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IMPORTANCIA DE LAS ZONAS RIPARIAS PARA LA COMUNIDAD DE MURCIÉLAGOS EN EL BOSQUE TROPICAL HÚMEDO EN EL SURESTE DE MÉXICO. IMPLICACIONES DE MANEJO Y CONSERVACIÓN

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ERIKA IVETEE DE LA PEÑA CUÉLLAR

TUTORA PRINCIPAL DE TESIS:
DRA. JULIETA BENÍTEZ MALVIDO
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

COMITÉ TUTOR:
DR. MIGUEL MARTÍNEZ RAMOS
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

DR. ALEJANDRO ESTRADA MEDINA
INSTITUTO DE BIOLOGÍA, UNAM

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COORDINACIÓN

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted, que el Subcomité de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, en su sesión ordinaria del día **22 de enero de 2018**, aprobó el jurado para la presentación del examen para obtener el grado de **DOCTORA EN CIENCIAS** a la alumna **DE LA PEÑA CUÉLLAR ERIKA IVETEE,** con número de cuenta **508010679**, con la tesis titulada, **"Importancia de las zonas riparias para la comunidad de murciélagos en el bosque tropical húmedo en el sureste de México. Implicaciones de manejo y conservación"**, realizada bajo la dirección de la **DRA. JULIETA BENITEZ MALVIDO:**

Presidente:	Dr. Vinicio de Jesús Sosa Fernández
Vocal:	Dr. Luis Daniel Ávila Cabadilla
Secretario:	Dr. Miguel Martínez Ramos
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Sin otro particular, quedo de usted.

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"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mex., a 05 de noviembre de 2018

COORDINACIÓN

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

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CONTENIDO

RESUMEN

Debido al proceso de globalización y la cambiante dinámica demográfica, los bosques tropicales enfrentan amenazas tradicionales (ganadería, agricultura) y emergentes (agricultura moderna basada en OGM, biocombustibles), así como nuevas oportunidades de urbanización presentando altas tasas de deforestación y cambio de uso de suelo a nivel mundial. Esta presión ha dado lugar a una constante pérdida de hábitat y un incremento en su fragmentación como parte del paisaje. La región de la selva Lacandona en Chiapas es una de las zonas prioritarias para México, ya que constituye el remanente más grande del ecosistema tropical y la región con más alta diversidad biológica en México. Se estima que el 31% de la superficie forestal se perdió durante la década de los noventas. Uno de los principales retos en materia de conservación es el mantenimiento de la biodiversidad dentro de paisajes modificados por las actividades humanas, en los cuales se presenta un mosaico integrado por fragmentos de bosque primario y secundario, tierras agrícolas, pastizales para ganado, vegetación riparia y zonas de asentamientos humanos.

Los murciélagos son peculiarmente importantes en los Neotrópicos ya que contribuyen con casi el 50% de las especies de mamíferos. Además debido a su amplio espectro trófico participan en procesos ecosistémicos primordiales como la regeneración de bosques en la en las zonas tropicales La presente investigación plantea que dentro de los paisajes agropecuarios la vegetación riparia posee características estructurales de la vegetación más complejas que el resto de la matriz agropecuaria, lo que en comparación le confiere mayor diversidad de recursos alimenticios y sitios de refugio para la comunidad de murciélagos. Por lo tanto, documentar la importancia de la vegetación riparia para la comunidad de murciélagos puede representar un eje fundamental para el diseño de estrategias de conservación enfocadas a la comunidad de murciélagos en un paisaje agropecuario.

La presente tesis se llevó a cabo en la región de la selva Lacandona, México, dónde se realizaron muestreos de murciélagos utilizando redes de niebla en cuatro tipos de hábitat: 1) vegetación riparia dentro del bosque continuo, 2) vegetación riparia dentro de pastizal, 3) bosque contínuo alejado de vegetación riparia y, 4) pastizal activo. Teniendo como pregunta central ¿Qué importancia tienen las zonas riparias para las comunidades de murciélagos? y si existen variables ligadas a la estructura de la vegetación que determinan la composición de la comunidad de murciélagos en un paisaje dominado por el hombre

Como primera aproximación evaluamos el papel de la vegetación riparia en la conservación de especies, donde se encontraron diferencias en la riqueza de especies y la

abundancia de murciélagos filostómidos entre hábitat riparios y no riparios. Se concluyó además que la presencia de árboles de mayor área basal en la vegetación riparia favorece la diversidad en la composición de especies de murciélagos. También, contrario a otros hallazgos que sugieren que la subfamilia Phyllostominae es un indicador ecológico para la modificación del hábitat debido a la fuerte asociación con bosques preservados, nuestros resultados sugieren que las especies abundantes y capaces de utilizar diferentes coberturas de vegetación (generalistas), como la subfamilia Stenodermatinae pueden ser mejores indicadores ecológicos. Esto corrobora que la vegetación riparia, permite la persistencia de especies sensibles a la perturbación del hábitat., y demuestra la importancia de mantener diferentes tipos de vegetación y así permitir la conservación de la diversidad de murciélagos en paisajes con uso de suelo agrícola.

