ecolocalización de rango corto (por medio del cual detectan objetos a través del eco de los sonidos que ellos mismos producen), afrontan restricciones en áreas abiertas por la distancia a los objetos y atenuación del sonido (Fenton 1999; Fenton 2002; Pettersson 2002), de tal manera que se consideran más vulnerables a la pérdida y fragmentación de los bosques naturales y a su conversión hacia usos del suelo sin diversificación de la vegetación (e.g. monocultivos), caracterizados por ausencia de cobertura arbórea (e.g. Heim et al. 2015).

1.4. Sistemas de detección ultrasónica para el estudio de murciélagos insectívoros aéreos: método complementario de estudio

En general, los murciélagos insectívoros aéreos utilizan el eco como un sistema de orientación y para distinguir presas (Richarz y Limbrunner 1993). La visión limita la ubicación de presas móviles en la oscuridad, mientras que la ecolocalización es efectiva en este sentido, aún cuando los murciélagos tienen que producir pulsos ultrasónicos de intensidad alta para recibir ecos audibles de objetivos como insectos pequeños (Jones y Rydell 2003). La evolución del vuelo activo (impulsado con las alas en contraste con el vuelo planeado o pasivo) y la ecolocalización presentaron oportunidades para el forrajeo nocturno en hábitats previamente libres de depredadores, con disponibilidad de recursos alimenticios (Schnitzler y Kalko 2001).

El estudio de la ecolocalización permitió el desarrollo de dispositivos de registro como los detectores de ultrasonido, los cuales ofrecen alternativas a métodos convencionales de captura como las redes de niebla (Kunz 2002). Estos dispositivos permiten identificar especies y facilitan las mediciones de actividad

relativa (Kunz y Brock 1975; Seidman y Zabel 2001), con la finalidad de comparaciones espaciales y temporales. Los detectores disponibles en el mercado varían, entre otras cosas, en el ancho de banda de detección, la técnica para la obtención de la información espectral del sonido y la resolución de las grabaciones, de tal manera que la información que se puede extraer del llamado de ecolocalización depende de su grado de sofisticación electrónica (Parsons et al. 2000). Los detectores de banda ancha permiten la grabación en un intervalo amplio de frecuencias, permitiendo así el estudio de varias especies simultáneamente, o bien ensambles. En varios estudios se ha evidenciado la importancia de la detección ultrasónica en la complementación de los inventarios de murciélagos (e.g. Kunz y Brock 1975; O'Farrell y Gannon 1999; Flaquer et al. 2007).

En la región Neotropical, específicamente en el sur-sureste de México, es posible citar varios ejemplos de la utilidad de la detección acústica para el estudio de los murciélagos (MacSwiney et al. 2008; García-García et al. 2009; Pech-Canché et al. 2010; Kraker y Pérez 2012). Por ejemplo, MacSwiney et al. (2008) compararon la utilidad de los detectores ultrasónicos para el registro de especies, simultáneamente con el uso de redes de niebla y trampas de arpa, determinando que en todos los sitios hubo una diferencia significativa entre el registro de especies por medio de detección acústica y métodos de captura combinados, en comparación con el registro exclusivo de métodos de captura.

Por otro lado, varios estudios en la región han contemplado la detección acústica para la comparación de los niveles de actividad relativa de murciélagos insectívoros aéreos con enfoques espaciales y temporales (MacSwiney et al. 2009; Williams-Guillén y Perfecto 2011; Kraker-Castañeda et al. 2013). Estos cálculos están basados en la evidencia de las especies en períodos de tiempo constantes, como una medida relativa que no es equivalente a un índice de abundancia, ya que por ejemplo, diez grabaciones de una misma especie pueden representar llamados de diez individuos, de un individuo que pasó frente al micrófono en diez ocasiones, o un número intermedio (Frick 2013). Con base en esta consideración, se han desarrollado índices que permiten calcular con el menor sesgo posible la intensidad de la actividad de una misma especie (e.g. Miller 2001), cálculo que no es comparable entre especies debido a la variación en la estructura de los llamados de ecolocalización (ver Stahlschmidt y Brühl 2012).

1.5. Variables explicativas a nivel local de la riqueza de especies y actividad relativa de murciélagos insectívoros aéreos: disponibilidad de alimento

Distintos factores a nivel local han sido abordados para explicar la riqueza de especies y las tasas de actividad relativa de los murciélagos insectívoros aéreos. En particular, la disponibilidad de alimento en cuerpos de agua, medida indirectamente como la abundancia o biomasa de insectos voladores nocturnos, ha sido una de las variables más exploradas, encontrándose evidencia de su valor predictivo en varios estudios (e.g. MacSwiney et al. 2009; Hagen y Sabo 2012; Kraker-Castañeda et al. 2013).

Por ejemplo, MacSwiney et al. (2009) evaluaron la actividad de murciélagos insectívoros aéreos en pastizales y bosques con presencia y ausencia de cenotes (depresión geológica inundada de origen kárstico). En su estudio, el número promedio de especies de murciélagos y la actividad fueron mayores en los sitios con presencia de cenotes, con especies exclusivas. Estos autores proponen que los sitios con cuerpos de agua son importantes para forrajeo, debido a la correlación con la abundancia de insectos.

Sin embargo, la evidencia proporcionada en estos estudios no es concluyente (o totalmente precisa), principalmente por que se trata de inferencias sobre lo que podría ser el alimento para los murciélagos insectívoros aéreos. La dificultad para capturar individuos en vuelo libre, la obtención de muestras de su dieta y su identificación taxonómica, son unas de las principales limitaciones para el estudio del efecto de la disponibilidad de alimento. Aún así, con base en la colecta de grupos taxonómicos específicos (e.g. lepidópteros, dípteros, coleópteros), es posible una aproximación sobre la importancia de las presas potenciales.

1.6. Variables explicativas del paisaje para la riqueza de especies y actividad relativa de murciélagos insectívoros aéreos: respuestas especie-específicas

La respuesta de los murciélagos insectívoros aéreos a la distribución espacial de los recursos está determinada en gran parte por la morfología alar y capacidad de vuelo (Norberg y Rayner 1987; Bader et al. 2015), así como por el rango efectivo de su sistema sonar (Jakobsen et al. 2013; Frey-Ehrenbold et al. 2013). En general, estudios previos coinciden que la vagilidad (capacidad de un organismo para moverse en un área) puede ser utilizada como variable proximal para explorar la

sensibilidad a la pérdida y fragmentación de los bosques y la vulnerabilidad a la extinción local (e.g. Estrada-Villegas et al. 2010; Fuentes-Montemayor et al. 2013).

Por ejemplo, Estrada-Villegas et al. (2010) encontraron en su área de estudio que las respuestas fueron diferenciales a nivel de especie, y además sugieren un efecto basado en la permeabilidad de la matriz e historia de fragmentación, ya que una matriz poco permeable (en su caso dominada por agua) y de contraste alto con los fragmentos puede ser percibida como hostil. Estos autores encontraron que las especies con preferencia por espacios abiertos no fueron afectadas por la fragmentación, lo cual pueden atribuir a sus adaptaciones específicas (carga alar y relación de aspecto del ala mayor), que les confieren un vuelo más rápido sobre extensiones amplias, en contraste con las especies de vuelo lento que tienen gastos energéticos mayores. Por su parte, Fuentes-Montemayor et al. (2013) plantearon en su área de estudio que las especies con maniobrabilidad menor serían más afectadas por condiciones locales, en contraste con las de maniobrabilidad mayor que serían más afectadas por elementos del paisaje en extensiones espaciales amplias. Estos autores encontraron nuevamente que la extensión espacial y magnitud del efecto de las variables evaluadas variaron entre especies, y aquellas con maniobrabilidad mayor respondieron al paisaje sobre extensiones amplias.

En este sentido, los elementos de un paisaje, ya sean de composición y/o configuración, deben ser explorados con un enfoque de escalas espaciales anidadas (e.g. Pinto y Keitt 2008), esto para establecer su valor predictivo tomando en cuenta que la percepción hacia la distribución espacial de los recursos en el ambiente es especie-específica y dependiente de la escala. De esta manera, se aumenta la probabilidad de encontrar respuestas diferenciales en un paisaje geográfico.

1.7. El Parque Nacional Lagos de Montebello: escenario para el estudio del efecto de variables locales y de paisaje en los murciélagos insectívoros aéreos

El Parque Nacional Lagos de Montebello (PNLM) es un área natural protegida incluida en la convención RAMSAR (sitio no. 1325) como humedal de importancia internacional. El PNLM está ubicado en una elevación intermedia (~1500 m), la vegetación predominante está compuesta por coníferas y bosques mixtos (pino-encino-liquidámbar), y sus superficies de agua son característicamente lagos, cenotes y aguajes (CONANP 2007); estos últimos, se tratan de ecotopos compuestos por superficies de agua permanente y con estacionalidad marcada,

respectivamente. El término “ecotopo”, puede definirse como la unidad de territorio más pequeña posible, relativamente homogénea, basada en factores abióticos y bióticos como vegetación, suelo, hidrología, entre otros (Zonneveld 1989; Forman 1995; Van der Molen et al. 2003). Por otro lado, la zona de influencia del PNLM está caracterizada por paisajes agrícolas de contraste alto y zonas urbanas (con una tendencia hacia la pérdida y fragmentación de bosques e incremento de áreas abiertas), y en porcentaje menor remanentes de bosque como propiedad ejidal (terreno con manejo para explotación comunal). Sin embargo, la influencia humana también se hace presente dentro de los límites del PNLM a través de la extracción de recursos, por presión del avance de la frontera agrícola y desarrollo turístico.

El Programa de Conservación y Manejo del PNLM incluye un componente de paisaje que reconoce que los patrones espaciales pueden afectar los procesos ecológicos (CONANP 2007). Dicho componente tiene como objetivos identificar las áreas afectadas por actividades antropogénicas (e.g. avance de la frontera agrícola), monitorear los cambios físicos de los paisajes transformados (e.g. aislamiento de los fragmentos de hábitat original) y establecer las bases para un programa de recuperación (CONANP 2007).

Por estas razones, diseñamos un estudio considerando el PNLM y su zona de influencia como escenario para estudiar la respuesta de los murciélagos insectívoros aéreos a variables locales como ecotopos específicos (e.g. superficies de agua) y disponibilidad de alimento (e.g. presas potenciales), así como a variables de paisaje, específicamente características que pueden mantener continuidad física del hábitat. Nuestra intención fue, a través de la selección de este grupo de estudio y las variables explicativas potenciales, entender los efectos de la transformación del ecosistema en la actividad relativa de los murciélagos insectívoros aéreos, con el fin de contribuir a las estrategias futuras para la protección y recuperación de ecotopos específicos y paisajes.

Desarrollamos este estudio a través de tres componentes interconectados, presentados como artículos científicos. El primer componente, consideró información generada con métodos complementarios para el estudio de murciélagos. Específicamente, presentamos datos generados con el uso de redes de niebla operadas simultáneamente con los dispositivos acústicos, cuyo fin original era aumentar la posibilidad de captura de murciélagos insectívoros aéreos para llevar a cabo grabaciones semi-controladas y crear la biblioteca de referencia acústica para

el área. Contrario a la expectativa, la cantidad de capturas de este grupo de murciélagos por medio de redes de niebla fue extremadamente baja y sesgada fuertemente hacia representantes de la familia Phyllostomidae (murciélagos frugívoros, nectarívoros y sanguívoros), lo que provee evidencia nueva de la importancia de métodos alternativos para el estudio de los ensambles de murciélagos. Sin embargo, estos datos fueron aprovechados y analizados con un enfoque dirigido a determinar el efecto del cambio de cobertura boscosa en el nivel de ensambles y conjuntos de murciélagos filostómidos, con un enfoque de generalización de atributos ecológicos que se propone puede ser útil en estrategias de conservación de taxa ricos en especies. Asimismo, los patrones observados sirvieron como punto de comparación con la respuesta de los murciélagos insectívoros aéreos estudiados por medio de detección acústica.

El segundo componente, se enfocó en la importancia de la caracterización acústica de las especies de murciélagos insectívoros aéreos previo al monitoreo en campo. Específicamente, abordó la importancia de identificar adecuadamente los parámetros acústicos que discriminan individuos y las tasas de clasificación correcta previo a su monitoreo en vuelo libre en un área específica. Se llevó a cabo un ejercicio sobre el poder de discriminación acústica a nivel intra-específico, explorando fuentes de variación intrínseca que pueden provocar confusión en la identificación (e.g. categoría de edad) y extrínsecas con base en restricciones del hábitat (e.g. ecolocalización en áreas abiertas o con obstáculos como vegetación de fondo). A través de este análisis demostramos la importancia de los métodos cuantitativos para la clasificación de especies con un enfoque que es objetivo y reproducible, en contraste con enfoques cualitativos que pueden acarrear errores de identificación. Asimismo, enfatizamos la importancia de las bibliotecas de llamados de ecolocalización basadas en el efecto del espacio acústico para una misma especie, como fuente de sesgo en la asignación taxonómica, también conocidas como “clutter-based acoustic libraries”.

Por último, el tercer componente nos lleva al tema central de la investigación. Específicamente, se trató de la exploración del valor explicativo potencial de variables a nivel local (hábitats específicos y disponibilidad de alimento) y nivel de paisaje (métricas de composición y configuración), sobre la actividad relativa de murciélagos insectívoros aéreos que exhiben un sistema de ecolocalización de rango corto (variable respuesta), estudiados a través de medios acústicos. Aquí,

además de la importancia relativa de las variables locales, en el nivel espacial se consideraron las respuestas especie-específicas, que pueden estar basadas en atributos ecológicos (e.g. vagilidad de las especies), tomando en cuenta el cambio de las extensiones de análisis del paisaje. De esta manera, identificamos la contribución independiente de las variables en la actividad relativa de este grupo de murciélagos e identificamos la importancia de ecotopos específicos, presas potenciales y características del ambiente circundante, cuya protección puede ser relevante para la persistencia de sus poblaciones.

1.8. Áreas y Sitios de Importancia para la Conservación de los Murciélagos: una propuesta para acreditación internacional

La Red Latinoamericana para la Conservación de los Murciélagos (RELCOM) ha establecido criterios para la acreditación de zonas de interés por su diversidad biológica. Específicamente, ha creado las figuras de Área de Importancia para la Conservación de Murciélagos (AICOM) y Sitio de Importancia para la Conservación de Murciélagos (SICOM) (<http://www.relcomlatinoamerica.net>). Para la acreditación de las primeras, los criterios son los siguientes: 1) El área contiene especies de interés de conservación nacional o regional (incluye especies amenazadas y casi amenazadas en listas rojas de los países, especies en la lista de UICN, endémicas, migratorias, raras, con datos deficientes, papel importante en el funcionamiento ecosistémico, especies con rangos de distribución pequeña o restringida e incluye especies presentes en su límite de distribución); 2) El área contiene refugios con una o varias especies de interés para la conservación y que sean usados de manera permanente o temporal, que sea usado en parte significativa de su ciclo de vida, como en el caso de refugios de maternidad o sitios de agregación por migración (puede ser un sistema de cuevas, refugios específicos como construcciones antrópicas, entre otros); 3) El área contiene una riqueza de especies alta independientemente de su amenaza. Los segundos, se diferencian del AICOM en que son sitios mucho más pequeños y puntuales que presentan poblaciones de murciélagos de interés para la conservación; pueden ser cuevas, cuerpos de agua o sitios de aprovisionamiento importantes (parques u otros) y construcciones antrópicas (casas, puentes, túneles, minas abandonadas).

Con base en nuestros hallazgos, hacemos énfasis en la pertinencia de la acreditación del PNLM y de ecotopos con superficie de agua estacional en su zona

de influencia; específicamente, proponemos la consideración de AICOM y SICOMs, respectivamente. Este tipo de acreditación serviría como plataforma para un programa permanente de investigación, educación ambiental y conservación, tomando en cuenta la participación de actores locales, organizaciones civiles sin fines de lucro e instituciones de gobierno vinculadas con las áreas naturales protegidas.

1.9. Literatura citada

Arrhenius O. 1921. Species and area. *J Ecol.* 9:95–99.

Bader E, Jung K, Kalko EKV, Page RA, Rodríguez R, Sattler T. 2015. Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biol Conserv.* 186:97–106.

Bennett AF, Saunders DA. 2010. Habitat fragmentation and landscape change. In: Sodhi NS, Ehrlich PR, editors. *Conservation Biology for all*. New York (US): Oxford University Press. p. 88–106.

Cleveland CJ, Betke M, Federico P, Frank JD, Hallam TG, Horn J, López Jr JD, MacCracken GF, Medellín RA, Moreno-Valdez A, Sansone CG, Westbrook JK, Kunz TH. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Front Ecol Environ.* 4(5):238–243.

[CONANP] Comisión Nacional de Áreas Naturales Protegidas. 2007. Programa de Conservación y Manejo del Parque Nacional Lagunas de Montebello, México. México (MX): Secretaría de Ambiente y Recursos Naturales. 189 p.

Diamond JM. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol Conserv.* 7(2):129–145.

Dunning JB, Groom MJ, Pulliam HR. 2006. Species and landscape approaches to conservation. In: Groom MJ, Meffe GK, Carroll CR, editors. *Principles of Conservation Biology*. Massachusetts (US): Sinauer Associates. p. 419–465.

Estrada-Villegas S, Meyer CF, Kalko EKV. 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biol Conserv.* 143(3):597–608.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S.* 34:487–515.

- Faria D. 2006. Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. *J Trop Ecol.* 22(5):531–542.
- Farneda FZ, Rocha R, López-Baucells A, Groenenberg M, Silva I, Palmeirim JM, Bobrowiec PED, Meyer CFJ. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. *J Appl Ecol.* 52(5):1381–1391.
- Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM, Adkins B. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica.* 24(3):440–446.
- Fenton MB. 1999. Describing the echolocation calls and behaviour of bats. *Acta Chiropterol.* 1(2):127–136.
- Fenton MB. 2002. Bat natural history and echolocation. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. *Bat echolocation research: Tools techniques and analysis.* Texas (US). Bat Conservation International. p. 2–6.
- Fischer J, Lindenmayer DB, Fazey I. 2004. Appreciating ecological complexity: Habitat contours as a conceptual landscape model. *Conserv Biol.* 18(5):1245–1253.
- Fischer J, Lindenmayer DB. 2006. Beyond fragmentation: The continuum model for fauna research and conservation in human-modified landscapes. *Oikos.* 112(2):473–480.
- Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: A synthesis. *Global Ecol Biogeogr.* 16(3):265–280.
- Forman RTT. 1995. *Land Mosaics. The ecology of landscapes and regions.* New York (US): Cambridge University Press. 632 p.
- Franklin JF, Lindenmayer DB. 2009. Importance of matrix habitats in maintaining biological diversity. *P Natl Acad Sci USA.* 106(2):349–350.
- Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J Appl Ecol.* 50(1):252–261.
- Frick WF. 2013. Acoustic monitoring of bats, considerations of options for long-term monitoring. *Therya.* 4(1):69–78.
- Fuentes-Montemayor E, Goulson D, Cavin L, Wallace JM, Park KJ. 2013. Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agr Ecosyst Environ.* 172:6–15.

- García-García JL, Santos-Moreno A, Hernández-Cruz, AE, Pérez-Lustre M. 2009. Murciélagos de La Ventosa, Oaxaca: comparación entre el método de muestreo convencional y el muestreo acústico. *Naturaleza Desarro*. 7(1):19–29.
- García-García JL, Santos-Moreno A, Kraker-Castañeda C. 2014. Ecological traits of phyllostomid bats associated with sensitivity to tropical forest fragmentation in Los Chimalapas, Mexico. *Trop Conserv Science*. 7(3):457–474.
- Gardner RH, Milne BT, Turner MG, O'Neill RV. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landsc Ecol*. 1:5–18.
- Gleason HA. On the relation between species and area. *Ecology*. 3(2):158-162.
- Groom MJ, Vynne CH. 2006. Habitat degradation and loss. In: Groom MJ, Geffe GK, Carroll CR, editors. *Principles of Conservation Biology*. Massachusetts (US): Sinauer Associates. p. 173–212.
- Gurevitch J, Fox GA, Fowler NL, Graham CH. 2016. Landscape demography: population change and its drivers across spatial scales. *Q Rev Biol*. 91(4):459–485.
- Hagen EM, Sabo JL. 2012. Influence of river drying and insect availability on bat activity along the San Pedro river, Arizona. *J. Arid Environ*. 84:1–8.
- Hanski I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*. 87(2):209–219.
- Heim O, Treitler JT, Tschapka M, Knörnschild M, Jung K. 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS ONE*. 10(7):e0134443.
- Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr*. 54(2):187–211.
- Jakobsen L, Brinkløv S, Surlykke A. 2013. Intensity and directionality of bat echolocation signals. *Front Physiol*. 4:89.
- Jones G, Rydell J. 2003. Attack and defense: Interactions between echolocating bats and their insect prey. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. Chicago (US): The University of Chicago Press. p. 301–345.
- Jules ES, Shahani PC. 2003. A broader ecological context to the fragmentation frenzy: Why matrix habitat is more important than we thought. *J Veg Sci*. 14(3):459–464.