Posteriormente, para tratar de entender la asociación entre la proporción de hembras y la vegetación riparia, se utilizaron las seis especies de murciélagos con más capturas (*Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina* y *Platyrrhinus helleri*). Comparando las tasas de captura de hembras y machos en los diferentes tipos de hábitat, se encontró que más de la mitad de los individuos capturados fueron hembras. Además, se demuestra la relación estrecha entre las hembras de *A. lituratus* y la calidad del hábitat, así como también que la presencia de hembras de *G. soricina* está influida por atributos específicos de la vegetación como árboles de gran altura y mayor área basa, esto parece respaldar la idea de que debido a los costos energéticos asociados a la reproducción y la necesidad de encontrar refugios temporales para dejar a sus crías durante el forrajeo, las hembras de ambas especies restringen sus movimientos hacia los sitios con mayores disponibilidad de recursos alimenticios y de refugio. Se encontró también que la estacionalidad resulta particularmente importante para las hembras de *A. lituratus* y *S. lilium*, lo cual reside en las diferencias en la abundancia o diversidad de los recursos alimenticios entre las estaciones húmedas y secas, al parecer, durante la estación seca, cuando los recursos alimenticios suelen ser escasos, las hembras tienden a aumentar los movimientos de forrajeo en áreas de bosques secundarios ricos en recursos. Estas respuestas específicas de las hembras de murciélagos conllevan importantes implicaciones para la comprensión de la adaptabilidad de los murciélagos a las modificaciones del hábitat. Las altas demandas energéticas de las hembras asociadas a la reproducción podrían llevar a un aumento de los movimientos de forrajeo en la vegetación riparia aumentando la importancia de conservación de la misma a largo plazo.

Finalmente, se evaluaron cuatro componentes de la diversidad funcional: riqueza funcional, equidad funcional, divergencia funcional, y especialización funcional, para los cuatro tipos de hábitat. Registrando los valores más altos de divergencia funcional para el hábitat de vegetación riparia dentro del bosque continuo y vegetación riparia dentro de pastizal. En contraste, el valor más bajo para la divergencia funcional se registró en el pastizal activo, esto indica que las especies registradas para este hábitat repiten los

atributos ya existentes y existe poca especialización. Además con la finalidad de conocer si el tipo de hábitat tiene un efecto específico sobre ciertos atributos de la comunidad de murciélagos, se analizó cuáles de estos están siendo filtrados por los diferentes tipos de hábitat. Los atributos de las especies seleccionados estuvieron relacionados con el tamaño, carga alar, fuerza de la mordida, tipo de ecolocación, nivel trófico y preferencia de forrajeo. Se encontró que especies frugívoras de tamaño pequeño y con carga alar alta son más comunes en ambientes perturbados; dichos atributos les permiten ser voladores rápidos y eficientes para viajes de larga distancia en espacios abiertos.

Los resultados de la tesis demuestran que el comportamiento de la comunidad de murciélagos en el paisaje transformado del bosque tropical lluvioso del sureste mexicano, depende de las características de los diferentes elementos del paisaje, como el tipo de hábitat y aspectos específicos de la estructura vegetal como altura y área basal de los árboles, además de la estacionalidad y disponibilidad de sitios de refugio y percha. Esto sugiere que las estrategias de conservación para la comunidad de murciélagos en la región de la Selva Lacandona requieren tanto de la conservación de la vegetación de bosque maduro como de estrategias de manejo sustentable de las zonas de sujetas a actividades de agricultura y ganadería. En particular, la vegetación riparia presentó gran similitud con el bosque maduro en cuánto a la diversidad de especies y diversidad funcional, así como los recursos alimenticios y de refugio esenciales para las hembras de murciélagos en especial durante la etapa reproductiva. Debido a que los ecosistemas riparios se ven fuertemente afectados por las actividades humanas, y a fin de mantener las poblaciones de murciélagos y los servicios ecosistémicos que brindan, los esfuerzos de conservación en el Neotrópico deben incluir a las zonas de vegetación riparia dentro de sus programas de manejo.

SUMMARY

Because of the process of globalization and the changing demographic dynamics, tropical forests face traditional threats (livestock and agriculture) and emergent ones (modern agriculture based on GMOs and biofuels), as well as new opportunities for urbanization that present high rates of deforestation and land-use change on a worldwide scale. This pressure has given rise to a sustained loss of habitat and an increase in its fragmentation as part of the landscape. The Lacandona rainforest in Chiapas is one of the priority areas for Mexico because it constitutes the largest remnant of tropical ecosystem and the region with the highest biological diversity in Mexico. It is estimated that 31% of the forest cover was lost during the 1990s. One of the main challenges for conservation is the maintenance of biodiversity within landscapes modified by human activity, in which a mosaic is presented that is composed of fragments of primary and secondary forest, farmland, pastureland for livestock, riparian vegetation and areas of human settlement.

Bats are particularly important in the Neotropics because they contribute almost 50% of the mammal species. In addition, because of their wide trophic spectrum they participate in essential ecosystem processes, such as the regeneration of forests in tropical zones. This study suggests that within agricultural landscapes the riparian vegetation possesses more complex vegetation structure characteristics than the rest of the agricultural matrix, which in comparison bestows greater diversity of food resources and refuge areas for the bat community. Therefore, documenting the importance of riparian vegetation for the bat community can represent a main focus for the design of conservation strategies focused on the bat community in a human dominated landscape.

This study was conducted in the Lacandon Jungle rainforest in Mexico, where bat sampling was performed using mist nets in four types of habitat: 1) riparian vegetation within mature continuous forest, 2) riparian vegetation in open pastures, 3) mature continuous forest away far from riparian vegetation and, 4) active pastureland. Having as a central question how important are the riparian areas for the bat communities and if variables linked to the vegetation structure that determines the composition of the bat community in a landscape dominated by agricultural practices.

As a first approach, we evaluated the role of riparian vegetation in species conservation, where differences in species richness and the abundance of Phyllostomidae bats between riparian and non-riparian habitats were found. It was also concluded that the presence of trees with a large basal area in riparian vegetation favors diversity in the composition of bat species. In addition, contrary to other findings that suggest that the subfamily Phyllostominae is an ecological indicator for habitat modification because of the strong association with preserved forests, our results suggest that species that are abundant and capable of using different vegetation cover (generalists), such as the subfamily Stenodermatinae, can be better ecological indicators. This corroborates that riparian vegetation permits the persistence of a species sensitive to habitat disturbance and

demonstrates the importance of maintaining different types of vegetation and ,therefore, allowing the conservation of bat diversity in a human-dominated landscape.

Afterward, to try to understand the association between the proportion of females and the riparian vegetation, the six bat species with the most captures were used: (*Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina* and *Platyrrhinus helleri*). Comparing the capture rate of females and males in the different types of habitat, it was found that more than half of the captured individuals were females. In addition, the close relationship between the females of *A. lituratus* and the quality of the habitat is demonstrated, as well as that the presence of females of *G. soricina* is influenced by specific attributes of the vegetation, such as tall trees with a large basal area. This seems to support the idea of that because of the energy costs associated with reproduction and the need to find temporary refuge to leave their offspring during foraging the females of both species restrict their movements toward the sites with the greater availability of food and refuge resources. It was also found that seasonality becomes particularly important for the *A. lituratus* and *S. lilium* females, which lies in the differences in the abundance or diversity of the food sources between the rainy and dry seasons. Apparently during the dry season when the food sources are usually scarce, the females tend to increase their foraging movements in areas of secondary forests rich in resources. These specific responses of female bats involve important implications for the understanding of the bats adaptability to habitat changes. The females' high energy demands associated with reproduction could lead to an increase of foraging movements in the riparian vegetation, confirming the importance of conservation of this vegetation cover in the long term.

Finally, four components of functional diversity were evaluated: functional richness, functional evenness functional divergence, and functional specialization, for the four habitat types .The highest values of functional divergence was recorded for the habitat of riparian vegetation within the continuous forest and riparian vegetation within the pastureland. In contrast, the lowest value for functional divergence was recorded in the active pastureland. This indicates that the species recorded for this habitat repeat the existing traits, and little specialization exists. In addition, to know if the type of habitat has a specific effect on certain attributes of the bat community, the traits filtered through the different types of habitat were analyzed. The characteristics of the selected species were related to size, wing loading, bite force, type of echolocation call, trophic level and foraging preference. It was found that small frugivorous species with high wing loading are most common in disturbed environments; these characteristics permit them to be fast and efficient flyers for long distance travel in open spaces.