- Kraker C, Pérez S. 2012. Detección ultrasónica de murciélagos insectívoros en cafetales de la Antigua Guatemala, Guatemala. *Revista Científica del Instituto de Investigaciones Químicas y Biológicas*. 22(1):43–53.
- Kraker-Castañeda C, Santos-Moreno A, García-García JL. 2013. Riqueza de especies y actividad relativa de murciélagos insectívoros aéreos en una selva tropical y pastizales en Oaxaca, México. *Mastozool Neotrop*. 20(2):255–267.
- Kunz TH, Brock CE. 1975. A comparison of mist nets and ultrasonic detectors for monitoring flight activity of bats. *J Mammal*. 56(4):907–911.
- Kunz TH. 2002. Foraging habits of North American insectivorous bats. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. *Bat echolocation research, tools, techniques and analysis*. Texas (US): Bat Conservation International. p. 13–25.
- Kunz TH, Braun de Torrez E, Bauer D, Lobo T, Fleming TH. 2011. Ecosystem services provided by bats. *Ann N Y Acad Sci*. 1223:1–38.
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am*. 15(3):237–240.
- Lindenmayer DB, Burgman M. 2005. *Practical Conservation Biology*. Australia: CSIRO Publishing. 609 p.
- MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. New Jersey (US): Princeton University Press. 224 p.
- MacIntire S, Barrett GW. 1992. Habitat variegation, an alternative to fragmentation. *Conserv Biol*. 6(1):146–147.
- MacSwiney MC, Clarke FM, Racey PA. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *J Appl Ecol*. 45(5):1364–1371.
- MacSwiney MC, Bolívar B, Clarke FM, Racey PA. 2009. Insectivorous bat activity at cenotes in the Yucatan Peninsula, Mexico. *Acta Chiropterol*. 11(1):139–147.
- Manning AD, Lindenmayer DB, Nix HA. 2004. Continua and umwelt: Novel perspectives on viewing landscapes. *Oikos*. 104(3):621–628.
- Medellín RA, Equihua M, Amin MA. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conserv Biol*. 14(6):1666–1675.

- Meyer CFJ, Fründ J, Pineda Lizano W, Kalko EKV. 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J Appl Ecol.* 45(1):381–391.
- Miller BW. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterol.* 3(1):93–105.
- Norberg U, Rayner J. 1987. Ecological morphology and the flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philos T R Soc B.* 316(1179):335–427.
- O’Farrell MJ, Gannon WL. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *J Mammal.* 80(1):24–30.
- Parsons S, Boonman AM, Obrist MK. 2000. Advantages and disadvantages of techniques for transforming and analyzing chiropteran echolocation calls. *J Mammal.* 81(4):927–938.
- Patterson BD, Atmar W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc.* 28(1-2):65–82.
- Pech-Canché JM, MacSwiney C, Estrella E. 2010. Importancia de los detectores ultrasónicos para mejorar los inventarios de murciélagos Neotropicales. *Therya.* 1(3):227–234.
- Perfecto I, Vandermeer J. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. *Conserv Biol.* 16(1):174–182.
- Pettersson L. 2002. The properties of sound and bat detectors. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. *Bat echolocation research: Tools techniques and analysis.* Texas (US). Bat Conservation International. p. 9–12.
- Pinto N, Keitt TH. 2008. Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos.* 117:1725–1731.
- Price B, McAlpine CA, Kutt AS, Phinn SR, Pullar DV, Ludwig JA. 2009. Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach. *Ecography.* 32(5):745–756.
- Pulliam HR. 1988. Sources, sinks, and population regulation. *Am Nat.* 132(5):652–661.
- Rainho A, Palmeirim JM. 2011. The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS ONE.* 6(4):e19227.

- Reiskind MH, Wund MA. 2009. Experimental assessment of the impacts of northern long-eared bats on ovipositing *Culex* (Diptera: Culicidae) mosquitoes. *J Med Entomol.* 46(5):1037–1044.
- Richarz K, Limbrunner A. 1993. *The world of bats: The flying goblins of the night.* New Jersey (US): TFH Publications. 192 p.
- Schnitzler H-U, Kalko EKV. 2001. Echolocation by insect-eating bats. *BioScience.* 51(7):557–569.
- Seidman V, Zabel C. 2001. Bat activity along intermittent streams in Northwestern California. *J Mammal.* 82(3):738–747.
- Seip KL, Wenstøp F. 2006. *A primer on environmental decision-making. An integrative quantitative approach.* The Netherlands: Springer. 492 p.
- Sodhi NS, Brook BW, Bradshaw CJA. 2009. Causes and consequences of species extinctions. In: Levin SA, Carpenter SR, Godfray HCJ, Kinzig AP, Loreau M, Losos JB, Walker B, Wilcove DS, editors. *The Princeton Guide to Ecology.* New Jersey (US): Princeton University Press. p. 514–520.
- Stahlschmidt P, Brühl CA. 2012. Bats as bioindicators – the need of a standardized method for acoustic bat activity surveys. *Methods Ecol Evol.* 3(3):503–508.
- Turner MJ, Gardner RH, O'Neill RV. 2001. *Landscape Ecology in Theory and Practice.* New York (US): Springer. 401 p.
- Vandermeer J, Carvajal R. 2001. Metapopulation dynamics and the quality of the matrix. *Am Nat.* 158(3):211–220.
- Van der Molen DT, Geilen N, Backx JJGM, Jansen BJM, Wolfert HP. 2003. *Water ecotope classification for integrated water management in the Netherlands.* Official Publication of the European Water Association. 14 p.
- Williams-Guillén K, Perfecto I. 2011. Ensemble composition and activity levels of insectivorous bats in response to management intensification in coffee agroforestry systems. *PLoS ONE.* 6:e16502.
- Zonneveld IS. 1989. The land unit – A fundamental concept in landscape ecology, and its applications. *Land Ecol.* 3(2):67–86.

Capítulo II

Responses of phyllostomid bats to forest cover in tropical highland landscapes in Chiapas, southeast Mexico

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Abstract

Forests are a key habitat for many bats, but tend to be lost and fragmented in some agri-environment schemes. We studied the effects of forest cover change on phyllostomid bats in agricultural landscapes with increment of open areas in an upland region in Chiapas, southeast Mexico. We tested whether with forest cover increase there is a directly proportional response on assemblage species diversity measures, on the capture success and body condition of particular ensembles. Depending on the spatial analysis window, and presumably on vagility, we found positive and significant associations with the sanguivore ensemble's capture success, as well as with the nectarivore and shrub frugivore ensembles' body condition. We support the idea that appropriate amounts of forest over small geographic extents may propitiate favorable environments for some phyllostomids, also which can provide important ecological services. Furthermore, the arrangement

of ecologically similar species proved to be valuable for exploring adaptive traits, and adequate for conservation strategies of species-rich taxa.

Keywords: assemblage; chiropterans; deforestation; ensemble; vagility

Introduction

The ongoing loss of biodiversity because of human activities is an issue of great concern, and the object of much of contemporary research. The loss and fragmentation of natural areas lead to adverse environments for sensitive species, and often a decrease in their survival probability (Groom & Vynne 2006; Bennett & Saunders 2010; Ávila-Gómez et al. 2015). While facing habitat disruption, the resilience of many organisms depends on traits as abundance and mobility, among others (e.g. García-García et al. 2014; Bader et al. 2015). Consequently, different species require different amounts of habitat to persist in a given landscape, and likely exhibit differential susceptibilities to local extinction (Fahrig 2003; Fischer & Lindenmayer 2007).

When studies of animal communities are based on the basic idea that these are collections of organisms living in the same place and time, delimited naturally or arbitrarily (e.g. all organisms in a plot), concepts such as phylogeny, geography and resource use may provide operational definitions that can be a valuable field of ecological inquiry (Jaksić 1981; Fauth et al. 1996). For instance, phylogenetically related groups within a community (this is the intersection between phylogeny and geography) are termed “assemblages” (Fauth et al. 1996). Similarly, phylogenetically related groups that use a similar set of resources within a community (this is the intersection between phylogeny, geography and resource use) are termed “ensembles” (Fauth et al. 1996). Approaches such as these allow the identification of patterns of community structure, and understanding of factors that underlie its organization (Kalko et al. 1996; Schnitzler & Kalko 2001; Denzinger & Schnitzler 2013).

Bats are an ideal study system for investigating consequences of habitat loss and fragmentation because most are colonial, central-place foragers or depend on scattered resources across landscapes (Pinto & Keitt 2008; Rainho & Palmeirim 2011). They are also known to be useful indicators of disturbance because of their high abundance and ecological, taxonomical, and trophic representation (Fenton et

al. 1992; Medellín et al. 2000). Moreover, their sensitivity to habitat disruption can be addressed by specific traits (e.g. Meyer et al. 2008; García-García et al. 2014; Farneda et al. 2015).

For instance, the bat's foraging behavior can be described by mobility traits during flight (similarly in birds) in terms of wing loading (body mass per wing area) and wing shape (as a function of wing length to width) (Norberg & Rayner 1987; Bader et al. 2015). The foraging behavior and the associated traits affect the bat's ability to access particular habitats such as cluttered vegetation, and consequently their ability to access food (Fenton et al. 1992; Marciente et al. 2015). Less mobile species with slow flight but high maneuverability exhibit large-surfaced, broad wings, and are thereby adapted for the use of cluttered habitats and covering short distances (Norberg & Rayner 1987; Fenton et al. 1992; Bader et al. 2015). In contrast, more mobile species with fast flight but less maneuverability exhibit small-surfaced, narrow wings, adapted for open spaces, and are able to cover long distances at low energetic cost (Norberg & Rayner 1987; Bader et al. 2015; Rodríguez-San Pedro & Simonetti 2015).

Likewise, body condition can provide a proxy for eco-physiological responses to food shortage in the environment, and it can offer insights into consequent animal stress (Fleming 1988; Ramos et al. 2010). Body condition indices are generally calculated as the relationship between body mass and a linear aspect of the animal (e.g. forearm length in bats), and can be related to habitat quality (Speakman 2008). For instance, Ramos et al. (2010) found a decline in body condition of the phyllostomid *Artibeus planirostris* when fruits were scarcer, which might indirectly reflect a decrease of the amount of suitable habitat in the given landscape.

Here, we investigated phyllostomid bats in a region exposed to human activity that has left few forested areas, which are immersed in agricultural landscapes with increment of open areas. Our aim was to provide evidence of the importance of forest cover for this group of bats. We used concentric spatial analysis windows (hereafter buffers) to analyze the effect of forest cover (hereafter FC) as a predictor variable on assemblage-level, and ensemble-level measures. We began with the hypothesis that the increase of FC is directly proportional to assemblage species diversity measures, on the capture success and body condition of particular ensembles.

The predictions with the increase of FC are: a) higher richness that incorporates rare species because of potential increment in environmental heterogeneity; b) higher equitability with lower dominance of generalist species because of presumably decrease in disturbance; c) higher capture success and body condition in some ensembles because of possibly more resource availability. Finally, we highlight that the arrangement of ecologically similar species can be a valuable approach in conservation strategies.

Material and methods

Study area

The study area is located on a plateau in a tropical highland region in Chiapas, southeast Mexico (Figure 1). It falls within and extends beyond the Lagos de Montebello National Park (hereafter PNLM) (Figure 1). Average elevation in the PNLM is 1,500 m asl (above sea level) and its extension covers 6,425 ha, with estimations of water surface during the dry season ranging between 1,030 ha and 1,219 ha (CONANP 2007). There was no considerable variation in elevation in the study area (1,460 m–1,540 m asl), which prevented this variable from being a confounding factor (Carrara et al. 2015).

The predominant vegetation type in the PNLM is coniferous forest, and the most frequent species are pines (Pinaceae), with *Pinus oocarpa* in the driest areas and *P. maximinoi* in wetter areas. Nevertheless, oaks (Fagaceae: *Quercus* spp.), cypresses (Cupressaceae: *Cupressus* spp.), and sweetgum (Altingiaceae: *Liquidambar styraciflua*) are also common in mixed associations (CONANP 2007). The surroundings of the PNLM are mostly characterized by agricultural activities (extensive cornfields), livestock husbandry (grasslands), human settlements, and scattered forest remnants. The cornfields, grasslands, and human settlements lack tree cover (i.e. they are characterized by open space), and hence we consider these as unsuitable environments for forest specialists. In the area, distinct levels of secondary vegetation are not distinguishable by satellite imagery and, when present, they are mixed into the forests as a result of land management practices.

Bat sampling

Field work was carried out monthly between July 2014–July 2015 during nights close to new moon, in order to avoid effects of lunar phobia (Santos-Moreno et al. 2010;

Saldaña-Vázquez & Munguía-Rosas 2013). In total, we sampled nine points within and beyond the PNLM (Table 1; Figure 1). Each sampling point was visited twice (once in both wet and dry seasons), for three consecutive nights each visit.

Sampling events were conducted in the understory using three 12 m long and 2.5 m high mist nets (Ecotone®, Gdynia, Poland), during 4 hour periods beginning at sunset. Mist netting effort was calculated with the area of the nets deployed (length by height in meters) divided by the number of hours sampled, giving an effort of 2,160 m²/h in each sampling point and a total sampling effort of 19,440 m²/h.

The bats captured were identified using the field key of Medellín et al. (2008), weighed to the nearest 0.1 g with a 100 g scale (Pesola AG®, Baar, Switzerland), and their forearms were measured to the nearest 0.1 mm with a digital caliper (Mitutoyo®, Illinois, US). Bat taxonomy was based on Ramírez-Pulido et al. (2014). We also registered reproductive activity (non-pregnant, pregnant, lactating) and age (juvenile, sub-adult, adult); the latter was based on the degree of fusion of the metacarpal epiphysis (Anthony 1988). For each individual captured, we obtained a 4 mm diameter biopsy of the wing membrane using a dermatological punch (Biopunch®, Ted Pella, Inc., California, US) at a standardized position between the fourth and fifth digits in order to allow recognition of re-captures and avoid re-measuring (Ripperberg et al. 2014). Samples were stored in 96% ethanol for future analyses.

Spatial analyses

A non-supervised classification of the study area was available in the Laboratory of Geographic Information and Statistic Analysis of ECOSUR, which was based on multispectral SPOT satellite images of 2011, with a spatial resolution of 10 m. This classification was verified during 2014–2015 through 211 control points around the sampling points and within the buffers, which allowed for polygons rectification using the software ArcView® version 3.2 (ESRI, Inc.). We chose to base our analysis on FC, because it is a variable highly correlated to other measures of habitat loss and fragmentation (Fahrig 2003). The FC was corroborated in the field by the presence of woody plants and a distinguishable canopy.

The sampling points were established with the intention of avoiding spatial autocorrelation, because if they are too close to one another observations can be spatially correlated, and the assumption of independence is violated (Popescu &

Gibbs 2010); in other words, as distance between sampling points decreases, similarity among samples increases. Information about Neotropical bats home ranges is scarce; however, *Carollia perspicillata* is a phyllostomid with body size comparable to some of the species previously registered in the study area, and has average flight distances from day roosts to feeding areas of 1.6 km (Heithaus & Fleming 1978). Therefore, the minimum distance between sampling points was set starting from ~ 3.5 km.

Several authors have provided evidence that a single buffer may fail to recognize phyllostomids species-level, assemblage-level, and ensemble-level perceptions of their surroundings and resource distribution (e.g. Pinto & Keitt 2008; Klingbeil & Willig 2009; Avila-Cabadilla et al. 2012; Bolívar-Cimé et al. 2013). Therefore, we constructed concentric buffers around the sampling points with 0.5 km, 1 km, and 1.5 km radius (Figure 1). These were non-overlapping in order to avoid re-measuring of land units (Popescu & Gibbs 2010). The minimum radius was chosen to encompass the home range of the smallest species in the study area, perhaps as wide as 0.5 km for *Glossophaga soricina* (Lemke 1984; Gorresen & Willig 2004). These focal buffers also facilitate comparison with previous research on phyllostomid spatial-dependent associations (e.g. Pinto & Keitt 2008; Ávila-Gómez et al. 2015). We measured FC in square kilometers (km²) in each buffer using the software ArcView® version 3.2 (ESRI, Inc.), and include the calculations in Table 1.

Delimitation of variables and statistical analyses

Assemblage-level: species diversity measures

The number of species or species richness (S) in a sample is among the simplest descriptors of community structure (Maurer & MacGill 2011). It is an essential, intuitive and natural index, for which many calculation methods have been proposed (Gotelli & Colwell 2011). Given that our samples differed in the number of captured individuals, we calculated the assemblage S with rarefaction, hereafter referred to as interpolation (Gotelli & Colwell 2011). This calculation was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004).

Theoretically, if the species in an assemblage are equally common or equivalent in number, then the diversity (as a combination of S and equitability) has to be proportional to the specific richness (Moreno et al. 2011). Nevertheless this is improbable, and the estimation of changes in diversity are useful when comparing

samples spatially and/or temporarily (Moreno et al. 2011). Therefore, we calculated the Shannon diversity index (H') with rarefaction in order to control for sample differences (Gotelli & Entsminger 2004), but transformed these calculations into effective number of species (1D), also known as "true diversity" (Jost 2006; Moreno et al. 2011). The 1D measure conserves intuitive properties of the diversity concept and allows for direct comparison of magnitudes among assemblages (Moreno et al. 2011). The calculation of H' was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004), and the calculation of 1D using Microsoft® Office Excel.

Finally, we include an evenness measure which attempts to examine how abundance is apportioned among species. Such measures rely on the basic concept that evenness is highest when an assemblage is not dominated by a few species of very high abundance, or equivalently that all species have an equal abundance (Maurer & MacGill 2011). We calculated the Hurlbert's PIE index (Probability of an Interspecific Encounter), which calculates the probability that two randomly sampled individuals from the assemblage represent two different species, and is unbiased by sample size (Gotelli & Entsminger 2004; Maurer & McGill 2011). This calculation was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004).

Ensemble classification allocation procedure

We classified species into the Highly Cluttered Space Gleaning "guild" following Kalko et al. (1996), Kalko & Handley (2001), Sampaio et al. (2003), and Morim et al. (2014). For those species lacking in the latter classification, we considered information of foraging height, capture height, and diet elements, comparing species in the same genus based on Reid (2009) and Rex (2011): canopy frugivore; shrub frugivore; nectarivore; sanguivore; carnivore. Nevertheless, the guild definition by Root (1967), later described by Fauth et al. (1996), is interpreted as a resource-bounded but non-taxonomically circumscribed set of species (e.g. foliage gleaners). Because the study area species are phylogenetically related groups that use a similar set of resources, they therefore fulfill the characteristics of an ensemble (see Fauth et al. 1996), and we use the latter term instead of guild.

Ensemble-level: capture success and body condition

Once all the species registered in the study area were classified into ensembles, we calculated the capture success at each sampling point as a surrogate for abundance

(Pinto & Keitt 2008). We considered the total number of individuals belonging to a particular ensemble divided by the mist netting effort (2,160 m²/h).

We calculated a body condition index (BCI) for the members in each ensemble at each sampling point (sub-adults, adults, and non-pregnant individuals), based on the relationship between body mass and forearm length, in g/mm (Speakman 2008). Our initial assumption was that species grouped in the same ensemble behave similarly, specifically forage in similar habitats in similar ways for similar foods (Kalko and Handley 2001), and that members reflect the sustenance capacity of the habitat (e.g. larger and better conditioned bats demand more food in the environment). We are aware that this approach may be biased because different species differ in physiology, and distinct resources might not be energetically equivalent. Nevertheless, we consider that it may offer insights about resources in the environment in general terms (e.g. availability of forest-associated floral nectar). We include the median BCI as a measure of central tendency, and to minimize the effect of the outliers.

Variables' responses to forest cover change

In order to measure the direction, magnitude, and significance of association between FC, the assemblage species diversity measures, ensembles' capture success and body condition, we calculated the Spearman non-parametric correlation coefficient in each focal buffer. This coefficient is adequate for small samples, and makes no assumptions about the data distribution. We excluded the carnivore ensemble because of insufficient samples (registered in a single sampling point). These calculations were performed in the software STATISTICA® version 8.0 (StatSoft, Inc. 2007), which also provides probability tests for statistical significance. All the tests were considered statistically significant with $p \leq 0.05$.

Results

Assemblage-level: species diversity measures

We captured a total of 264 phyllostomids, registered 4 subfamilies, 10 genera and 14 species (Table 2). Between sampling points, overall abundance ranged between 12 and 77 individuals (Table 2). The values of S differed between sites, and the lowest ¹D and Hurlbert's PIE index values were detected in sampling points characterized by a high capture rate of *A. jamaicensis* and *Sturnira parvidens* (constituting 91% of

captures), and *A. jamaicensis* and *Anoura geoffroyi* (80% of captures), respectively (Table 3). The highest 1D was 4.76, more than twice as large as in the sampling point with the lowest value (2.27).

Ensemble-level: capture success and body condition

The maximum value in overall capture success was 0.036, and the minimum was 0.005. Capture successes in each sampling point are presented in Table 4. The median BCI in each sampling point is presented in Table 5. The average BCI was highest for the canopy frugivore's (0.77; $\sigma = 0.11$), followed in rank order by the sanguivore's (0.59; $\sigma = 0.07$), shrub frugivore's (0.48; $\sigma = 0.06$), and nectarivore's (0.32; $\sigma = 0.06$).

Variables' responses to forest cover change

In the smallest buffers, the sampling points with more than 80% of forest cover showed higher values of interpolated S (with one exception), and the addition of rare species (e.g. *Chiroderma salvini*, *Diphylla ecaudata*, *Chrotopterus auritus*). The sampling point with least forest cover (< 50%), exhibited the lowest values of interpolated S and 1D , and it was dominated by *A. jamaicensis* and *S. parvidens*. Besides the latter, the sampling point with less forest cover in the intermediate and largest buffers, below 40% and 30% respectively, exhibited the lowest 1D and Hurlbert's PIE values, and it was dominated by *A. jamaicensis*.

In Table 6, we present the correlations between FC, the assemblage species diversity measures, ensembles' capture success and body condition. We did not find assemblage-level statistically significant associations, except a weak, positive, and marginally non-significant correlation with the interpolated S ($\rho = 0.66$; $p = 0.053$).

In the smallest buffers we found strong, positive, and significant correlations with the nectarivore's BCI ($\rho = 0.72$; $p = 0.044$), as shown in Figure 3. In the intermediate buffer we found strong, positive, and significant correlations with the sanguivore's capture success ($\rho = 0.86$; $p = 0.006$), and with the shrub frugivore's BCI ($\rho = 0.87$; $p = 0.002$). In the largest buffer we also found strong, positive, and significant correlations with the shrub frugivore's BCI ($\rho = 0.85$; $p = 0.003$).

Discussion

Variables' responses to forest cover change

With regard to the predictions of the effect of increase of FC at the assemblage-level, specifically a directly, proportional response on species richness and equitability, we did not find statistically significant associations, and hence we can not support this hypothesis in the study area. This lack of response might possibly be due to buffers failing to detect patterns which may be present over larger spatial extents. For instance, nested distribution of habitats is a possible cause of nested species assemblages (e.g. Calmé & Desrochers 1999), and may be stronger over wider areas with increasing FC. Moreover, the degree of habitat degradation may be high in the area, with a consequent dominance of generalist species (e.g. *A. jamaicensis*, *S. parvidens*).

At the ensemble-level, we found that the canopy frugivore members, who are presumed to be more vagile, did not respond to FC in the focal buffers in the study area. Nevertheless, dependent on buffers we found various statistically significant associations with the rest of the ensembles, composed of less mobile species, which are described below.

In the smallest buffers (0.5 km radius), we found a significant positive response in the nectarivore's BCI, which corroborates the prediction that with increase in FC, the body condition of some phyllostomids is higher. The lowest values were associated with sampling points with less than 70% of FC. In accordance, Ávila-Gómez et al. (2015) found in their study area that *G. soricina*, which is a member of the nectarivore ensemble, was more frequent in areas with more than 70% arboreal cover. The glossophagines consume floral nectar using a hovering flight mode, and have to ingest large amounts of nectar each night in order to fulfill the high energetic requirements of this foraging behavior (Voigt & Winter 1999; Von Helversen & Winter 2003). Assuming that FC might be correlated with the quantity of floral resources, low availability of floral nectar in landscapes with low FC might affect both abundance and body condition of glossophagines. Lemke (1984) also indicates that individuals of *G. soricina* adopt an energetically costly territorial behavior in response to low plant diversity and food reliability, which could lead to stress and consequently poor body condition.

In the intermediate buffers (1 km radius), we found a significant positive response in the sanguivore ensemble capture success, which corroborates the prediction that with increase in FC the abundance of some species may be higher. The lowest values were associated to the sampling points with less than 60% of FC.

For this ensemble, the most abundant member was *Desmodus rotundus*, while *D. ecaudata* was captured in low abundance, and at only two sampling points; the latter is considered to be locally rare, and its population small in size (Greenhall et al. 1984; Elizalde-Arellano et al. 2007). Ávila-Gómez et al. (2015) suggest that *D. rotundus* requires landscapes in which a high percentage of forest has been preserved, but is more frequent where canopy cover is low. In other words, it benefits from areas with a high amount of forest and low tree density, which may improve flight performance. Nevertheless, the latter finding may only be true as long as food sources (e.g. livestock) and roosts are available nearby. Even more, *D. rotundus* is known to be present in low abundance or absent from areas of continuous forest, and it was not captured in the sampling point with 95.5% of FC (AZAR), which is located within the PNLM.

In both the intermediate and largest buffers (1.5 km radius) we found a significant positive response of the shrub frugivore BCI, which indicates that with increase in FC the shrub frugivore's body condition is also higher. The lowest values were found in the sampling points with less than 75% of forest cover. The *Sturnira* species, which were the most abundant members of this ensemble, are known to respond to the amount of secondary and primary forest over small geographic extents (Pinto & Keitt 2008; Mena 2010). This genus is strongly associated with vegetation succession elements, specifically pioneer plants in the genera *Solanum* and *Piper*, which produce edible, fleshy fruits (Bolívar-Cimé et al. 2013; Kraker-Castañeda et al. 2016). Nevertheless, pioneer plants in the study area are mixed into forests complicating the spatial characterization of secondary vegetation, and consequently the inference of its relative importance for this particular ensemble.

Ecological generalization in conservation strategies

Here, we considered the arrangement of ecologically similar species in order to explore the effects of FC in high contrast agricultural landscapes. By pooling species into sets based on ecological traits, we explored an alternative to the species-specific approach, and offered an insight into the responses of phyllostomids. This way, “keystone ensembles” can be considered useful in conservation strategies of species-rich taxa by protecting species that behave similarly. Nevertheless, it is important to recognize that a generalized approach may obscure specialized interactions which can be ecologically relevant (Ávila-Gómez et al. 2015), and which

may also be at risk of being disrupted by habitat loss and fragmentation. Moreover, bats presence does not only depend on landscape context (e.g. FC), and other extrinsic factors (e.g. habitat variables) might be involved (Bader et al. 2015).

Understanding of phyllostomid responses to landscape features in the region is usually based on lowland species, and general conclusions are drawn from these environments (e.g. Bolívar-Cimé et al. 2013; García-García & Santos-Moreno 2014; Arroyo-Rodríguez et al. 2016). Nevertheless, the importance of forests may be context-dependent, and as Rodríguez-San Pedro & Simonetti (2015) point out, the type of matrix can influence the direction, magnitude, and spatial extent operating on species. Therefore, we highlight that more research effort should be directed towards upland ecosystems, which also benefit from ecological services provided by this group of mammals. Finally, as Ávila-Gómez et al. (2015) discuss, we agree that estimating appropriate amounts of habitat for target species (or ensembles as an alternative approach) is a necessity in conservation planning, and for the selection of places to protect in transformed landscapes.

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References

- Anthony ELP. 1988. Age determination in bats. In: Kunz TH, editor. Ecological and behavioral methods for the study of bats. Washington DC (US): Smithsonian Institution Press; p. 47–58.
- Arroyo-Rodríguez V, Rojas C, Saldaña-Vásquez RA, Stoner KE. 2016. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. *Biol Cons.* 198:84–92.
- Avila-Cabadilla LD, Sanchez-Azofeifa GA, Stoner KE, Alvarez-Añorve MY, Quesada M, Portillo-Quintero CA. 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forests. *PLoS ONE.* 7(4):e35228.
- Ávila-Gómez ES, Moreno CE, García-Morales R, Zuria I, Sánchez-Rojas G, Briones-Salas M. 2015. Deforestation thresholds for phyllostomid bat populations in tropical landscapes in the Huasteca region, Mexico. *Trop Conserv Science.* 8(3):646–661.
- Bader E, Jung K, Kalko EKV, Page RA, Rodriguez R, Sattler T. 2015. Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biol Conserv.* 186:97–106.
- Bennett AF, Saunders DA. 2010. Habitat fragmentation and landscape change. In: Sodhi NS, Ehrlich PR, editors. Conservation biology for all. New York (US): Oxford University Press; p. 88–106.
- Bolívar-Cimé B, Laborde J, MacSwiney G MC, Muñoz-Robles C, Tun-Garrido J. 2013. Response of phytophagous bats to patch quality and landscape attributes in fragmented tropical semi-deciduous forest. *Acta Chiropterol.* 15(2):399–409.
- Calmé S, Desrochers A. 1999. Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia.* 118(3):361–370.
- Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L. 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biol Conserv.* 184:117–126.
- [CONANP] Comisión Nacional de Áreas Naturales Protegidas. 2007. Programa de conservación y manejo del Parque Nacional Lagunas de Montebello, México. México DF (México): Secretaría de Ambiente y Recursos Naturales; 194 p.

- Denzinger A, Schnitzler H-U. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front Ecol Environ.* 4(164):1–15.
- Elizalde-Arellano C, López-Vidal JC, Arroyo-Cabrales J, Medellín RA, Laundré JW. 2007. Food sharing behavior in the hairy-legged vampire bat *Diphylla ecaudata*. *Acta Chiropterol.* 9(1):314–319.
- Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol, Evol Syst.* 34:487–515.
- Farneda FZ, Rocha R, López-Baucells A, Groenenberg M, Silva I, Palmeirim JM, Bobrowiec PED, Meyer CFJ. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. *J Appl Ecol.* 52(5):1381–1391.
- Fauth JE, Bernardo J, Camara M, Resetarits WJ Jr., Van Buskirk J, McCollum SA. 1996. Simplifying the jargon of community ecology: a conceptual approach. *Am Nat.* 147(2):282–286.
- Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM, Adkins B. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica.* 24(3):440–446.
- Findley JS, Studier EH, Wilson DE. 1972. Morphological properties of bat wings. *J Mammal.* 53:429–444.
- Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: A synthesis. *Global Ecol Biogeogr.* 16:265–280.
- Fleming TH. 1988. The short-tailed fruit bat. A study in plant-animal interactions. Chicago (US): The University of Chicago Press; 365 p.
- García-García JL, Santos-Moreno A, Rodríguez-Alamilla A. 2010. Population dynamics of the bat *Dermanura tolteca* (Chiroptera: Phyllostomidae) in a tropical forest in Mexico. *Int J Trop Biol.* 58(4):1323–1334.
- García-García JL, Santos-Moreno A. 2014. Efectos de la estructura del paisaje y de la vegetación en la diversidad de murciélagos filostómidos (Chiroptera: Phyllostomidae) de Oaxaca, México. *Int J Trop Biol.* 62(1):217–239.
- García-García JL, Santos-Moreno A, Kraker-Castañeda C. 2014. Ecological traits of phyllostomid bats associated with sensitivity to tropical forest fragmentation in Los Chimalapas, Mexico. *Trop Conserv Science.* 7(3):457–474.
- Gorresen PM, Willig MR. 2004. Landscape responses of bats to habitat fragmentation in Atlantic Forest of Paraguay. *J Mammal.* 85:688–697.

- Gotelli NJ, Entsminger GL. 2004. EcoSim: Null model software for ecology. Version 7.71. Available from: www.garyentsminger.com/ecosim.
- Gotelli NJ, Colwell RK. 2011. Estimating species richness. In: Magurran AE, McGill BJ, editors. Biological diversity. Frontiers in measurement and assessment. New York (US): Oxford University Press; p. 39–54.
- Greenhall AM, Schmidt U, Joermann G. 1984. *Diphylla ecaudata*. Mamm Species. 227:1–3.
- Groom MJ, Vynne CH. 2006. Habitat degradation and loss. In: Groom MJ, Meffe GK, Carroll CR, editors. Principles of conservation biology. 3rd Edition. Sunderland, Massachusetts (US): Sinauer Associates; p. 173–212.
- Heithaus R, Fleming TH. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomidae). Ecol Monogr. 48(2):127–143.
- Horváth A, Vidal-Lopez R, Sarmientos-Aguilar R. 2001. Mamíferos del Parque Nacional Lagunas de Montebello. Rev Mex Mastozool. 5:6–26.
- Jaksić FM. 1981. Abuse and misuse of the term “guild” in ecological studies. Oikos. 37(3):397–400.
- Jost L. 2006. Entropy and diversity. Oikos. 113:363–375.
- Kalko EKV, Handley CO Jr., Handley D. 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. In: Cody ML, Smallwood JA, editors. Long-term studies of vertebrate communities. San Diego, California (US): Academic Press; p. 503–553.
- Kalko EKV, Handley CO Jr. 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. Plant Ecol. 153:319–333.
- Klingbeil BT, Willig MR. 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J Appl Ecol. 46(1):203–213.
- Kraker-Castañeda C, Cajas-Castillo JO, Lou S. 2016. Opportunistic feeding by the little yellow-shouldered bat *Sturnira lilium* (Phyllostomidae, Stenodermatinae) in northern Guatemala: a comparative approach. Mammalia. 80(3):349–352.
- Lemke TO. 1984. Foraging ecology of the Long-nosed bat, *Glossophaga soricina*, with respect to resource availability. Ecol. 65(2):538–548.

- Marciente R, Bobrowiec PED, Magnusson WE. 2015. Ground-vegetation clutter affects phyllostomid bat assemblage structure in lowland Amazonian forest. *PLoS ONE*. 10(8):e0136226.
- Maurer BA, McGill BJ. 2011. Measurement of species diversity. In: Magurran AE, McGill BJ, editors. *Biological diversity. Frontiers in measurement and assessment*. New York (US): Oxford University Press; p. 55–65.
- Medellín RA, Equihua M, Amin MA. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conserv Biol*. 14(6):1666–1675.
- Medellín RA, Arita HT, Sánchez O. 2008. Identificación de los murciélagos de México, clave de campo. México DF (México): Instituto de Ecología, Universidad Nacional Autónoma de México; 79 p.
- Mena JL. 2010. Respuestas de los murciélagos a la fragmentación del bosque en Pozuzo, Perú. *Rev Peru Biol*. 17(3):277–284.
- Meyer CFJ, Fründ J, Pineda Lizano W, Kalko EKV. 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J Appl Ecol*. 45(1):381–391.
- Moreno CE, Barragán F, Pineda E, Pavón NP. 2011. Reanalyzing alpha diversity: alternatives to understand and compare information about ecological communities. *Rev Mex Biodivers*. 82:1249–1261.
- Morim RL, de Souza R, de França R, Gregorin R. 2014. Bat assemblage in remnants of Atlantic Forest in Minas Gerais State, southeastern Brazil. *Neotrop Biol Conserv*. 9(1):20–26.
- Norberg UM, Rayner JM. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos Trans R Soc Lond, Ser B: Biol Sci*. 316:335–427.
- Pinto N, Keitt TH. 2008. Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*. 117:1725–1731.
- Popescu VD, Gibbs P. 2010. Landscape ecology and GIS methods. In: Kenneth C Jr., editor. *Amphibian ecology and conservation: A handbook of techniques*. New York (US): Oxford University Press; p. 339–360.
- Rainho A, Palmeirim JM. 2011. The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS ONE*. 6(4):e19227.
- Ramírez-Pulido J, González-Ruiz N, Gardner AL, Arroyo-Cabrales J. 2014. List of recent land mammals of Mexico, 2014. *Spec Pub, Mus Tex Tech Univ*. 63:1–69.

- Ramos MJ, Tiago Marques J, Palmeirim JM. 2010. Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests. *Biotropica*. 42(6):680–687.
- Reid FA. 2009. A field guide to the mammals of Central America and southeast Mexico. 2nd. Edition. New York (US): Oxford University Press; 346 p.
- Rex K, Michener R, Kunz TH, Voigt CC. 2011. Vertical stratification of Neotropical Leaf-nosed bats (Chiroptera: Phyllostomidae) revealed by stable carbon isotopes. *J Trop Ecol*. 27:211–222.
- Ripperberg SP, Tschapka M, Kalko EKV, Rodríguez-Herrera B, Mayer F. 2014. Resisting habitat fragmentation: High connectivity among populations of the frugivorous bat *Carollia castanea* in an agricultural landscape. *Agric Ecosyst Environ*. 185:9–15.
- Rodríguez-San Pedro A, Simonetti JA. 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? *Landsc Ecol*. 30:1561–1572.
- Root RB. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol Monogr*. 37:317–350.
- Saldaña-Vázquez RA, Munguía-Rosas MA. 2013. Lunar phobia in bats and its ecological correlates: A meta-analysis. *Mamm Biol*. 78(3):216–219.
- Sampaio EM, Kalko EKV, Bernard E, Rodríguez-Herrera B, Handley CO Jr. 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of central Amazonia, including methodological and conservation considerations. *Stud Neotrop Fauna Environ*. 38(1):17–31.
- Santos-Moreno A, Ruiz-Velásquez E, Sánchez-Martines A. 2010. Efecto de la intensidad del viento y de la intensidad de la luz lunar en la actividad de murciélagos filostómidos de Mena Nizanda, Oaxaca, México. *Rev Mex Biodivers*. 81(3):839–845.
- Schnitzler H-U, Kalko EKV. 2001. Echolocation by insect-eating bats. *BioScience*. 51(7):557–569.
- Speakman JR. 2008. Body composition analysis of animals. A handbook of non-destructive methods. Cambridge (UK): Cambridge University Press; 260 p.
- StatSoft, Inc. 2007. STATISTICA (data analysis software system). Version 8.0. Available from: www.statsoft.com.

- Voigt CC, Winter Y. 1999. The energetic costs of hovering flight in nectar-feeding bats (Phyllostomidae, Glossophaginae) and its scaling in sphingid moths, hummingbirds and bats. *J Comp Physiol B*. 169:38–48.
- von Helversen O, Winter Y. 2003. Glossophagine bats and their flowers: costs and benefits for plants and pollinators. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. Chicago (US): University of Chicago Press; p. 346–397.

Tables

Table 1. Phyllostomid bat sampling points and corresponding forest cover (FC) calculated in square kilometers (km²) in concentric buffers (0.5 km, 1 km, and 1.5 km radius) in landscapes in a tropical highland region in Chiapas, southeast Mexico. For each buffer the FC is indicated along with its percentage in parenthesis, according to the total surface. Abbreviations: TS = total surface.

	W	N	0.5 km radius (TS = 0.79 km ²)	1 km radius (TS = 3.14 km ²)	1.5 km radius (TS = 7.07 km ²)
CAMP	-91°52'17.39"	16°8'3.15"	0.53 km ² (67.1%)	1.2 km ² (38.2%)	2 km ² (28.3%)
TALL	-91°44'33.39"	16°5'55.39"	0.68 km ² (86.1%)	2.3 km ² (73.2%)	4.7 km ² (66.5%)
AKAS	-91°49'42.76"	16°5'27.96"	0.67 km ² (84.8%)	1.4 km ² (44.6%)	2.1 km ² (29.7%)
ESPE	-91°48'42.37"	16°8'49.92"	0.53 km ² (67.1%)	2.1 km ² (66.9%)	4.3 km ² (60.8%)
LICA	-91°48'9.46"	16°5'36.56"	0.35 km ² (44.4%)	1.7 km ² (54.1%)	4.4 km ² (62.2%)
LEBA	-91°46'22.37"	16°6'45.2"	0.47 km ² (59.5%)	1.3 km ² (41.4%)	2.3 km ² (32.5%)
CAMA	-91°45'28.44"	16°8'38.5"	0.69 km ² (87.3%)	2 km ² (63.7%)	4 km ² (56.6%)
PERO	-91°40'11.82"	16°6'53.85"	0.58 km ² (73.4%)	2.4 km ² (76.4%)	5.5 km ² (77.8%)
AZAR	-91°42'50.51"	16°6'40.32"	0.75 km ² (94.9%)	3 km ² (95.5%)	6.1 km ² (86.3%)

Table 2. Number of phyllostomid bats registered in a tropical highland region in Chiapas, southeast Mexico. Abbreviations: CF = Canopy Frugivore; SF = Shrub Frugivore; Ne = Nectarivore; Sa = Sanguivore; Ca = Carnivore.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR	Total	Guild
Stenodermatinae											
<i>Artibeus lituratus</i>	-	-	3	1	1	-	-	-	-	5	CF
<i>Artibeus jamaicensis</i>	16	9	19	8	22	3	-	-	-	77	CF
<i>Chiroderma salvini</i>	-	1	1	-	2	-	-	-	-	4	CF
<i>Dermanura azteca</i>	-	1	1	1	-	-	-	1	-	4	SF
<i>Dermanura tolteca</i>	-	-	-	-	-	2	1	2	1	6	SF
<i>Sturnira hondurensis</i>	1	1	-	-	-	-	3	10	7	22	SF
<i>Sturnira parvidens</i>	2	-	1	5	48	6	2	-	-	64	SF
<i>Centurio senex</i>	1	-	-	1	-	-	-	-	-	2	SF
Glossophaginae											
<i>Anoura geoffroyi</i>	4	1	3	2	1	3	4	2	2	22	Ne
<i>Glossophaga soricina</i>	-	-	-	3	1	-	-	-	1	5	Ne
<i>Glossophaga commissarisi</i>	-	-	1	-	-	-	1	-	-	2	Ne
Desmodontinae											
<i>Desmodus rotundus</i>	1	5	3	16	2	3	5	13	-	48	Sa
<i>Diphylla ecaudata</i>	-	1	1	-	-	-	-	-	-	2	Sa
Phyllostominae											
<i>Chrotopterus auritus</i>	-	-	-	-	-	-	-	-	1	1	Ca
Total individuals (n)	25	19	33	37	77	17	16	28	12	264	

Table 3. Phyllostomid bat assemblage diversity measures in landscapes in a tropical highland region in Chiapas, southeast Mexico. S = species richness; 1D = effective number of species; Hurlbert's PIE = Hurlbert's Probability of Interspecific Encounter index.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
S (observed)	6	7	9	8	7	5	6	5	5
S (interpolation)	4.1	5.2	5.1	5.1	3	4.9	5.4	3.8	5
1D	2.80	3.82	3.39	3.94	2.27	4.39	4.76	2.97	3.42
Hurlbert's PIE	0.58	0.73	0.66	0.76	0.53	0.82	0.83	0.67	0.67

Table 4. Phyllostomid bat ensembles capture success (total number of individuals divided by the mist netting effort) in landscapes in a tropical highland region in Chiapas, southeast Mexico. Abbreviations: CF = Canopy Frugivore; SF = Shrub Frugivore; Ne = Nectarivore; Sa = Sanguivore

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
CF	0.0074	0.0046	0.0106	0.0042	0.0116	0.0014	-	-	-
SF	0.0019	0.0009	0.0009	0.0032	0.0222	0.0037	0.0028	0.0060	0.0037
Ne	0.0019	0.0005	0.0019	0.0023	0.0009	0.0014	0.0023	0.0009	0.0014
Sa	0.0005	0.0028	0.0019	0.0074	0.0009	0.0014	0.0023	0.0060	-

Table 5. Median body condition of phyllostomid bat ensembles in landscapes in a tropical highland region in Chiapas, southeast Mexico. Condition was calculated through an index that considers body mass and forearm length (g/mm). Abbreviations: CF = Canopy Frugivore; SF = Shrub Frugivore; Ne = Nectarivore; Sa = Sanguivore.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
CF	0.77	0.72	0.77	0.86	0.78	0.79	-	-	-
SF	0.46	0.50	0.46	0.48	0.47	0.44	0.45	0.55	0.62
Ne	0.33	-	0.36	0.25	0.28	0.32	0.33	0.37	0.37
Sa	0.64	0.63	0.60	0.65	0.53	0.59	0.58	0.55	-

Table 6. Spearman correlation coefficients (ρ) between forest cover (FC), phyllostomid bat assemblage diversity measures, ensembles capture success and body condition index (BCI) in landscapes in a tropical highland region in Chiapas, southeast Mexico. Abbreviations: S = species richness; 1D = effective number of species; Hurlbert's PIE = Hurlbert's Probability of Interspecific Encounter index; CF = Canopy Frugivore; SF = Shrub Frugivore; Ne = Nectarivore; Sa = Sanguivore. The asterisks indicate statistically significant correlations ($p \leq 0.05$).