The results of the thesis demonstrate that the behavior of the bat community in the modified landscape of the tropical rain forest in southeastern Mexico depends on the characteristics of the different elements of the landscape, like the type of habitat and specific aspects of plant structure such as height and the trees' basal area, in addition to seasonality and the availability of refuge and perching sites. This suggests that conservation strategies for the bat community in the Lacandon rainforest region require

both the conservation of mature forests and sustainable management strategies for the areas subjected to agriculture activities. In particular, the riparian vegetation showed a strong similarity to the mature forest regarding species diversity and functional diversity, as well as the essential food sources and refuge for the female bats especially during the reproductive stage. Given that the riparian ecosystems are strongly affected by human activities, and for the purpose of maintaining the bat populations and ecosystem services that they offer, the conservation efforts in the Neotropics must include areas of riparian vegetation within management programs.

INTRODUCCIÓN GENERAL

Los bosques tropicales son uno de los ecosistemas más diversos del planeta y aportan casi el 50% de las especies conocidas a nivel global (Dirzo & Raven 2003), no obstante son también una de las regiones más importantes en la producción de alimentos. Actualmente las políticas públicas implementadas para el sector agrícola se enmarcan dentro de tratados internacionales, provocando que la dinámica entre los productores y sus tierras esté direccionado hacia el abastecimiento del mercado internacional (principalmente Asia), dejando como última instancia la producción para consumo local (Grau & Aide 2008)

Debido al proceso de globalización y la cambiante dinámica demográfica enfrentan amenazas tradicionales (ganadería, agricultura) y emergentes (agricultura moderna basada en OGM, biocombustibles), así como nuevas oportunidades de urbanización (Grau & Aide 2008). Esto ha provocado una tendencia generalizada al reemplazo de grandes extensiones de bosque maduro por remanentes de selva, bosques secundarios, tierras agrícolas, pastizales para ganado y zonas de asentamientos humanos (Chazdon 2003).A Esta presión para el cambio de uso de suelo, ha dado lugar a una constante pérdida de hábitat e incremento del aislamiento de los remanentes de hábitat en todo el mundo (Henle *et al.* 2004). Dentro del proceso de fragmentación del paisaje, los efectos implicados en los cambios en la biodiversidad son: disminución de hábitat disponible, el incremento en el número de parches, la disminución en el tamaño de parches y la pérdida de conectividad entre estos (Fahrig 2003). La reducción de la cubierta vegetal ocasiona modificaciones en el ciclo hidrológico y cambios regionales de los regímenes de temperatura y precipitación, favoreciendo con ello el calentamiento global y la disminución en el secuestro de bióxido de carbono (Chazdon 2003).Además del alimento, la vegetación proporciona elementos estructurales del hábitat para muchos animales, como son:

sitios de percha, refugio, zonas de anidamiento, además de cobertura para protección contra los depredadores y las condiciones climáticas adversas. Asimismo, es un suministro directo de recursos alimentarios (Ober & Hayes 2008). Los procesos correlacionados con la pérdida y fragmentación del hábitat son considerados las más graves amenazas a la biodiversidad y la causa principal de la crisis actual de extinción (Laurance, Bierregaard & Moritz 1997).Uno de los principales retos en las regiones tropicales es conservar la biodiversidad dentro de paisajes altamente deforestados y fragmentados y se ha señalado ya que algunas especies nativas pueden continuar viviendo en ambientes que, aunque están sujetos a actividades productivas, mantienen la estructura y funciones básicas del ecosistema original (Laurance *et al.* 2002).