	0.5 km radius	1 km radius	1.5 km radius
S (interpolation)	0.66	0.18	-0.09
1D	0.36	0.12	-0.05
Hurlbert's PIE	0.31	0.19	0.04
CF	-0.09	-0.03	-0.03
SF	-0.42	0.24	0.48
Ne	0.10	-0.32	-0.56
Sa	0.44	0.86*	0.62
CF-BCI	-0.70	-0.14	-0.09
SF-BCI	0.39	0.87*	0.85*
Ne-BCI	0.72*	0.33	0.24
Sa-BCI	0.13	-0.17	-0.40

Figures

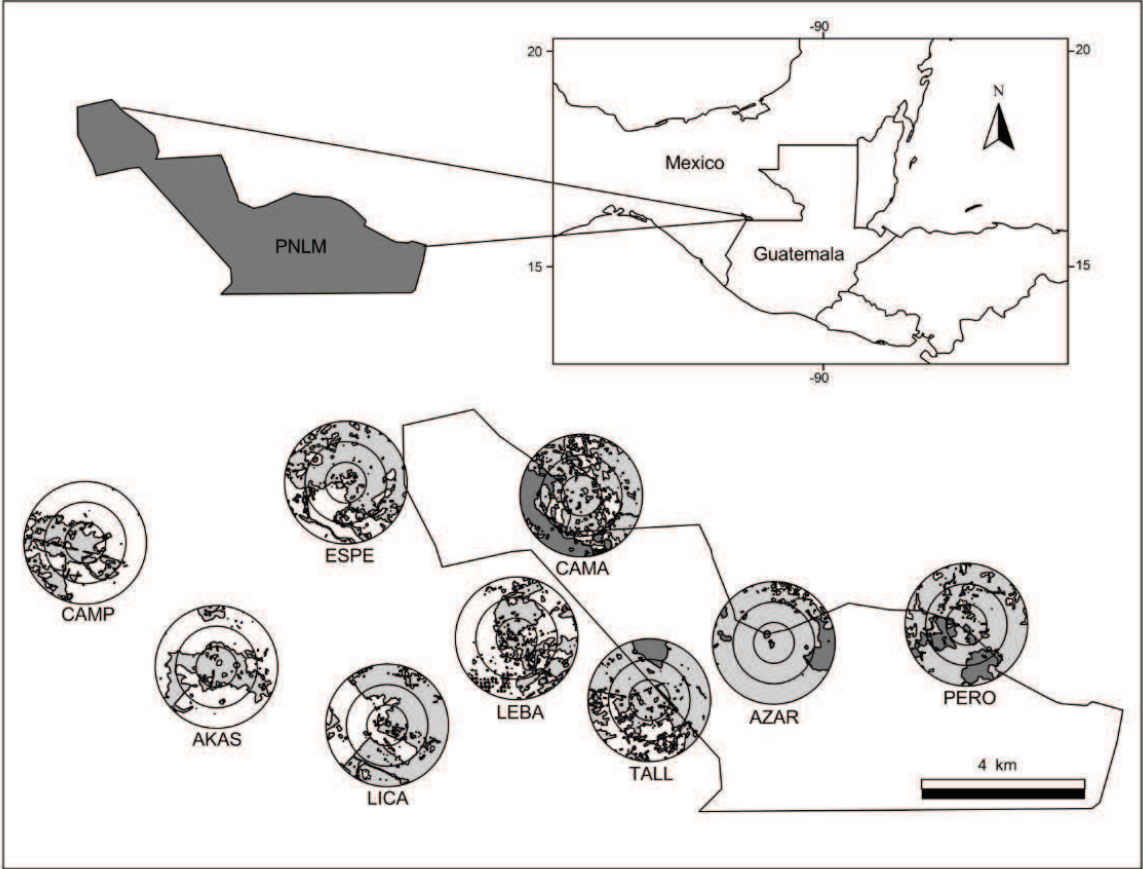


Figure 1. Study area in a tropical highland region in Chiapas, southeast Mexico. The Lagos de Montebello National Park is highlighted next to the Guatemalan border. The sampling points are surrounded by concentric buffers of 0.5 km, 1 km, and 1.5 km radius. Light gray = forest cover; Dark gray = water; White = open areas.

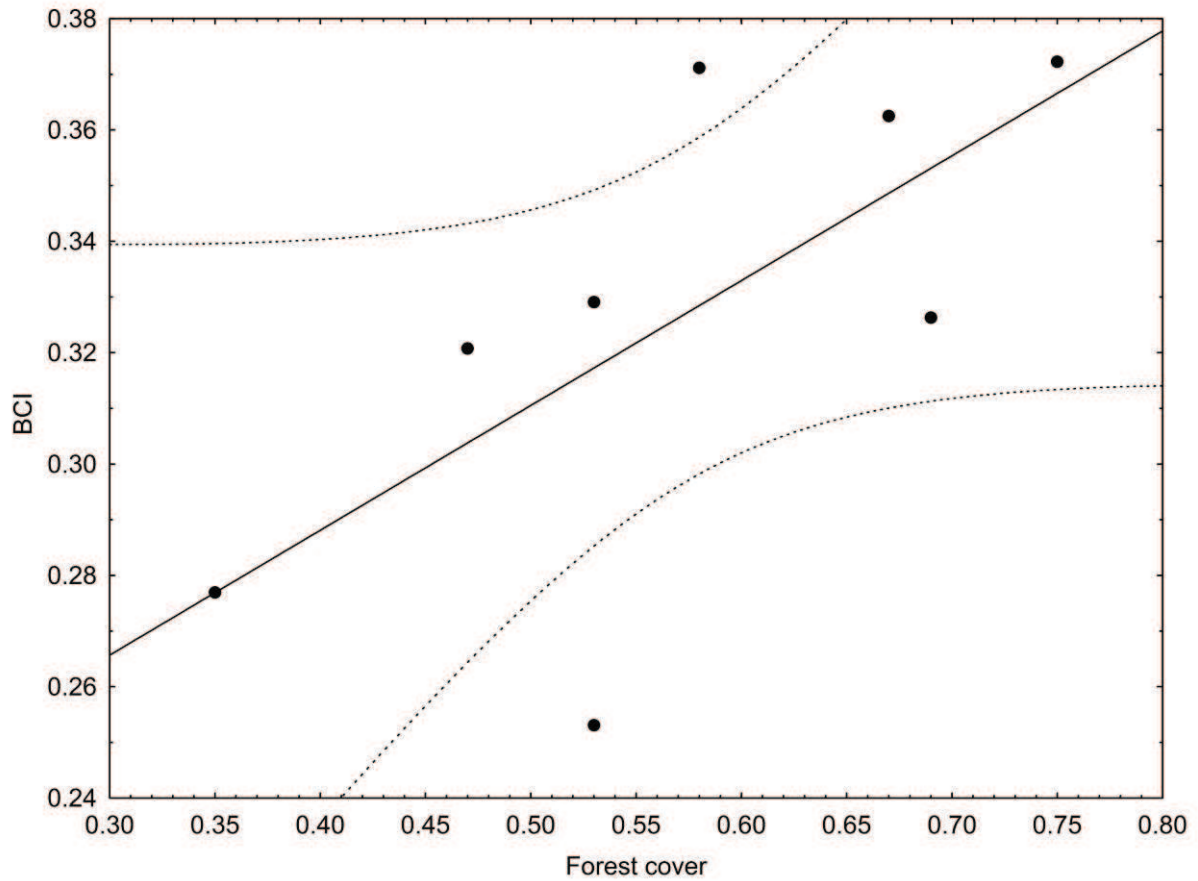


Figure 2. Plot with a linear model adjusted showing the strong positive association between forest cover (FC) in square kilometers (km^2), and the nectarivore's body condition index (BCI), measured in 0.5 km radius buffers in landscapes in a tropical highland region in Chiapas, southeast Mexico. The discontinuous lines represent the 95% confidence intervals.

Capítulo III

The effects of extrinsic and intrinsic factors on the echolocation calls plasticity of *Myotis pilosatibialis* LaVal 1973 (Chiroptera: Vespertilionidae)

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Abstract

The success of bat acoustic surveys relies on adequate measuring of acoustic parameters, recognition of key discriminating variables, and estimations of classification accuracy. Moreover, intrinsic and extrinsic factors may produce convergence in calls, adding uncertainty in species identification. Therefore, we examined within *Myotis pilosatibialis* LaVal 1973 (Chiroptera: Vespertilionidae) sources of acoustic variation in terms of the effect of age group (juveniles vs. adults), and acoustic space (open area vs. background vegetation) in an upland area in Chiapas, southeast Mexico. We found a significant discrimination of adult's calls in open space based on the interpulse interval, which is higher on average in contrast to calls along background vegetation. The latter finding may be explained by habitat constraints, specifically less demand of returning information through echo of the surroundings. The classification rates were below 75%, as to be considered as confounding factors in the study area. We agree that whenever possible, clutter-specific call libraries should be developed before attempting recognition of free-flying bats in a given area, to reject sources of potential error in species recognition.

Keywords: classification accuracy; clutter-based acoustic library; Discriminant Function Analysis; echolocating bats

Introduction

High intensity ultrasounds, such as the echolocation calls emitted by many bats (hereafter calls), can be studied either by transformation into audible sounds using a detector, or directly through high-speed recording systems; after signals are recorded, sound analysis can be performed in a variety of ways using computational software (Pettersson 2002). Many bat species exhibit vocal signatures, and may be identified qualitatively by visual inspection of calls and quick examination of acoustic parameters (O'Farrell and Miller 1999; Jones et al. 2000), while others exhibit similar calls with variation at several levels, meriting a quantitative analysis (Barclay 1999). Either way, ultrasound detection has become a promising tool increasingly used for bat inventories in the Neotropics, mainly because traditional study methods (e.g. mist nets) do not provide a full representation of assemblages (MacSwiney et al. 2008; Pech-Canche et al. 2010). However, ultrasound detection is only effective if the calls recorded in field can be unequivocally assigned to a given species, and in most study areas there is a poor knowledge of the acoustic repertoire of bats (Rodríguez-San Pedro and Simonetti 2013).

While the qualitative method rely on the ability to recognize sequences of complete search phase calls, along with the recognition of features such as shape (linearity and slope), frequency-based and time-based acoustic parameters as sufficient information for distinguishing among free-flying bats (Barclay 1999; O'Farrell et al. 1999; O'Farrell and Miller 1999), with potential bias by the observer's expertise (e.g. Betts 1998), the use of quantitative methods (classification techniques) may offer objectivity and repeatability (Vaughan *et al.* 1997; Jones *et al.* 2000; Zamora-Gutierrez *et al.* 2016). The inclusion of multiple and interacting characteristics of the calls provides an estimate of the confidence that a species has been identified correctly, taking into account the variation that may occur among and within species (Barclay 1999; Parsons and Jones 2000).

Aside from patterns that help distinguish echolocating bats acoustically (mainly to family and genus levels), it is recognized that there can be geographic, habitat, and individual variation in calls (e.g. Barclay et al. 1999; Kazial et al. 2001), which may obscure differences among species, and greatly affect classification accuracy

(Betts 1998; Murray et al. 2001). For instance, the demands of certain acoustic tasks can cause convergence in calls (Parsons and Jones 2000), and the acoustic parameters can be affected by vegetation clutter as a result of the physical constraints of sound propagation (Wund 2006). As clutter increases, calls may show an increase in frequency, the duration becomes shorter and more broadband (with a steeper frequency modulation), and the repetition rate increases (Schnitzler and Kalko 2001). This way, bats avoid overlap between outgoing calls and echoes from objects in close proximity, in keeping with short range target detection strategies (Schnitzler and Kalko 2001; Wund 2006).

Here, we provide a detailed description of the acoustic parameters of the calls of *Myotis pilosatibialis* LaVal 1973 (for the last taxonomy see Mantilla-Meluk and Muñoz-Garay 2014), recorded for the first time in an upland area in Chiapas, southeast Mexico. We based the acoustic characterization on the hypothesis that within this species the calls can be discriminated based on intrinsic and extrinsic factors. Therefore, we examined sources of variation in terms of the effect of age group (juveniles vs. adults), and acoustic space (open area vs. background vegetation). Finally, we highlight that clutter-specific call libraries should be developed before attempting recognition of free-flying bats in a given area, in order to reject sources of potential error in species taxonomic recognition.

Materials and methods

Study area and recording conditions

The study area is located in an upland region in Chiapas, southeast Mexico. Specifically, we worked in the Lagos de Montebello National Park (hereafter NP), which is located between -91°37'40"W, -91°47'40"W, and 16°04'40"N, 16°10'20"N, has an average elevation of 1,500 m asl (above sea level), and its extension covers 6,425 ha, with estimations of water surface during the dry season ranging between 1,030 ha and 1,219 ha (CONANP 2007). The predominant vegetation type in the NP is coniferous forest, and the most frequent species are pines (Pinaceae), with *Pinus oocarpa* in the driest areas and *P. maximinoi* in wetter areas. Nevertheless, oaks (Fagaceae: *Quercus* spp.), cypresses (Cupressaceae: *Cupressus* spp.), and sweetgum (Altingiaceae: *Liquidambar styraciflua*) are also common in mixed associations (CONANP 2007).

The recording sessions were carried out from hand-released mist-netted individuals. The individuals were captured at their night roost, and recorded in two conditions nearby the capture location: 1) in open space, specifically in an area with absence of vegetation cover over an approximately 50 m radius; 2) along background vegetation, specifically in an approximately 3 m wide path inside the forest.

Species taxonomic identification and processing

The bats were identified with the help of taxonomic keys (Medellín et al. 2008; Álvarez-Castañeda et al. 2015). All individuals were weighed to the nearest 0.1 g with a 100 g scale (Pesola AG®, Baar, Switzerland), and their forearms measured to the nearest 0.1 mm with a digital caliper (Mitutoyo®, Illinois, US). The juvenile individuals were characterized by forearm lengths from 34.49 to 37.27 mm ($n = 18$) and body mass from 4 to 6 g ($n = 17$), and adult individuals by forearm lengths from 34.02 to 39.09 mm ($n = 27$) and body mass from 5 to 7 g ($n = 26$). We also registered age (juvenile or adult), based on the degree of fusion of the metacarpal epiphysis (Anthony 1988). Temporary marks, specifically a 4 mm diameter biopsy of the wing membrane at a standardized position between the fourth and fifth digits (see Ripperberg et al. 2004), allowed us to recognize recaptures, and so avoid pseudo-replication of individual's recordings.

Ultrasonic detector configuration and sampling technique

For the recording we used a Pettersson Ultrasound Detector D1000X (Pettersson Elektronik AB, Uppsala, SE). The D1000X is a broadband detector that has a built-in high speed recording system that uses a Compact Flash (CF) card (type I) for recording sound, and for temporary storage. During the recording sessions, the D1000X was configured as follows: 1) manual recording mode; 2) sampling frequency of 384 kHz; 3) pre-trigger time off; 4) pos-trigger in manual mode; 5) auto save mode; 6) manual replay mode; 7) ultrasonic signal as trigger source of the recording system.

The detector performed direct ultrasound sampling, and we stored full spectrum calls for further quantitative analysis. The direct sampling is the acquisition of signals in real time without the use of a technique for lowering the signal's frequency (Jones et al. 2000). Independently, we switched to the frequency division

ultrasound conversion system in order to hear the signals through the detectors speaker, which helped us locate the trajectory of the signal, and obtain higher quantity and quality of calls in the recordings.

Software configuration and acoustic parameter analysis

The shape, frequency-based, and time-based acoustic parameters of the calls were visualized using BatSound Standard – Sound Analysis v. 3.31 (Pettersson Elektronik AB, Uppsala, SE). The calls were analyzed using three kinds of display: 1) oscillogram (amplitude vs. time); 2) spectrogram (frequency vs. time); 3) power spectrum (loudness vs. frequency). Because display affects the visual perception of calls, we proceeded to change the configuration settings for comparison with other call libraries (e.g. MacSwiney et al. 2009): 1) we set the oscillogram amplitude magnitude to 100%; 2) we set the spectrogram to a maximum frequency of 150 kHz, Fast Fourier Transformation (FFT) size of 512 samples, FFT Hanning window, FFT overlap of 99%, threshold of 10, and amplitude contrast of 3 (MacSwiney et al. 2009; Rodríguez-San Pedro and Simonetti 2013); 3) we set the power spectrum to a minimum level of -50 dB SPL (Biscardi et al. 2004), and a maximum frequency of 150 kHz.

During the procedure, we always measured the harmonic call with most energy (Parsons and Jones 2000). We only selected one sequence of calls per individual in order to avoid pseudo-replication (Vaughan et al. 1997; Russo and Jones 2002; Biscardi et al. 2004). We considered sequences of a minimum of three, and a maximum of five complete successive search phase calls (we avoided files with approximation phase calls and feeding buzzes). This way, we always obtained an average of at least two readings of interpulse (intercall) intervals. We only measured calls with good signal-to-noise ratio, with peak intensity more than 20 dB above noise level in the power spectrum (Rodríguez and Mora 2006).

For each call, we manually measured the following parameters: 1) frequency with most energy (FMAXE) in kHz, measured from the peak of the power spectrum (Fenton 2002; Biscardi et al. 2004); 2) lowest frequency (LF) in kHz, taking -50 dB as the criterion for isolation, measured in the power spectrum (Biscardi et al. 2004); 3) highest frequency (HF) in kHz, taking -50 dB as the criterion for isolation, measured in the power spectrum (Biscardi et al. 2004); 4) duration (DUR) in milliseconds (ms), as the time between the start and end of a call, measured in the oscillogram (Fenton

2002; Rodríguez-San Pedro and Simonetti 2013); 5) interpulse interval (IPI) in ms, from the beginning of one call to the start of the next call, measured in the oscillogram (Rodríguez-San Pedro and Simonetti 2013). For each parameter we calculated descriptive statistics by age group and acoustic space (average, range, and coefficient of variation).

Statistical analysis of the acoustic parameters

Prior to the analyses, we explored the data graphically through their quartiles (box plots) and excluded the extreme values, as these may represent atypical measures influenced by the hand-release condition. For our purpose, we performed a Discriminant Function Analysis (DFA). We considered a five variable model with FMAXE, LF, HF, DUR, and IPI. Before the DFA computation we proceeded with a transformation (standardization) by subtracting each value from the sample mean, and dividing it by the standard deviation for 'normalization'; even though, multivariate analysis are somewhat robust from departures of normality (Russo and Jones 2002).

We established the discriminatory power of the overall model based on the Wilks' Lambda, the independent variable contributions through the Partial Lambdas, the statistical significance of the Discriminant Functions, the weighing of variables, and the percent of correct classifications through cross-validation (observed vs. predicted). All calculations were performed in the STATISTICA® software, v. 8.0 (StatSoft, Inc. 2007).

Results

We captured a total of 45 individuals of *M. pilosatibialis*. Specifically, we obtained a total of 18 sequences from juveniles ($n = 83$ calls), 9 in open space ($n = 42$ calls) and 9 along background vegetation ($n = 41$ calls), and 27 from adults ($n = 118$ calls), 11 in open space ($n = 46$ calls) and 16 along background vegetation ($n = 72$ calls). We include an oscillogram/spectrogram showing two search phase calls in open space (Fig. 1), as well as the power spectrum corresponding to the first call (Fig. 2). All acoustic parameters overlapped regardless of age group and acoustic space. There was a trend of lower average DUR and IPI along background vegetation (Table 1). The FMAXE and LF had the lowest coefficients of variation, and the HF, DUR and IPI had the highest coefficients of variation (Table 1).

The discrimination power of the model was significant ($n = 45$; Wilks' Lambda = 0.3; $F = 2.7$; $p = 0.001$). The DFA indicated that only IPI had a significant ($p = 0.02$) contribution. The first Discriminant Function proved to be statistically significant and mostly weighed by IPI, and therefore interpreted. The second Discriminant Function was not significant, although weighed by FMAXE. The first Function accounted 75% of explained variance, discriminating the calls of adult individuals in open space (Fig. 3), which on average show higher IPI in comparison with the calls of adult's along background vegetation. The second Function accounted 20% of explained variance, for a total cumulative of 95%. We obtained 55.6% correct classifications for juvenile's calls along background vegetation, 44.4% for juvenile's calls in open space, 75% for adult's calls along background vegetation, and 63.6% for adult's calls in open space.

Discussion

Here, we illustrated a common classification procedure based on a conventional statistic technique such as DFA (Parsons and Jones 2000; Preatoni et al. 2005). This is a multivariate technique that has been previously used for individual classification of recorded bats (e.g. Betts 1998; Kazial et al. 2001; Rodríguez and Mora 2006). The application of DFA to separate call databases from cluttered and open situations may be considered to reduce the influence of confounding factors and therefore enhance the resolution power for some species (Russo and Jones 2002).

We did not find a significant discrimination by age group as previously noted for other vesper bats (e.g. Kazial et al. 2001). Kazial et al. (2001) found significantly higher correct classifications rates for adults (74%) than for juveniles (69%), suggesting more stability with aging. Nevertheless, this was a trend observed in our study, with adult's calls with a higher classification rate than for juveniles (63.6 % vs. 44.4 % in open space and 75 % vs. 55.6 % along background vegetation).

On the other hand, we found a significant discrimination of adult's calls based on the acoustic space, with effect on time-based acoustic parameters. This finding allow us to suggest that *M. pilosatibialis* may partially resolve the issue of avoiding obstacles while echolocating near background vegetation by shortening the time between calls, and hence increasing information of the surroundings through the returning echoes. Other authors exploring similar predictions found shorter duration of calls when bats where foraging within vegetation, than when foraging in open areas (e.g. Barclay et al. 1999; Broders et al. 2004; Wund 2006), while Wund (2006)

found higher frequencies, and steeper frequency modulations in calls recorded in cluttered conditions.

The percentage of correct classification rates may be useful for 'quality threshold', and scores less than 80% to 90% may insure a minimal risk of mistaken species recognition (Barclay 1999; Russo and Jones 2002). After acoustic characterization, clutter-based acoustic libraries may be useful in order to address plastic echolocators which may be potentially confused as distinct species. This way, researchers may consider labeling calls as unidentified or lumping into larger taxonomic groups (Russo and Jones 2000).

The classification rates calculated for *M. pilosatibialis* turned to be low (< 75%), as to be considered as confounding factors for species recognition in the study area. But for instance, Broders et al. (2004) found more than 94% correct classifications of *M. lucifugus* calls in highly cluttered vegetation, which points to the possibility of missclassifications while recording in other conditions. Therefore, characterization of calls taking into account various sources of variation is recommended before attempts of identification of free-flying bats.

As Zamora-Gutierrez *et al.* (2016) emphasize, standardized identification tools offer the opportunity for objective and repeatable identification of monitoring 'units', to identify changes in time and space. However, it is important to recognize that the use of quantitative methods does not guarantee correct results, although it maximizes the probability of correct identifications (Parsons and Jones 2000). Broders et al. (2004) suggest that clutter-specific call libraries should be developed whenever possible, in order to improve species classification accuracy. This way, a solid basis for taxonomic identification is provided in acoustic monitoring programs.

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Disclosure statement

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References

- Álvarez-Castañeda ST, Álvarez T, González-Ruiz N. 2015. Keys for identifying mammals of Mexico in the field and in the laboratory. Guadalajara, Jalisco (México): Asociación Mexicana de Mastozoología A. C.
- Anthony ELP. 1988. Age determination in bats. In: Kunz TH, editor. Ecological and behavioral methods for the study of bats. Washington DC (US): Smithsonian Institution Press; p. 47–58
- Barclay RMR. 1999. Bats are not birds—A cautionary note on using echolocation calls to identify bats: A comment. *J Mammal*. 80(1):290–296. doi:10.2307/1383229
- Barclay RMR, Fullard JH, Jacobs DS. 1999. Variation in the echolocation calls of the Hoary bat (*Lasiurus cinereus*): influence of body size, habitat structure, and geographic location. *Can J Zool*. 77:530–534. doi:10.1139/z99-008
- Betts BJ. 1998. Effects of interindividual variation in echolocation calls on identification of Big Brown and Silver-haired bats. *Journal Wildlife Manage*. 62:1003–1010. doi:10.2307/3802553
- Biscardi S, Orprecio J, Fenton MB, Tsoar A, Ratcliffe JM. 2004. Data, sample sizes and statistics affect the recognition of species of bats by their echolocation calls. *Acta Chiropterol*. 6(2):347–363. doi:10.3161/001.006.0212
- Broders HG, Findlay CS, Zheng L. 2004. Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. *J Mammal*. 85(2):273–281. doi:10.1644/BWG-102

- [CONANP] Comisión Nacional de Áreas Naturales Protegidas. 2007. Programa de conservación y manejo del Parque Nacional Lagunas de Montebello, México. México DF (México): Secretaría de Ambiente y Recursos Naturales; 194 p.
- Fenton MB. 2002. Reporting: essential information and analysis. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. Bat Echolocation Research. Tools, techniques and analysis. Austin, Texas (US): Bat Conservation International; p. 133–140
- Jones G, Vaughan N, Parsons S. 2000. Acoustic identification of bats from directly sampled time expanded recordings of vocalizations. *Acta Chiropterol.* 2(2):155–170.
- Kazial KA, Burnett SC, Masters WM. 2001. Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *J Mammal.* 82:339–351. doi:10.1644/1545-1542(2001)082<0339:IAGVIE>2.0.CO;2
- MacSwiney G MC, Clarke FM, Racey PA. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bats assemblages. *J Appl Ecol.* 45:1364–1371. doi:10.1111/j.1365-2664.2008.01531.x
- MacSwiney G MC, Bolívar C B, Clarke FM, Racey PA. 2009. Insectivorous bat activity at cenotes in the Yucatan Peninsula. *Acta Chiropterol.* 11(1):139–147. doi:10.3161/150811009X465758
- Mantilla-Meluk H, Muñoz-Garay J. 2014. Biogeography and taxonomic status of *Myotis keaysi pilosatibialis* LaVal 1973 (Chiroptera: Vespertilionidae). *Zootaxa.* 3793:60–70. doi:10.11646/zootaxa.3793.1.2
- Medellín RA, Arita HT, Sánchez O. 2008. Identificación de los murciélagos de México, clave de campo. México DF (México): Instituto de Ecología, Universidad Nacional Autónoma de México.
- Murray KL, Britzke ER, Robbins LW. 2001. Variation in search-phase calls of bats. *J Mammal.* 82(3):728–737. doi:10.1644/1545-1542(2001)082<0728:VISPCO>2.0.CO;2
- O'Farrell MJ, Miller B. 1999. Use of vocal signatures for the inventory of free-flying Neotropical bat. *Biotropica.* 31(3):507–516. doi:10.1111/j.1744-7429.1999.tb00394.x

- O'Farrell MJ, Miller B, Gannon WL. 1999. Qualitative identification of free-flying bats using the Anabat detector. *J Mammal.* 80(1):11–23. doi:10.2307/1383203
- Parsons S, Jones G. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *J Exp Biol.* 203:2641–2656.
- Pech-Canche JM, MacSwiney G MC, Estrella E. 2010. Importancia de los detectores ultrasónicos para mejorar los inventarios de murciélagos Neotropicales. *Therya.* 1(3): 227–234. doi:10.12933/therya-10-17
- Pettersson L. 2002. Bat-specific signal analysis software – BATSOUND. In: Brigham RM, Kalko, EKV, Jones G, Parsons S, Limpens HJGA, editors. *Bat Echolocation Research. Tools, techniques and analysis.* Austin, Texas (US): Bat Conservation International; p. 130–133.
- Preatoni DG, Nodari M, Chirichella R, Tosi G, Wauters LA, Martinoli A. 2005. Identifying bats from time-expanded recordings of search calls: comparing classification methods. *Journal Wildlife Manage.* 69:1601–1614. doi:10.2193/0022-541X(2005)69[1601:IBFTRO]2.0.CO;2
- Rodríguez A, Mora, EC. 2006. The echolocation repertoire of *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in Cuba. *Caribb J Sci.* 42(1):121–128.
- Rodríguez-San Pedro A, Simonetti JA. 2013. Acoustic identification of four species of bats (Order Chiroptera) in central Chile. *Bioacoustics.* 22(2):165–172. doi:10.1080/09524622.2013.763384
- Russo D, Jones G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J Zool.* 258:91–103. doi:10.1017/S0952836902001231
- Schnitzler H-U, Kalko EKV. 2001. Echolocation by insect-eating bats. *Bioscience.* 51(7):557–569. doi:10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO
- StatSoft Inc. 2007. STATISTICA (data analysis software system). Version 8.0. Available from: www.statsoft.com.
- Vaughan N, Jones G, Harris S. 1997. Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics.* 7:189–207. doi:10.1080/09524622.1997.9753331
- Wund MA. 2006. Variation in the echolocation calls of Little Brown bats (*Myotis lucifugus*) in response to different habitats. *Am Midl Nat.* 156:99–108. doi:10.1674/0003-0031(2006)156[99:VITECO]2.0.CO;2

Zamora-Gutierrez V, Lopez-Gonzalez C, MacSwiney G MC, Fenton MB, Jones G, Kalko EKV, Puechmaille SJ, Stathopoulos V, Jones KE. Acoustic identification of Mexican bats based on taxonomic and ecological constraints on call design. *Method Ecol Evol.* doi: 10.1111/2041-210X.12556.

Tables

Table 1. Summary statistics of the acoustic parameters of 45 individuals of *Myotis pilosatibialis* LaVal 1973 ($n = 201$ calls) categorized by age group and acoustic space, recorded in an upland area in Chiapas, southeast Mexico. OSp = open space; BVe = background vegetation; FMAXE = frequency of maximum energy; LF = lowest frequency; HF = highest frequency; DUR = duration; IPI = interpulse (intercall) interval; CV = coefficient of variation.

Juveniles OSp	Average	Range	CV	Juveniles BVe	Average	Range	CV
$n = 42$ calls				$n = 41$ calls			
FMAXE	51.8	49.9-54.6	2.7		53.8	50.7-57.5	2.8
LF	48.6	45.4-52.3	3.7		50	46.8-52.9	3.4
HF	78.5	62.7-98.6	12.3		84.9	69.5-107.5	9.9
DUR	5.1	3.8-6.9	14.5		4.4	3-5.8	15.5
IPI	82.9	58-102.6	13.7		64.5	47.7-87.1	16.3
Adults OSp				Adults BVe			
$n = 46$ calls				$n = 72$ calls			
FMAXE	52.5	49.8-56.2	3		52.5	49.9-55.4	2.5
LF	49.5	45.4-52.9	3.5		48.9	46.3-52.3	2.6
HF	80	60.5-95.6	11.5		90.2	70.1-117.4	14
DUR	5.1	3.2-6.6	17.4		4.3	3.2-.8	13
IPI	82.5	58.2-95.1	11.4		67.7	50.5-91	15.7

Figures

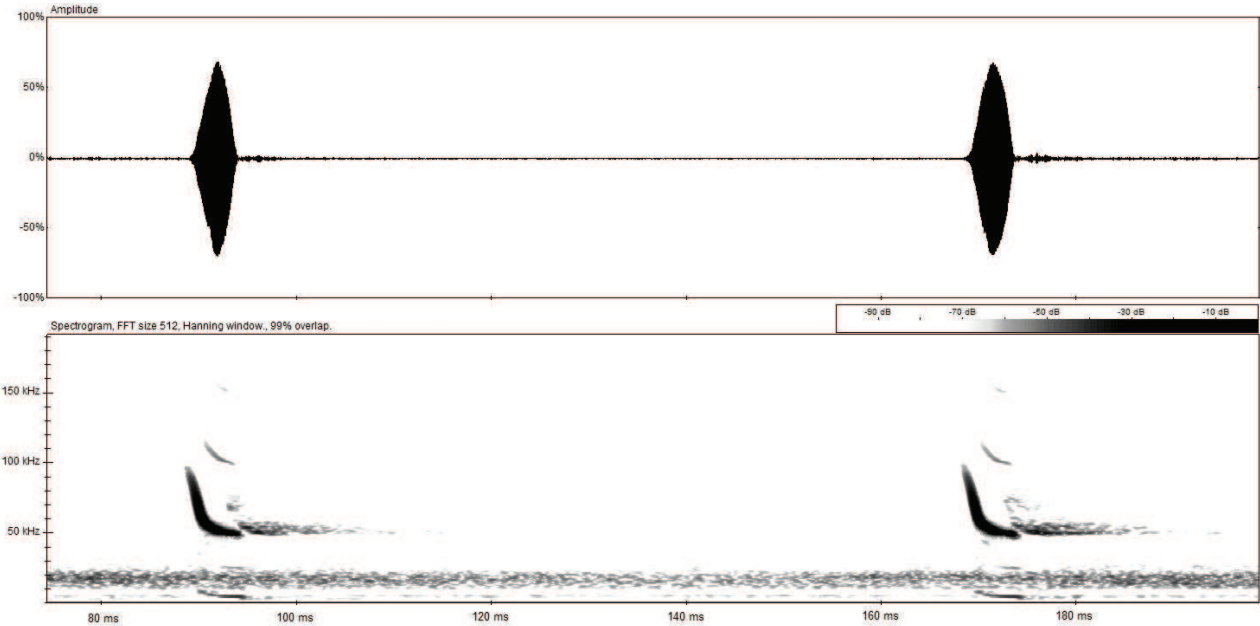


Figure 1. Visual representation of two search phase calls of *Myotis pilosatibialis* LaVal 1973, displayed as oscillogram (above) and spectrogram (below), recorded in open space in the National Park Lagos de Montebello, Chiapas, southeast Mexico.

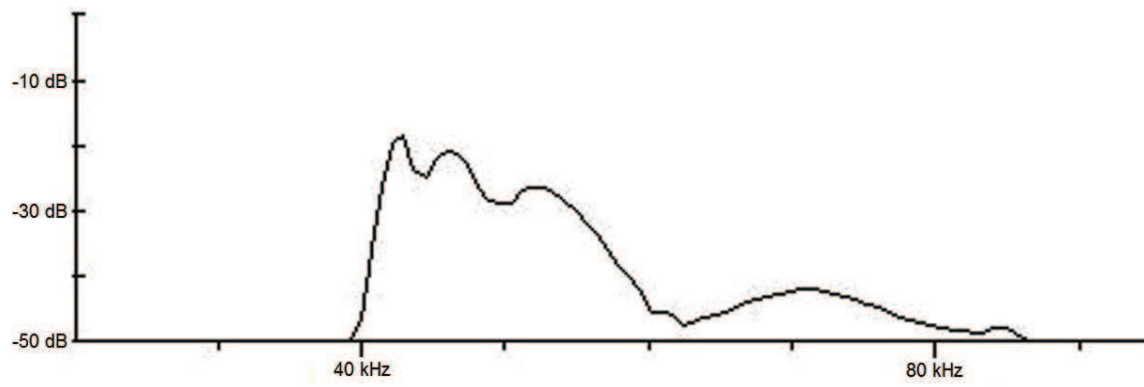


Figure 2. Power spectrum display showing the energy in one call of *Myotis pilosatibialis* LaVal 1973. The frequency of maximum energy (FMAXE) is measured at the peak of the calls.

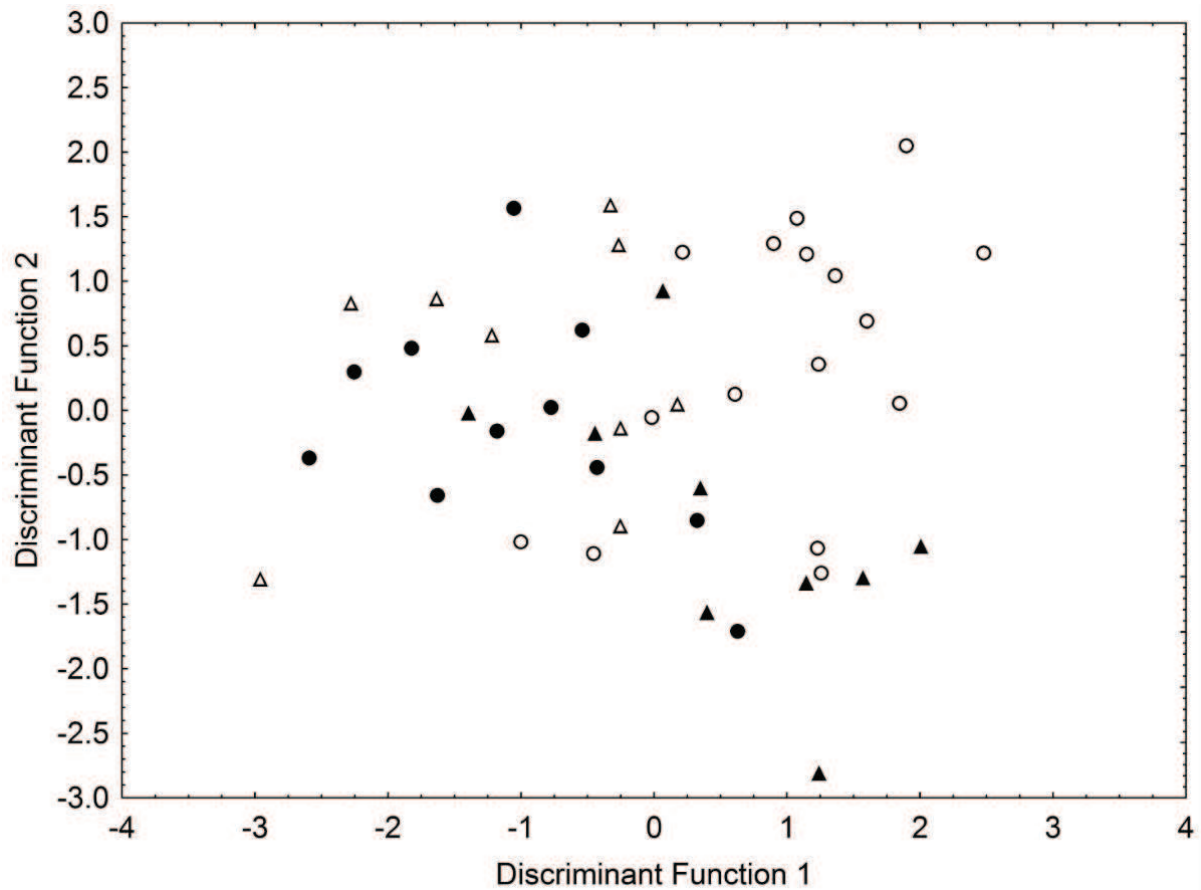


Figure 3. Discriminant Functions (DF) plot showing echolocation calls of *Myotis pilosatibialis* LaVal 1973 categorized by age group and acoustic space. The first DF proved to be statistically significant, accounted for 75% of explained variance, and was weighed by the interpulse interval (IPI) which discriminates the adult's calls in open space from those along background vegetation. Symbology: adult's calls in open space (solid circles); adult's calls along background vegetation (open circles); juvenile's calls in open space (open triangles); juvenile's calls along background vegetation (solid triangles).

Capítulo IV

Local and landscape determinants for relative activity of short range echolocating aerial insectivorous bats in tropical highland Chiapas, southeast Mexico

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Abstract

Some human induced landscapes are scenarios where the loss and fragmentation of forests can have negative effects on biodiversity. In such landscapes, it is important to identify local and landscape features that may back away bat population declines, and ecological service contributions. At the local level, specific features of the environment may offer resources (e.g. water, roosts, food), and at the landscape level some patterns may provide physical continuity (e.g. increasing forest patch density). The aerial insectivorous bats with short range echolocation are known to be benefited by water supply, and highly dependent on forest. Therefore, we studied the change on relative activity of this group of bats in response to local and landscape variables, focusing on three ecotopes (water sinkholes, flooded surface, forested sites), all of which are subject to modification by human activity, specifically increment of open area in the surroundings. For *Myotis pilosatibialis*, we found at the local level a habitat-specific preference for water sinkholes and flooded habitats,

while at the landscape level a positive association with increase of mean forest patch area over small geographic extents. For *Mormoops megalophylla* and *Pteronotus mesoamericanus*, we found at the local level a positive association with the biomass of the super-order Amphiesmenoptera (Lepidoptera and Trichoptera). We suggest that the protection of water surface ecotopes and the nearby forests in the study area can have a key role for the persistence of this group of bats.

Keywords: bats vagility; forested habitats; insect biomass; open area; water surfaces

Introduction

Forests are key habitats for bats throughout the world (Siebold et al. 2013; Rodríguez-San Pedro and Simonetti 2015), but the expansion of some forms of agriculture (e.g. extensive monocultures) has led to their widespread loss and fragmentation (Fuentes-Montemayor et al. 2013). Therefore, it is important to understand the effect of features at local and landscape levels as determinants for species distribution and activity, and identify their potential to back away target species population declines, and decreasing ecosystem service contributions (Heim et al. 2015).

Aerial insectivorous bats (AIB hereafter) use echolocation calls (calls hereafter) in analogy to a sonar system (Schnitzler et al. 2003; Denzinger and Schnitzler 2013), and hunt airborne prey such as nocturnal flying insects (Fenton 1999). Typically, the AIB with short range calls (SRE bats hereafter) exhibit frequency modulated sound pulses over 50 kHz, and call durations less than 7 ms (Frey-Ehrenbold et al. 2013), which are of low intensity presumably to minimize the return of confusing echoes in cluttered environments (Waters and Jones 1995; Jones 1999). Such calls are not beneficial in open areas because they are subject to attenuation (Fenton 1999; Fenton 2002; Heim et al. 2015), which is the loss of acoustic energy in the media. Moreover, for the slower species flight away from vegetation cover may impose higher energetic costs due to stronger wind (Heim et al. 2015). Therefore, SRE bats are thought to be more sensitive to forest cover loss and fragmentation (e.g. Frey-Ehrenbold et al. 2013).

We chose to work with SRE bats in the Lagos de Montebello National Park (NP hereafter) and its surroundings in upland Chiapas, Mexico, as scenario to test

predictions about the effects of human activities on this group of bats. The main reasons for the selection of the study area are that the NP is included in the RAMSAR Convention (site no. 1325) as a wetland of importance (of presumably high importance for SRE bats because of the presence of water surface ecotopes), and that its surroundings are characterized by high contrast agricultural landscapes (with a trend towards the loss and fragmentation of forests, and increment of open area), where habitat disruption may occur for SRE bats.

The NP established in its Conservation and Management Program a landscape component which recognizes that spatial patterns may affect ecologic processes (CONANP 2007). This component has the goals of identifying areas affected by anthropogenic activities, monitoring the physical changes in the transformed landscapes (e.g. habitat isolation), and establishing the basis for a recovery program (CONANP 2007). Therefore, considering SRE bats relative activity as response variable, we designed a study including local level (ecotope type and potential flying insect prey availability), and landscape level predictive variables. Our intention is to contribute to future strategies regarding protection/recovery of specific ecotopes and landscapes, and their associated biota.

Our aims were to: 1) establish the SRE bats preference for ecotopes as measured through increase of relative activity, 2) determine if potential flying insect prey is associated with the SRE bats relative activity, 3) identify landscape elements and patterns that may favor the SRE bats relative activity. The corresponding hypotheses are that: 1) the relative activity of some SRE bats is associated with water surface ecotopes, 2) the SRE bats will have higher relative activity with increase of potential flying insect prey, 3) the SRE bats relative activity increases in landscapes with elements that propitiate physical continuity.

Material and methods

Study area description

The study area is located in a plateau in a tropical highland region in Chiapas, southeast Mexico (Figure 1). The sampling points were located inside and beyond the NP. The average elevation in the NP is 1500 m (there was no considerable variation in the study area, between 1460 to 1540 m above sea level), and its extension covers 6425 ha (CONANP 2007). The climate in the area is markedly with a dry season (approximately from March to June), rainy season (approximately from

July to October), and windy season locally known as “nortes” (approximately from November to February).

The predominant vegetation type in the NP is the pine-oak-sweetgum forest, which is characterized by high species richness, forming a two stratum structure with a canopy between 20 to 35 m, composed mainly by *Pinus* spp. (Pinaceae), *Quercus* spp. (Fagaceae), and in less proportion *Liquidambar styraciflua* (Altingiaceae), *Clethra* spp. (Clethraceae) and *Persea* spp. (Lauraceae), and a forest interior species-rich tree stratum below 20 m height (González and Ramírez 2013). The surroundings of the NP are mostly characterized by agricultural activities (extensive cornfields), livestock (grasslands), human settlements, and scattered managed forest remnants. The cornfields, grasslands, and human settlements lack tree cover (they are characterized by open space), and hence we consider these as unsuitable environments for SRE bats which echolocate more efficiently within forests. Inside the NP there is a lacustrine system connected by a subterranean fluvial network, with estimations of water surface during the dry season ranging between 1,030 ha and 1,219 ha (CONANP 2007).

Landscape spatial characterization

We started from a supervised classification based on satellite imagery of the study area (multispectral SPOT satellite images of 2011, with a spatial resolution of 10 m). This classification was elaborated through a procedure in which pixels of known identity are used to assign pixels of unknown identity within training areas, and control points obtained in the field for verification and polygon rectification. We chose to base our spatial characterization on two classes: forest cover (FC hereafter) and water surfaces (WS hereafter). These classes have been suggested as relevant for many taxa, including SER bats (e.g. Fahrig 2003; Fuentes-Montemayor et al. 2013; Rodríguez-San Pedro and Simonetti 2015).

The FC class was corroborated in the field by the presence of woody plants and a distinguishable canopy. Following Fuentes-Montemayor et al. 2013, forest types were grouped together because, similarly to the study area of these authors, patches of one vegetation type were adjacent to (or immersed in) patches of a different type, resulting in confounding information. The WS class was comprised mainly by lakes, water sinkholes, and seasonal flooded habitats. The landscape

matrix was designated by open area, and ignored in the analysis as we consider it a barrier for SER bats movement.

SRE bats sampling points and recording conditions

Sampling was carried out monthly between July 2014 and July 2015, in nights close to new moon in order to avoid effects of lunar phobia (Santos-Moreno et al. 2010; Saldaña-Vásquez and Munguía-Rosas 2013). The sampling points were characterized by three ecotopes, with three repetitions each (Figure 1): 1) permanent water sinkholes locally known as “cenotes” (CAMA, PERO, AZAR), 2) seasonal flooded surfaces locally known as “aguajes” (ESPE, LICA, LEBA), 3) gaps and open trials within forested sites (CAMP, TALL, AKAS). During the a one year period each sampling point was visited twice, during three consecutive nights each visit.

For the bat recordings we used an Echo Meter EM3+ Ultrasonic Detector (Wildlife Acoustics, Inc.). This detector allows monitoring bats in real-time, and to simultaneously record using full spectrum technology. The EM3+ was configured as follows: 1) sample rate of 256 kHz, 2) WAV audio file format, 3) maximum duration of 15 seconds, 4) frequency trigger of 15 kHz; 5) amplitude trigger of 18 dB, 6) trigger window of 1 second, 7) gain of 30 dB. Finally, we located stationary points for short-term passive recording events which lasted 4 hours beginning at dusk, as this time period is sufficient for species representation (Duffy et al. 2000; Kraker-Castañeda et al. 2013). The detector was positioned on a 1 m pole with a 45° upward angle (Kraker-Castañeda et al. 2013; López-González et al. 2015), directed towards open space, and the recordings were stored in a 32 GB SD card (Kingston© Technology Corporation). The total recording effort was 432 hrs.

Recordings analysis and acoustic identification

The recordings were processed using the software Kaleidoscope Pro v. 4.0 and associated classifiers (Wildlife Acoustics, Inc.). In the Bat Analysis Mode, we configured automatic classification using the Auto ID for Bats, using the classifier Bats of the Neotropics. These SRE bats registered in the study area have the following classification rates (Wildlife Acoustics, Inc.): *Myotis pilosatibialis* (89%), *Mormoops megalophylla* (69%), *Pteronotus davyi* (97%), *Pteronotus mesoamericanus* (100%). The latter is the exception in the study area, as it is a high duty cycle species whose calls features differ from those of SRE bats (see Fenton

1999). Next, we set the signal parameters of interest (frequency 45 to 100 kHz, duration 2 to 10 ms, 2 pulses minimum), and proceeded with files processing. We automatically deleted noise files.

After scanning during the batch processing, we obtained a CSV file indicating the software's identification of species, along with additional information (e.g. acoustic parameter measures). Using the Kaleidoscope Viewer (Wildlife Acoustics, Inc.), we manually changed identifications whenever missclassifications were detected, and manually saved changes in the CSV file. Because automatic ID will produce false positive and false negative errors (see Help Topics in Kaleidoscope Pro v. 4.0), we carried out this procedure for each one of the files.

For the manual characterization of calls, we started with shape (linearity and slope) as a quick clue for family and genus discrimination, and then we considered the following acoustic parameters which represent unmistakable features for the recognition of the SRE bats in the study area, for which values are included in the Supplementary Material (Table S1): characteristic frequency (CF), maximum frequency (FMAX), minimum frequency (FMIN), duration (DUR). Nevertheless, we also compared our recordings with acoustic libraries of southeast Mexico (e.g. MacSwiney et al. 2008; Williams-Guillén and Perfecto 2011; Kraker-Castañeda et al. 2013), for corroboration of taxonomic identifications.

Landscape metrics calculation

Based on the FC and WS classes, we selected landscape metrics that might propitiate physical continuity (e.g. increase aggregation of FC, with decreasing distance between forest remnants), or might be a proxy for availability of resources (e.g. edge density of WS, which may be associated with potential flying insect prey). The metrics were grouped in two categories: composition and configuration (Turner et al. 2001). Those metrics that quantify composition are not usually spatially explicit, as they measure what is present and their relative amounts, without reference to where on the landscape they may be located (McGarigal et al. 2012). Those metrics that quantify configuration account for the spatial arrangement of patch types (McGarigal et al. 2012).

The landscape metrics were calculated independently for both FC and WS classes. We choose the following metrics because they capture aspects of the pattern that are relevant to the original question (physical continuity), while

minimizing redundancy (see Turner et al. 2001): percentage of landscape, patch density, mean patch area, edge density, Euclidean nearest neighbor distance, and patch cohesion index. For details about the calculation and interpretation of metrics see McGarigal et al. (2012). All metrics were calculated within concentric spatial analysis windows (buffers hereafter) of 500 m, 1000 m, and 1500 m radius from the sampling point, seeking for species-specific responses. The calculations were performed using the software FragStats v. 4 (McGarigal et al. 2012), and the results are included in the Supplementary Material (Tables S2, S3, S4).

Potential flying insect prey and biomass estimation

For the collection of potential flying insect prey we used a Malaise trap, which is appropriate for trapping airborne insects (Kunz 1988; Delfin et al. 2011). The trap was suspended on trees near the recording station (not more than 15 m), and when sampling around water surfaces located on the shore. It was installed approximately 1.5 m above ground, and it was operated simultaneously with the bat detector during every recording session. All the specimens collected were preserved in 70% alcohol inside plastic containers (Wickramasinghe et al. 2004), and labeled for posterior processing and identification.

In laboratory, we identified the specimens into the super-order Amphiesmenoptera (AMP), and the orders Diptera (DIP) and Coleoptera (COL), as these groups are among the most important food elements reported in literature for the SER bats registered in the study area (Whitaker 2004; Wickramasinghe et al. 2004; Feldhamer et al. 2009; Rolfe and Kurta 2012; Salinas-Ramos et al. 2015). The super-order AMP is composed by the orders Trichoptera and Lepidoptera, and we chose to pool data because of the difficulty of discrimination of alcohol preserved specimens, and the possibility of wrong classifications.

We counted the number of individuals of each taxa in the samples (see Queiroz de Oliveira et al. 2015). Then, the samples were dried in a stove at 70°C, during 48 hours (Bradley et al. 1993; Kraker-Castañeda et al. 2013). Finally, we obtained the dry weight using an Explorer[®] EP214C analytical balance (Ohaus Corporation, US) with 0.1 mg readability. Following Queiroz de Oliveira et al. (2015), we estimated the mean flying insect's biomass per sampling point dividing the mass by the number of insects; this way, higher values indicate larger insects.

Statistical analyses

SRE bats relative activity calculation

For the estimation of relative activity, we choose one minute blocks with evidence of SRE bat calls as index proposed by Miller (2001). Specifically, we considered the presence of a minimum of two consecutive calls independently of the number of files (MacSwiney et al. 2009; Heim et al. 2015). The mean relative activity was estimated at each sampling point as the number of active minute blocks per night. Data was omitted whenever the species of interest was not registered, and we did not considered zero values in our statistical analysis as we can not guarantee “true absences”.

Exploratory analyses for the detection of outliers (which were omitted) were performed using the software STATISTICA® v. 8.0 (StatSoft, Inc. 2007). The outliers are expected more frequently in random small samples and have strong effects on some statistical computations (e.g. sample mean). For the statistical comparisons we used the software GraphPad InStat® v. 3.10 (GraphPad Software, Inc. 2009), specifically Kruskal-Wallis tests (non-parametric ANOVA), and whenever we detected statistically significant differences, we proceeded with a paired multiple comparison post test (Dunn post test). Significance level was set to 95% ($\alpha = 0.05$) for comparability with other studies.

Predictive value of local and landscape level variables

In order to measure the independent contribution of each variable (local and landscape levels) on the SRE bats relative activity, we employed a hierarchical partitioning analysis (HP hereafter) in each spatial analysis window (e.g. Klingbeil & Willig 2008; García-García and Santos-Moreno 2014). The HP is a multivariate exploratory analysis that partitions a measure of association into variables whose independent correlation with a response variable may be important from variables that have little independent effect (Chevan and Sutherland 1991; Mac Nally 2002; Radford and Bennett 2007), addressing potential multicollinearity between the explanatory variables (Graham 2003; Olea et al. 2010). The HP was performed through the routine hier.part in the package hier.part v. 1.04 (Walsh and Mac Nally 2015), using the statistical computing environment R v. 3.3.2 (R Core Team 2016). Given that the response variable is continuous, the models were performed using Gaussian type errors, with goodness of fit based on R-squared (see Klingbeil and

Willig 2008). The statistical significance of the independent contributions was tested by comparison to randomization (1000 permutations) through the routine `rand.hp` in the package `hier.part` v. 1.04 (Mac Nally 2002; Walsh and Mac Nally 2015), using the statistical computing environment R v. 3.3.2 (R Core Team 2016), and significance level was set to 95% ($\alpha = 0.05$) for comparability with other studies. All data sets were transformed (standardized) prior to modeling in order to alleviate departures from “normality”, and allow reliable comparisons between measure scales. Finally, in order to identify the direction of the relationships between the response variable and each one of the variables with a significant independent contribution, we calculated Spearman rank correlation coefficients in order to avoid the effects of the outliers characteristic of small samples. Standardization and non-parametric correlations were performed using the software STATISTICA® v. 8.0 (StatSoft, Inc. 2007).

Results

SRE bats relative activity and ecotope preference

We recorded a total of 14631 files. After scanning during the batch processing and deletion of noise files, we obtained the following file numbers by species: *M. pilosatibialis* ($n = 7144$), *M. megalophylla* ($n = 142$), *P. davyi* ($n = 746$), *P. parnellii* ($n = 49$).

We determined that the relative activity of *M. pilosatibialis* between ecotopes was statistically significant (KW = 13.155, $p = 0.0014$), specifically between the water sinkholes and the forested sites (Figure 2). For *M. megalophylla*, the difference was not statistically significant between the flooded surfaces and the forested sites (KW = 3.333, $p = 0.1889$). For *P. davyi*, the relative activity per night between ecotopes was statistically significant (KW = 12.986, $p = 0.0015$), specifically between the water sinkholes and the flooded surfaces and forested sites (Figure 2). For *P. mesoamericanus*, the difference between flooded and forested sites was not statistically significant (KW = 2.447, $p = 0.2943$). The comparison of *M. megalophylla* and *P. mesoamericanus* relative activity in the water sinkholes was not possible because of too few values (1).

Flying insect's biomass predictive value on SRE bats relative activity

The description of the flying insect's collections is included in Table 1. Between ecotopes (water sinkholes, flooded surfaces, forested sites), the mean biomass per

night for AMP was not statistically significant (KW = 2.767, $p = 0.2507$), for DIP was statistically significant (KW = 10.315, $p = 0.0058$), specifically between the water sinkholes and the forested sites (Figure 3), and for COL was not statistically significant (KW = 0.6378, $p = 0.7269$).

In Table 2, we present the percentage of independent contributions of the flying insect's biomass for SRE bats relative activity. For *M. pilosatibialis*, we did not find significant independent contributions of insect biomass for any of the orders considered. For *M. megalophylla*, we found a significant independent contribution of AMP, with 65.2% of all explained variability. For *P. davyi*, we found a significant independent contribution of DIP, with 48.2% of all explained variability. For *P. mesoamericanus*, we found a significant independent contribution of AMP, with 71.4% of all explained variability.

Landscape metrics predictive value on SRE bats relative activity

In Table 3, we present the percentage of independent contributions of the landscape metrics for SRE bats relative activity. For *M. pilosatibialis*, based on the FC class in the smallest buffers, we found a significant independent contribution of mean patch area, with 32.35% of all explained variability. For *P. mesoamericanus*, based on the FC class in the intermediate buffers, we found a significant independent contribution of patch cohesion index, with 31.93% of all explained variability.

Discussion

SRE bats relative activity and ecotope preference

We found that the ecotope had importance for the relative activity of *M. pilosatibialis* and *P. davyi*. Specifically, for *M. pilosatibialis* we found a higher relative activity on water sinkholes and flooded surfaces, which supports our first hypothesis of preference for water surface ecotopes. For *P. davyi*, we found a higher activity within forested sites.

In general, bats may benefit from water surfaces, as this ecotope can offer a drinking supply, and feeding opportunities (MacSwiney et al. 2009; Seibold et al. 2013). The physiological characteristics of bats demand high amounts of water, mainly for reproductive success (Seibold et al. 2013), and the water supply and water edge vegetation may provide food such as aquatic and airborne insects. MacSwiney et al. (2009) found that the average number of AIB species and their corresponding

activity were higher in sites with presence of water sinkholes in comparison to those that lacked this ecotope, along with presence of exclusive species. López-González et al. (2015) found that water surfaces, specifically artificial ponds in rangelands, represent a seasonal limiting resource for AIB, whose activity decreased temporarily during the dry season and far away from this ecotope. Therefore, there is evidence that water surfaces may have a strong relationship with AIB, specifically with some SRE bats in the study area. Nevertheless, the water quality is decreasing in the area as consequence of the use of pesticides in the surroundings, and could have an important effect on insect's abundance. For instance, García-Estrada et al. (2006) found that insectivorous bats reduced their number in agroecosystems as pesticides were incorporated.

On the opposite, the preference of *P. davyi* for forested sites can be related to foraging opportunities, and this species capability of flight in background cluttered space (Schnitzler & Kalko 2001). Nevertheless, it remains unclear if the habitat selection is primarily based on prey availability and secondarily on habitat constraints, or vice versa (Morris et al. 2010).

Flying insect's biomass predictive value on SRE bats relative activity

In the study area, the water sinkholes are characterized by a higher biomass of DIP, not significantly different from the flooded surfaces, but significantly different from the forested sites. Although we did not find significant independent contributions of the flying insect's biomass for the activity of *M. pilosatibialis*, we found effects for the activity of *M. megalophylla*, *P. davyi* and *P. mesoamericanus*. Specifically, for *M. megalophylla* and *P. mesoamericanus* we found that AMP had predictive value, with a relationship in a positive direction. The former findings support our second hypothesis which states that flying insect's biomass may be a limiting factor for SRE bats relative activity. Contradictorily, for *P. davyi* we found that DIP had predictive value, with a relationship in a negative direction. This could possibly be a response to a third variable not considered or a suppressing effect, and might not reflect causality.

Bats eat a diverse range of insects, and although most representatives seem to be flexible in their diets, some species apparently specialize on certain taxa (Jones & Rydell 2003). MacSwiney et al. (2009) and Kraker-Castañeda et al. (2013) found a positive relationship of AIB relative activity over water surfaces with flying insect's

biomass. Also, MacSwiney et al. (2009) found a higher number of feeding buzzes in this ecotope, which might suggest a plausible causal effect. Accordingly, López-González et al. (2015) found that the emission of pulses was positively correlated with feeding buzzes (signals emitted during predation of airborne prey), which might be a reflection of foraging activity.

Therefore, we might suggest that the disproportional activity of *M. pilosatibialis* on water surfaces in our study area may be an indirect reflection of predation upon airborne insects, mostly because bat species in this genus are known to include DIP as an important component in their diet, although may include other insects taxa in their diet (Kurta and Whitaker 1998; Whitaker 2004). Nevertheless, there is evidence that the ratio of foraging activity to prey density between water surfaces and terrestrial habitats is more likely a reflection of the use of the water surface ecotopes as a source of drinking water rather than of prey (mainly in dry areas and low productive water surfaces); but this should be contextualized by the food supply relative to the surrounding areas (see Seibold et al. 2013).

Regarding the predictive value of AMP for the activity of *M. megalophylla* and *P. mesoamericanus*, Lepidoptera is known to be an important component in the diet of *Mormoops* and *Pteronotus* species (Rolfe and Kurta 2012; Salinas-Ramos et al. 2015). Nevertheless, there are dietary differentiations between species that may act as mechanisms for species coexistence (Rolfe and Kurta 2012), and diet may be driven by prey availability (Salinas-Ramos et al. 2015). It is important to notice that the effect of the sum of Trichoptera and Lepidoptera in the samples might obscure the effect of one or the other for SRE bats relative activity, and in the future their specific effects should be explored.

Landscape metrics predictive value on SRE bats relative activity

For *M. pilosatibialis*, we found a significant independent contribution of a metric in a positive direction. Specifically, we found that mean patch area based on the FC class had predictive value for this species relative activity in the smallest buffers. This finding supports our third hypothesis regarding that elements that propitiate physical continuity in the landscape are beneficial for SRE bats. Nevertheless, this metric represents the average condition, with variability in the number and size of patches, and therefore is probably best interpreted in conjunction with other metrics (McGarigal et al. 2012). In the study area, in the smallest buffers, mean patch area is

positively correlated with percentage of landscape; in other words, as the mean patch area increases the forest occupies a higher portion of the landscape, possibly reflecting more physical continuity.

Fuentes-Montemayor et al. (2013) proposed that less vagile species should be more influenced by local conditions, and small buffers could be considered as site-specific characteristics. In contrast to the lack of response of SRE bats relative activity to the WS based metrics in our study area, Fuentes-Montemayor et al. (2013) found that *Myotis* spp. abundance (which was correlated with activity), was strongly related to the water bodies decreasing Euclidean nearest neighbor distance.

For *P. mesoamericanus*, we found a significant independent contribution of a metric based on FC, although it showed a relationship in a negative direction which is counterintuitive, and contradicts our third hypothesis. The negative relationship of this species was with patch cohesion index in the intermediate buffers. This index resembles aggregation, measures the physical connectedness of the corresponding patch type and it increases as the patch type becomes more clumped in its distribution (MacGarigal et al. 2012). This species has the ability to traverse long distances through open areas (Estrada and Coates-Estrada 2001), condition from which may benefit (e.g. by exploitation of specific prey), and may not be satisfied in areas with clumping patches, therefore lacking or even showing negative responses in such landscapes.

Importance of local and landscape features in conservation strategies

The understanding of the use of water surfaces in human induced landscapes is important for conservation purposes (López-González et al. 2015), as these ecotopes provide various kinds of resources (e.g. water supply, food availability) for many taxa. The preservation of a continuous network of various types of water surfaces, even artificial ones, along with relevant local and landscape features may be essential for the protection of qualitatively rich bat faunas (Ciechanowsky 2002; Siebold et al. 2013; López-González et al. 2015). Nevertheless, in the surroundings of the NP there is intensive use of agricultural pesticides, which affect the water quality inside the protected area, with potential implications not yet explored on taxonomic groups such as the flying nocturnal insects, and consequently on the aerial insectivorous bats, among others.

We provide evidence that the water sinkholes and flooded surfaces are an important resource for SRE bats inside the NP as well as in its surroundings, as may be for other taxa associated to water surfaces (e.g. aquatic insects, anurans, aquatic birds). The water sinkholes may represent a permanent resource on the limits of the NP, while the flooded surfaces beyond the NP may represent a seasonal resource threatened by human activities (e.g. by infiltration of pesticides affecting water quality, by use of water supply for agriculture irrigation, by loss of surrounding forest cover), mainly if protection actions are not carried out in the near future. As López-González et al. (2015) point out, maintaining the characteristics of the water surfaces, relevant to local biodiversity, may contribute for continuity of local populations and ecological services.

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Disclosure statement

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References

- Bradley ES, Cooper RJ, Greer RD, Whitmore RC. 1993. Estimation of insect biomass by length and width. *Am Midl Nat.* 129:234–240.
- [CONANP] Comisión Nacional de Áreas Naturales Protegidas. 2007. Programa de conservación y manejo del Parque Nacional Lagunas de Montebello, México. México DF (México): Secretaría de Ambiente y Recursos Naturales; 194 p.
- Chevan A, Sutherland M. 1991. Hierarchical partitioning. *Am Stat.* 45(2):90–96.
- Ciechanowsky M. 2002. Community structure and activity of bats (Chiroptera) over different water bodies. *Mamm Biol.* 67:276–285.
- Delfín G H, Manrique S PC, Meléndez R V, Reyes N E. 2011. Insectos terrestres. 415–448, In *Técnicas de Muestreo para Manejadores de Recursos Naturales.* (Bautista Z F, Palacio P JL, Delfín G H, eds). Second Edition, Universidad Nacional Autónoma de México, México.
- Denzinger A, Schnitzler H-U. 2013. Bat guilds, a concept to classify the highly diverse foraging end echolocation behaviors of microchiropteran bats. *Front Physiol.* 4:164.
- Duffy AM, Lumsden LF, Caddle CR, Chick RR, Newell GR. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropterol.* 2:127–144.
- Estrada A, Coates-Estrada R. 2001. Bats in continuous forest, forest fragments and in agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biol Conserv.* 103:237–245.
- García Estrada C, Damon A, Sánchez Hernández C, Soto Pinto L, Ibarra Núñez G. 2006. Bat diversity in montane rainforest and shaded coffee under different Management regimes in southeastern Chiapas, Mexico. *Biol Conserv.* 132(3):351–361.
- González E M, Ramírez M N. 2013. Comunidades vegetales terrestres. 21–42, In *La biodiversidad en Chiapas: Estudio de Estado* (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Gobierno del Estado de Chiapas, México.
- Graham MH. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst.* 34:487–515.

- Feldhamer GA, Carter TC, Whittaker Jr JO. 2009. Prey consumed by eight species of insectivorous bats from southern Illinois. *Am Midl Nat.* 162(1):43–51.
- Fenton MB. 1999. Describing the echolocation calls and behaviour of bats. *Acta Chiropterol.* 1(2):127–136.
- Fenton MB. 2002. Bat natural history and echolocation. 2–6, In: *Bat echolocation research: Tools techniques and analysis* (Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, eds). Bat Conservation International, Texas, US.
- Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J Appl Ecol* 50:252–261.
- Fuentes-Montemayor E, Goulson D, Cavin L, Wallace JM, Park JK. 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agric Ecosyst Environ.* 172:6–15.
- Garcías-García JL, Santos-Moreno A. 2014. Efectos de la estructura del paisaje y de la vegetación en la diversidad de murciélagos filostómidos (Chiroptera: Phyllostomidae) de Oaxaca, México. *Rev Biol Trop.* 62(1):217–239.
- Heim O, Treitler JT, Tschapka M, Knörnschild M, Jung K. 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS ONE.* 10(7):e0134443.
- Herd RM. 1983. *Pteronotus parnellii*. *Mamm Species.* 209:1–5.
- Horváth A, Vidal-Lopez R, Sarmientos-Aguilar R. 2001. Mamíferos del Parque Nacional Lagunas de Montebello. *Revista Mexicana Mastozool.* 5:6–26.
- Jones G. 1999. Scaling echolocation call parameters in bats. *J Exp Biol.* 202:3359–3367.
- Klingbeil BT, Willig MR. 2008. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *J Appl Ecol.* 46(1):203–213.
- Kraker-Castañeda C, Santos-Moreno A, García-García JL. 2013. Riqueza de especies y actividad relativa de murciélagos insectívoros aéreos en una selva tropical y pastizales en Oaxaca, México. *Mastozool Neotrop.* 20(2):255–267.
- Kunz TH. 1988. Methods of assessing the availability of prey to insectivorous bats. 191–210, In *Ecological and Behavioral Methods for the Study of Bats* (Kunz TH, ed.). Smithsonian Institution Press, Washington DC, US.

- Kurta A, Whitaker Jr JO. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *Am Midl Nat.* 140(2):280–286.
- López-González C, Gómez-Ruiz EP, Lozano A, López-Wilchis R. 2015. Activity of insectivorous bats associated with cattle ponds at La Michilfa Biosphere Reserve, Durango, Mexico: implications for conservation. *Acta Chiropterol.* 17(1):117–129.
- Mac Nally R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers Conserv.* 11:1397–1401.
- McGarigal K, Cushman SA, Ene E. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Available from: <http://www.umass.edu>
- MacSwiney G MC, Vilchis L P, Clarke FM, Racey PA. 2007. The importance of cenotes in conserving bat assemblages in the Yucatan, Mexico. *Biol Conserv.* 36:499–509.
- MacSwiney G MC, Clarke FM, Racey PA. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bats assemblages. *J Appl Ecol.* 45:1364–1371.
- MacSwiney G MC, Bolívar C B, Clarke FM, Racey, PA. 2009. Insectivorous bat activity at cenotes in the Yucatan Peninsula. *Acta Chiropterol.* 11(1):139–147.
- Miller BW. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterol.* 3(1):93–105.
- Morris AD, Miller DA, Kalcounis-Rueppell MC. 2010. Use of forest edges by bats in a managed pine forest landscape. *J Wildl Manage.* 74(1):26–34.
- Olea PP, Mateo-Tomás P, de Frutos Á. 2010. Estimating and modelling bias of the hierarchical partitioning public-domain software: implications in environmental management and conservation. *PLoS ONE.* 5(7):e11698.
- Queiroz de Oliveira LQ, Marciente R, Magnusson WE, Bobrowiec PED. 2015. Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources and vegetation structure. *J Mammal.* 96(5):1036–1044.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.r-project.org/>

- Radford JQ, Bennett AF. 2007. The relative importance of landscape properties for woodland birds in agricultural environments. *J Appl Ecol.* 44:737–747.
- Rodríguez-San Pedro A, Simonetti JA. 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? *Landscape Ecol.* 30:1561–1572.
- Rolfe AK, Kurta A. 2012. Diet of mormoopid bats on the Caribbean island of Puerto Rico. *Acta Chiropterol.* 14(2):369–377.
- Salina-Ramos VB, Herrera M LG, León-Regagnon V, Arrizabalaga-Escudero A, Clare EL. 2015. Dietary overlap and seasonality in three species of mormoopid bats from a tropical dry forest. *Mol Ecol.* 24:5296–5307.
- Schnitzler H-U, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends Ecol Evol.* 18(8):386–394.
- Seibold S, Buchner J, Bäessler C, Müller J. 2013. Ponds in acidic mountains are more important for bats in providing drinking water than insect prey. *J Zool.* 290(4):302–308.
- StatSoft Inc. 2007. STATISTICA (data analysis software system). Version 8.0. Available from: <http://www.statsoft.com>.
- Turner MG, Gardner RH, O'Neill RV. Quantifying Landscape Pattern. 93-134, In *Landscape Ecology in Theory and Practice*. Springer, New York, US.
- Walsh C, Mac Nally R. 2015. Package 'hier.part': Hierarchical Partitioning. Available from: <https://cran.r-project.org/web/packages/hier.part/index.html>
- Waters DA, Jones G. 1995. Echolocation call structure and intensity in five species of insectivorous bats. *J Exp Biol.* 198:475–789.
- Whickramasinghe LP, Harris S, Jones G, Vaughan J N. 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv Biol.* 18(5):1283-1292.
- Whitaker Jr JO. 2004. Prey selection in a temperate zone insectivorous bat community. *J Mammal-* 85(3):460–469.
- Williams-Guillén K, Perfecto I. 2011. Ensemble composition and activity levels of insectivorous bats in response to management in response to management intensification in coffee agroforestry systems. *PLoS ONE.* 6:e16502.

Tables

Table 1. Number of individual insects, mass (g), and percentage of the mass of flying insects collected in three ecotopes (water sinkholes, flooded surfaces, forested sites) in the study area in a tropical highland region in Chiapas, southeast Mexico. For comparison purposes, we followed the table structure of Queiroz de Oliveira et al. (2015).

Taxon	Water sinkholes		Flooded surfaces		Forested sites		Total	
	n	mass (g) %	n	mass (g) %	n	mass (g) %	n	mass (g) %
Amphiesmenoptera	76	0.28 75.70	136	0.86 86.87	102	0.61 79.2	314	1.75 82.2
Diptera	170	0.06 16.20	157	0.07 7.07	196	0.05 6.5	523	0.18 8.5
Coleoptera	8	0.03 8.10	20	0.06 6.06	28	0.11 14.3	56	0.20 9.4
Total	254	0.37 100	313	0.99 100	326	0.77 100	893	2.13 100

Table 2. Percentage of independent contribution of flying insect's biomass on the relative activity of aerial insectivorous bats with short range echolocation in a tropical highland region in Chiapas, southeast Mexico. Values in bold represent significant effects with a confidence level of 90% (alpha = 0.1). The positive and negative signs indicate the direction of the relationship between variables.

Taxon	Amphiesmenoptera	Diptera	Coleoptera
<i>Myotis pilosatibialis</i>	82.9	22	4.8
<i>Mormoops megalophylla</i>	65.2 (+)	24.7	10.1
<i>Pteronotus davyi</i>	7.7	48.2 (-)	44.2
<i>Pteronotus mesoamericanus</i>	71.4 (+)	19	9.6

Table 3. Percentage of independent contribution of landscape metrics on the relative activity of aerial insectivorous bats with short range echolocation in concentric buffers of 500, 1000, and 1500 m radius in a tropical highland region in Chiapas, southeast Mexico. Values in bold represent significant effects with a confidence level of 95% (alpha = 0.05). FC = forest cover class; WS = water surface class; PLAND = percentage of landscape; PD = patch density; AREA = mean patch area; ED = edge density; ENN = Euclidean nearest neighbor distance; COH = patch cohesion index. The positive and negative signs indicate the direction of the relationship between variables.

		Composition			Configuration		
		PLAND	PD	AREA	ED	ENN	COH
<i>Myotis pilosatibialis</i>							
FC	500	16.96	7.76	32.35 (+)	16.66	10.31	15.95
	1000	16.39	5.24	29.19	18.65	13.10	17.43
	1500	26.35	18.55	12.61	9.14	18.23	15.12
WS	500	24.60	11.99	19.49	18.77	14.55	10.60
	1000	20.49	13.73	11.39	29.38	13.50	11.50
	1500	20.22	9.84	20.45	18.73	8.30	22.45
<i>Mormoops megalophylla</i>							
FC	500	22.76	7.56	7.85	6.76	22.03	33.05
	1000	14.19	6.08	12.06	18.30	21.31	28.07
	1500	21.10	17.25	13.44	12.02	16.83	19.35
WS	500	14.47	24.72	19.50	13.47	16.98	10.86
	1000	13.84	28.67	14.97	10.87	15.06	16.59
	1500	17.02	27.30	15.70	8.45	16.32	15.22
<i>Pteronotus davyi</i>							
FC	500	5.58	10.53	33.92	9.62	27.19	13.16
	1000	44.78	8.77	6.95	5.40	15.07	19.03
	1500	18.51	11.38	11.23	4.71	21.55	32.62
WS	500	17.85	17.53	13.60	20.01	24.30	6.70
	1000	8.27	8.51	9.16	10.52	38.70	24.84
	1500	15.87	7.49	13.94	24.16	14.22	24.32
<i>Pteronotus mesoamericanus</i>							
FC	500	25.65	17.64	9.74	9.31	17.01	20.66
	1000	13.23	7.36	12.07	10.87	24.54	31.93 (-)
	1500	18.21	15.31	23.01	17.46	16.15	9.86
WS	500	13.89	16.51	12.97	13.06	25.64	17.93
	1000	16.68	13.31	17.55	15.19	10.93	26.34
	1500	17.01	9.15	15.74	16.97	25.97	15.16

Figures

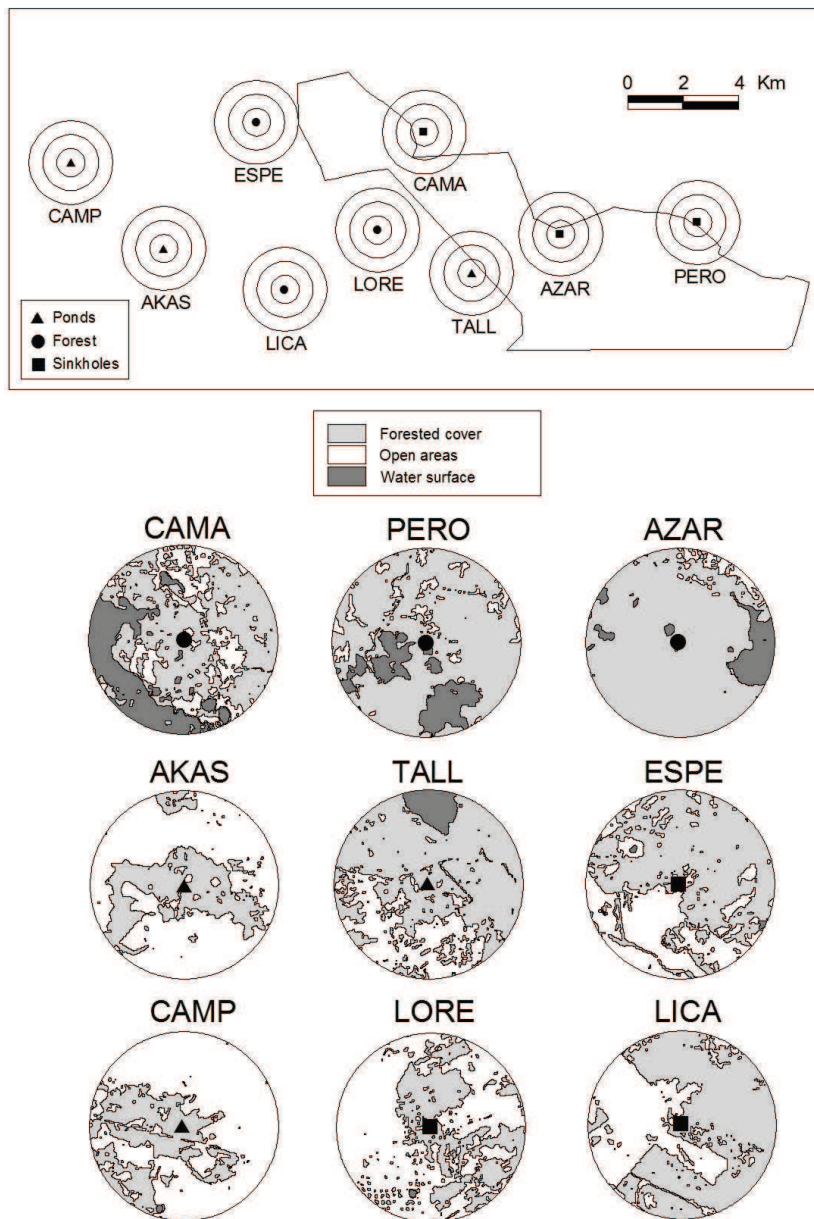


Figure 1. Study area in a tropical highland region in Chiapas, southeast Mexico. Above, the sampling points are surrounded by concentric buffers of 500, 1000 and 1500 m radius, inside and beyond the limits of the Lagos de Montebello National Park. Below, the sampling points are surrounded by a spatial analysis window of 1500 m radius, including the forested cover, open areas, and water surfaces.

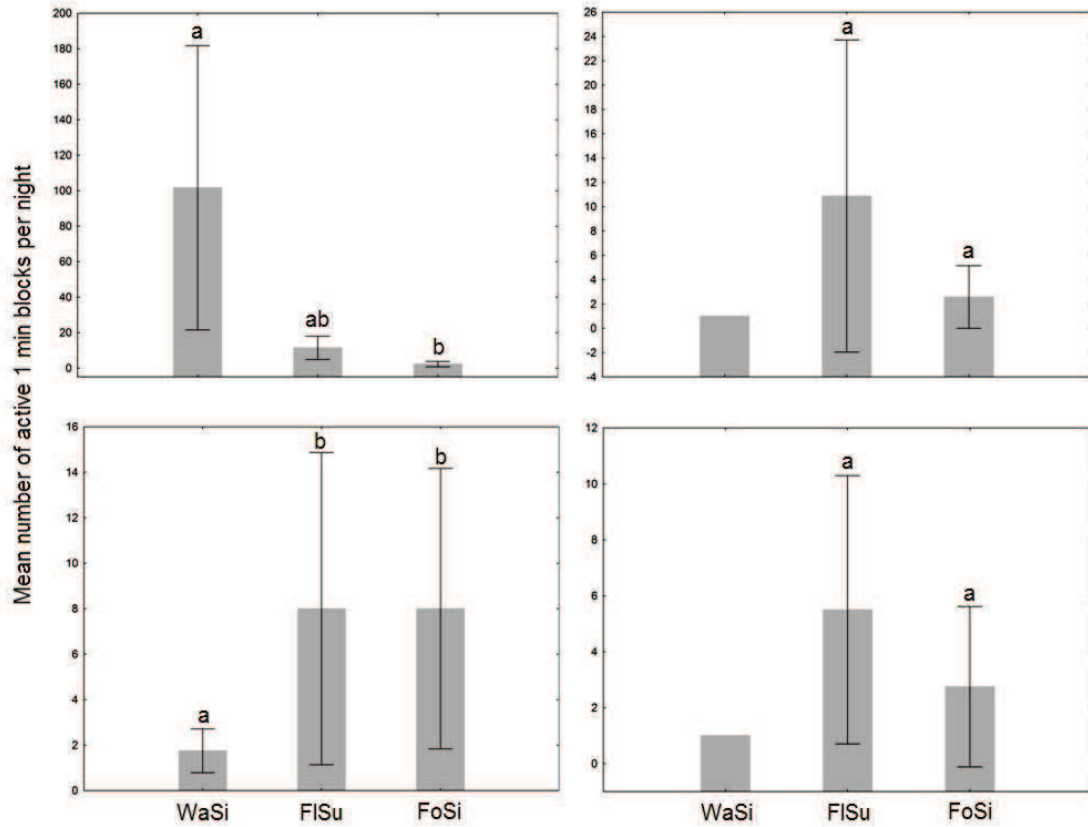


Figure 2. Mean number of active one minute blocks per night for aerial insectivorous bats with short range echolocation, pooled by ecotope (water sinkholes, flooded surfaces, forested sites) in a tropical highland region in Chiapas, southeast Mexico. *Myotis pilosatibialis* (up/left); *Mormoops megalophylla* (up/right); *Pteronotus davyi* (down/left); *Pteronotus mesoamericanus* (down/right). The whiskers represent the standard deviation, and distinct letters indicate statistically significant differences with a 95% confidence level (alpha = 0.05). WaSi = water sinkholes; FISu = flooded surfaces; FoSi = forested sites.

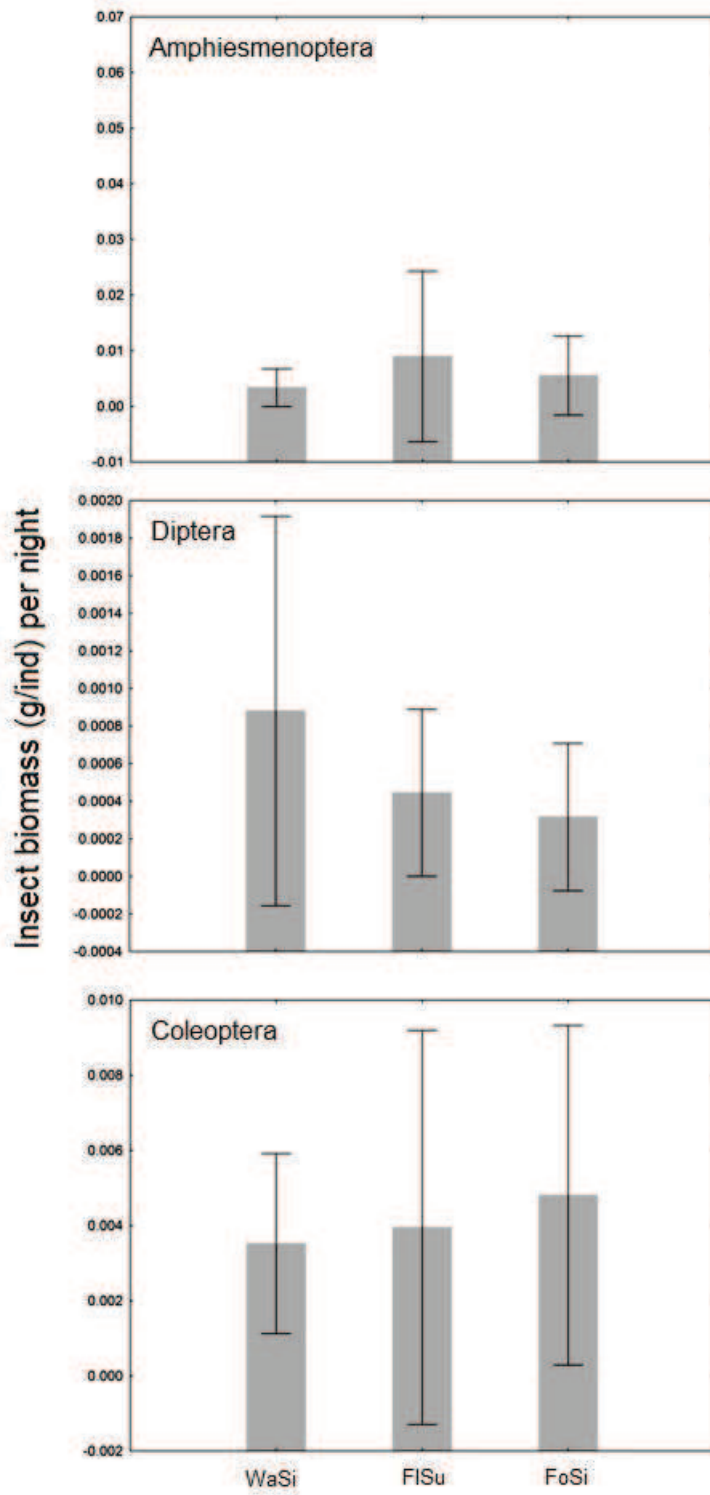


Figure 3. Mean flying insect's biomass (g/ind) per night, pooled by ecotope (water sinkholes, flooded surfaces, forested sites) in a tropical highland region in Chiapas, southeast Mexico. The whiskers represent the standard deviation. For Diptera, based on a Kruskal-Wallis test and a Dunn post test, we determined statistically significant differences between the water sinkholes and forested sites ($p = 0.001$). WaSi = water sinkholes; FISu = flooded surfaces; FoSi = forested sites.

Supplementary Material

Table S1. Aerial insectivorous bats echolocation calls acoustic parameters in the study area in a tropical highland region in Chiapas, southeast Mexico. The values represent mean, range, and coefficient of variation. n = number of pulses; Fc = characteristic frequency; Dur = duration; Fmax = maximum frequency; Fmin = minimum frequency.

Taxon	n	Fc	Dur	Fmax	Fmin
<i>Vespertilionidae</i>					
<i>Myotis pilosatibialis</i>	64	50.1; 46.2-55; 4.9	3.3; 2.3-4.7; 21.2	61.4; 48.9-83; 16	49.4; 45.1-53.9; 4.9
<i>Mormoopidae</i>					
<i>Mormoops megalophylla</i>	60	50.3; 49.4-51.7; 1.1	7; 3.5-9.8; 26.9	52; 50.5-53.7; 1.4	47.4; 45.1-49.9; 3
<i>Pteronotus davyi</i>	35	69.8; 61.6-78.2; 9	4.6; 4.3-5.3; 9.4	72.7; 63.6-79.9; 9.8	63.9; 57.4-70.5; 8.3
<i>Pteronotus mesoamericanus</i>	60	62.2; 61.2-62.7; 1.1	12.8; 8.6-17.4; 28.2	62.9; 62.1-63.6; 1.1	60; 58.6-61.4; 1.9

Table S2. Landscape metrics calculated in buffers of 500 m radius in the study area in a tropical highland region in Chiapas, southeast Mexico. FC = forest cover; WS = water surface; PLAND = percentage of landscape; PD = patch density; AREA = mean patch area; ED = edge density; ENN = Euclidean nearest neighbor distance; COH = patch cohesion index.

	PLAND ^{FC}	PD ^{FC}	AREA ^{FC}	ED ^{FC}	ENN ^{FC}	COH ^{FC}	PLAND ^{WS}	PD ^{WS}	AREA ^{WS}	ED ^{WS}	ENN ^{WS}	COH ^{WS}
AZAR	95.5476	1.2777	74.7838	18.8888		99.9651	4.0962	2.5553	1.603	15.5158	150.5032	91.0875
PERO	74.6996	3.8312	19.4975	99.4592	33.5914	99.6826	18.113	7.6625	2.3639	52.4268	70.159	95.184
CAMA	87.5612	2.5542	34.2817	79.2302	47.5933	99.8677	1.8024	8.9396	0.2016	15.846	154.9752	80.2269
ESPE	68.0321	2.5553	26.6239	78.0849	37.3352	99.6393	0.1113	1.2777	0.0871	1.6865		56.1159
LEBA	59.6616	21.7201	2.7468	143.1838	47.2024	99.211	0.6233	3.833	0.1626	6.4087	283.9878	72.2158
LICA	44.3703	15.325	2.8953	107.5508	64.6518	98.2654	1.4686	1.2771	1.15	6.4058		89.0187
AKAS	85.4853	3.833	22.3027	81.9639	40.7546	99.7946	0.0445	2.5542	0.0174	1.18	549.3484	0
CAMP	68.2911	6.3854	10.6949	99.9649	47.7385	99.503	0.2225	2.5542	0.0871	2.36	280.6358	60.9086
TALL	86.5821	5.1083	16.9492	97.7735	27.958	99.8547						

Table S3. Landscape metrics calculated in buffers of 1000 m radius in the study area in a tropical highland region in Chiapas, southeast Mexico. FC = forest cover; WS = water surface; PLAND = percentage of landscape; PD = patch density; AREA = mean patch area; ED = edge density; ENN = Euclidean nearest neighbor distance; COH = patch cohesion index.

	PLAND ^{FC}	PD ^{FC}	AREA ^{FC}	ED ^{FC}	ENN ^{FC}	COH ^{FC}	PLAND ^{WS}	PD ^{WS}	AREA ^{WS}	ED ^{WS}	ENN ^{WS}	COH ^{WS}
AZAR	97.0544	0.3202	303.1253	12.0029	99.9887	2.4268	1.6009	1.5159	8.7063	223.9488	90.844	
PERO	75.531	1.5998	47.2121	77.0795	54.6964	99.8552	2.8797	6.0694	32.3523	119.6471	97.6396	
CAMA	64.9105	7.0392	9.2213	117.9634	41.7971	99.6722	7.5486	4.7995	1.5728	26.566	151.3832	93.6868
ESPE	68.0948	3.8421	17.7231	66.6075	40.5159	99.622	0.4909	2.2413	0.219	4.015	226.259	77.0262
LEBA	41.1512	16.0054	2.5711	100.1002	54.8405	99.2144	0.1896	1.2804	0.1481	2.1127	332.5219	70.2535
LICA	54.8252	5.4394	10.0793	58.0314	64.3228	99.1732	0.3903	0.32	1.2197	1.8584	88.7101	
AKAS	43.5629	3.2	13.6134	61.6705	89.7711	99.2501	0.0446	0.6399	0.0697	0.7602	541.8435	52.8753
CAMP	39.1314	4.4795	8.7356	78.8112	64.6316	99.2741	1.3492	0.9599	1.4055	3.3366	454.7159	93.1024
TALL	74.2822	9.279	8.0054	84.344	43.3705	99.7079						

Table S4. Landscape metrics calculated in buffers of 1500 m radius in the study area in a tropical highland region in Chiapas, southeast Mexico. FC = forest cover; WS = water surface; PLAND = percentage of landscape; PD = patch density; AREA = mean patch area; ED = edge density; ENN = Euclidean nearest neighbor distance; COH = patch cohesion index.

	PLAND ^{FC}	PD ^{FC}	AREA ^{FC}	ED ^{FC}	ENN ^{FC}	COH ^{FC}	PLAND ^{WS}	PD ^{WS}	AREA ^{WS}	ED ^{WS}	ENN ^{WS}	COH ^{WS}
AZAR	86.9694	1.274	68.2634	30.2148	56.5556	99.9173	9.1335	1.4156	6.4521	12.7997	202.9503	97.5708
PERO	77.7657	1.132	68.6933	68.2881	45.6519	99.9054	14.135	1.415	9.9892	22.825	118.1963	97.827
CAMA	56.5346	8.0653	7.0096	107.1338	44.7831	99.6155	21.464	2.6884	7.9839	28.2776	117.4595	98.8069
ESPE	61.4132	3.3972	18.0774	81.7461	52.5705	99.5895	0.5229	2.2648	0.2309	4.0546	285.5476	78.7457
LEBA	31.9257	15.7138	2.0317	89.7146	59.6019	98.9445	0.2393	0.7078	0.338	1.5323	390.0875	81.9151
LICA	62.6116	4.1037	15.2574	61.5467	57.013	99.7346	0.1677	0.1415	1.1848	0.8219		88.3117
AKAS	29.0988	4.9531	5.8794	48.3817	103.813	99.1936	0.1652	0.566	0.2919	1.102	303.9218	81.0872
CAMP	27.7681	5.2353	5.304	59.4503	100.3479	99.0074	5.7296	1.2735	4.4993	4.5947	295.8595	97.8616
TALL	66.6626	8.4897	7.8521	80.9854	43.1755	99.595						

Capítulo V

Discusión

Complementación de métodos para el estudio de murciélagos

Con base en el uso de métodos complementarios de muestreo (redes de niebla y detectores ultrasónicos), proveemos evidencia nueva del sesgo de los dispositivos de registro como las redes de niebla y los detectores ultrasónicos. Particularmente en el área de estudio, las redes de niebla permitieron el registro de murciélagos frugívoros, nectarívoros, sanguívoros y carnívoros (Phyllostomidae), mientras que los detectores exclusivamente de murciélagos insectívoros aéreos. Atribuimos el sesgo de las redes de niebla a la capacidad de los murciélagos insectívoros aéreos de ubicar obstáculos por medio de su sistema de ecolocalización, a su vuelo en estratos superiores y a la actividad relativamente baja en los sitios donde fueron ubicadas las trampas (e.g. a lo largo de brechas dentro de los bosques), donde la cantidad de presas potenciales es menor en comparación con los ecotopos con superficie de agua.

Análisis de parámetros acústicos para clasificación de especies

Con respecto a la identificación taxonómica por medios acústicos, proveemos evidencia de la importancia de enfoques cuantitativos para la clasificación de especies, tomando en cuenta fuentes de variación intrínseca y extrínseca. A través del análisis multivariado fue posible identificar los parámetros acústicos con poder de discriminación en el nivel intraespecífico, basado en categorías de edad y espacio acústico. Estas fuentes de variación pueden originar confusión para la asignación de especies, por lo que la caracterización previa al monitoreo en vuelo libre debe ser considerada para proveer umbrales de confianza y, de presentarse el caso de tasas de clasificación alta para una misma especie en distintas condiciones, considerar con criterios objetivos agrupaciones a niveles taxonómicos superiores.

Modelos conceptuales para la representación de los paisajes

En este estudio utilizamos el modelo de parche-matriz-corredor como base teórica del análisis espacial del paisaje. Específicamente, adoptamos este modelo tomando en cuenta las características del área: matriz contrastante (predominancia de área abierta) y fragmentos discretos (bosques con

discontinuidad abrupta). Es importante reconocer que en la actualidad hay enfoques que toman en cuenta la importancia de la matriz en la continuidad física del paisaje; sin embargo, la selección del modelo debe ser contexto-específica (con base en el tipo de ecosistema y su patrón de cambio) y basarse en rasgos de las especies (e.g. especialización, vagilidad, entre otros). También debe reconocerse que la relevancia de los modelos puede ser especie-específica y una alternativa a la selección arbitraria es poner a prueba su idoneidad contrastando el valor explicativo en una misma especie, aunque esto depende de la disponibilidad de recursos y herramientas.

Diseño de escalas anidadas y respuestas especie-específicas

El diseño de escalas anidadas, probó ser una aproximación apropiada en la búsqueda de respuestas especie-específicas tanto para murciélagos filostómidos, como para los murciélagos insectívoros aéreos. A pesar de que los murciélagos tienen la capacidad de vuelo activo y por lo tanto se consideran animales muy móviles, la implementación de ventanas de análisis espacial concéntricas para el estudio de cambios en el contexto paisajístico en extensiones geográficas pequeñas, permitió revelar asociaciones escala-dependientes a distintos niveles de organización, tanto en conjuntos ecológicos como en especies.

Amenazas para el ecosistema en el área de estudio

En cuanto a las presiones sobre los ecotopos con superficie de agua, los cenotes se encuentran dentro del área natural protegida, lo que garantiza su protección y permanencia. Aún así, el área se encuentra amenazada por la filtración de pesticidas en el sistema lacustre, los cuales son administrados en las áreas agrícolas circundantes, lo que puede tener un efecto en la calidad del agua y presumiblemente en la fauna asociada; en este caso en particular, una potencial disminución en la abundancia de insectos acuáticos y consecuentemente en la actividad de los murciélagos insectívoros aéreos.

En el caso de los agujeros, estos son característicos de la zona de influencia y existe evidencia de fluctuaciones importantes en períodos de clima extremo (sequía), además de que su entorno está sujeto a cambio de uso del suelo, específicamente para pastoreo con aprovechamiento de la superficie de

agua, poniendo en riesgo su integridad ecológica. Los aguajes, junto con su fauna asociada, pueden ser considerados los ecotopos más amenazados en el área por el contexto ambiental.

Por otro lado, en la zona de influencia hay una tendencia hacia la pérdida y fragmentación de los bosques, con conversión hacia áreas abiertas (monocultivos, zonas de pastoreo, asentamientos humanos). Asimismo, los remanentes de bosque reflejan distintos grados de degradación como consecuencia de las prácticas locales de manejo. De seguir esta tendencia, muchos hábitats pueden disminuir su calidad y/o resultar aislados, involucrando la interrupción de la dinámica poblacional de varias especies.

Propuesta para la protección de ecotopos en el área de estudio

Con base en los hallazgos de este estudio y los criterios definidos por la RELCOM, proponemos el Parque Nacional Lagos de Montebello como Área de Importancia para la Conservación de Murciélagos (AICOM) y los aguajes en su zona de influencia como Sitio de Importancia para la Conservación de Murciélagos (SICOM). Las AICOM y los SICOM representan acreditaciones a nivel internacional que pueden respaldar el acceso a recursos financieros específicos (fondos semilla) para un programa de investigación, educación ambiental y conservación. Dicho programa debe tomar en cuenta la participación de actores locales (ejidatarios), organizaciones civiles sin fines de lucro e instituciones de gobierno. La finalidad es que a través de este grupo taxonómico se promueva el valor escénico-biológico de los ecotopos estudiados, con implicaciones en la salud del ecosistema y en el legado natural de las generaciones futuras.

Capítulo VI

Conclusiones

El enfoque de generalización ecológica basado en conjuntos de especies con rasgos similares, probó ser una alternativa potencial para las estrategias de conservación de grupos taxonómicos ricos en especies. De esta manera, los esfuerzos son dirigidos a especies que son ecológicamente similares: que se comportan de forma similar, que utilizan recursos similares y que pueden responder de forma similar a cambios en el ambiente.

Para las especies en el área de estudio, las respuestas a la fragmentación del paisaje se pueden relacionar con atributos como la vagilidad (capacidad de movilidad en el entorno), propiedades del sistema de ecolocalización (rango de detección) y factores contextuales (pérdida y fragmentación de la cobertura forestal). Asimismo, contrario a la expectativa general, se provee evidencia nueva que las respuestas en este grupo de mamíferos, a pesar de su capacidad de vuelo activo, pueden darse en extensiones geográficas pequeñas.

Para *Myotis pilosatibialis*, con base en el análisis cuantitativo de parámetros acústicos diferenciando categorías de edad y espacio acústico, las tasas de clasificación fueron bajas (< 75%) para considerarlas una fuente de confusión en la asignación de especie. Cuando las tasas de clasificación en una misma especie son altas (e.g. > 90%), el grado de diferenciación puede acarrear errores; por ejemplo, al confundir una misma especie entre hábitats, como especies distintas. Enfatizamos la importancia de la caracterización acústica de las especies tomando en cuenta variaciones ambientales locales (e.g. restricciones del espacio acústico), para proveer umbrales de confianza en la asignación de especies y evitar identificaciones incorrectas.

Las variables a nivel local y escala de paisaje tuvieron valor predictivo para la actividad relativa de los murciélagos insectívoros aéreos. Las respuestas fueron especie-específicas y escala-dependientes, relacionadas con el ecotopo, la disponibilidad de alimento y el paisaje circundante.

Los ecotopos con superficie de agua (cenotes y aguajes) destacaron por su efecto positivo en la actividad relativa de *M. pilosatibialis*, mientras que *Pteronotus davyi* estuvo asociado a las áreas forestadas, lo cual puede estar asociado a las distintas oportunidades de forrajeo.

A nivel local, para *Mormoops megalophylla* y *Pteronotus mesoamericanus* se observó una asociación positiva con la biomasa del superorden Amphiesmenoptera (Lepidoptera and Trichoptera). Por el contrario, en el caso de *P. davyi* se observó una correlación negativa con la biomasa del orden Diptera, sin embargo esto no determina una causalidad y puede ser efecto de otras variables no consideradas.

A la escala de paisaje, en la ventana de análisis espacial más pequeña, el tamaño promedio de los fragmentos de bosque presentó valor predictivo en una dirección positiva sobre la actividad relativa de *M. pilosatibialis*. En el área de estudio, el tamaño promedio de los fragmentos de bosque está correlacionado con el porcentaje que ocupan estos en el paisaje, lo que refleja una mayor continuidad física que puede ser beneficiosa para esta especie.

Por sus características, el PNLM y los agujajes en su zona de influencia son candidatos potenciales para área y sitios de conservación, respectivamente. Específicamente, contienen especies con datos deficientes que juegan un papel importante en servicios ecosistémicos, así como refugios que son utilizados permanentemente, incluso como refugios de maternidad. Este tipo de acreditación internacional permite el acceso a recursos para programas de investigación, educación ambiental y conservación, como base para la recuperación de sitios y paisajes con valor biológico y escénico alto en el área de estudio.