La selva Lacandona en Chiapas es una de las zonas prioritarias para la conservación en México, ya que es el remanente más grande del ecosistema de bosque tropical en nuestro país y la región con más alta diversidad biológica en el trópico (Medellín 1994). Esta zona, alberga una cobertura continua de bosques tropicales poco perturbados que se extienden a la región del Petén en Guatemala mediante el corredor Bonampak-Yaxchilán, y al noreste de Belice, formando parte del Corredor Biológico Mesoamericano (CBM) dando lugar a una de las zonas (“hot spot”) más importantes de biodiversidad Mesoamericana (Medellin Medellín 1994; Instituto Nacional de Ecología 2000). El CBM representa la mayor extensión de vegetación tropical en América Central y se estima que tiene una extensión aproximada de 768,000 km^2, equivalente al 0.5% de la superficie continental, albergando alrededor del 10% de la biodiversidad del planeta (Miller, Chang & Johnson 2001).El gobierno federal ha establecido Áreas Naturales Protegidas como: Parque Nacional Palenque (1771.95 ha), Monumento Natural Yaxchilán (2632 ha), Reserva de la Biósfera Montes Azules (331000 ha) y Reserva de la Biosfera

Lacantún (61874 ha) con el objetivo de conservar la biodiversidad de la región Lacandona, por otra parte, también se ha propiciado el cambio de uso de suelo de la región a través de la implementación de políticas públicas como el Programa de Apoyos Directos al Campo (PROCAMPO) cuyo objetivo es introducir el campo mexicano al mercado internacional, otorgando subsidios a los cultivos que representarían ventajas frente al mercado externo, y Proganadería (Progan) fortaleciendo la actividad ganadera, incluso incorporando a grupos de mujeres para el manejo de pequeños hatos, provocando un cambio radical en la organización del campo mexicano (Montoya Gómez *et al.* 2006), aumentando la presión antrópica sobre el bosque remanente. Se estima que el 31% de la superficie forestal de la Selva Lacandona (Chiapas) se perdió durante la década de los noventas provocado por actividades humanas (Instituto Nacional de Ecología 2000). Durante estas prácticas es común que se dejen remanentes de selva en lugares remotos o poco accesibles, sin embargo, para el establecimiento de potreros ganaderos, es habitual que se conserve la vegetación a lo largo de los arroyos. De tal manera que en la región puede observarse un mosaico de potreros activos e inactivos, parches de vegetación en sucesión secundaria, fragmentos con vegetación primaria y vegetación riparia (Warkentin, Greenberg & Ortiz 1995).

Una de las estrategias más empleadas para el mantenimiento de la conectividad en paisajes fragmentados es el establecimiento y conservación de los corredores de vida silvestre, los cuáles se definen como elementos lineales del paisaje que conectan dos o más parches de hábitat que han estado conectados en tiempo histórico y funcionan como un conducto para organismos (Soule & Gilpin 1991). Los elementos lineales de paisajes fragmentados, tales como cercas vivas y corredores de vegetación riparia, son importantes para la comunidad animal ya que proporcionan mayor disponibilidad de recursos, funcionan como rutas de vuelo, proveen sitios de refugio para protección contra depredadores y condiciones climáticas adecuadas (Cosson, Pons & Masson 1999; Estrada & Coates-Estrada 2001; Medina *et al.* 2007).

Vegetación riparia y biodiversidad en paisajes fragmentados

Las zonas de vegetación riparia son el intervalo entre sistemas terrestres y acuáticos, albergan una gran variedad de especies de flora y fauna, y muchas de ésas están restringidas a estas zonas (Naiman, Decamps & Pollock 1993; Sabo *et al.* 2005). La vegetación riparia provee numerosos servicios ecológicos, no sólo como hábitat para la fauna, sino también como control de la erosión, control de inundaciones y mantenimiento de los ciclos biogeoquímicos (Naiman *et al.* 1993). Además, son reconocidos como hábitat para diversas especies, y como corredores de organismos terrestres y voladores, fomentando la formación de redes de dispersión (Estrada & Coates-Estrada 2001). Se ha documentado que la composición de especies y densidad de fauna difiere considerablemente entre franjas de vegetación riparia y la matriz agropecuaria circundante (Warkentin *et al.* 1995; Pinto & Keitt 2008). Por lo anterior, en paisajes agrícolas, la conservación y manejo de las zonas de vegetación riparia parece un método eficaz y poco costoso para el mantenimiento de la diversidad biológica en general (Jobin *et al.* 2004). Diversos estudios corroboran la importancia de la vegetación riparia como hábitat para la comunidad de murciélagos en paisajes agrícolas y coinciden en recomendar el mantenimiento de una variedad y extensión de zonas de vegetación riparia para promover la conservación del mayor número de especies de murciélagos (Naiman *et al.* 1993; Harvey *et al.* 2005; Lloyd, Law & Goldingay 2006).

Importancia de los murciélagos en los ecosistemas Neotropicales

Los murciélagos son particularmente importantes en los Neotrópicos ya que constituyen entre el 40 y 50% de las especies de mamíferos, contribuyendo a la alta diversidad y riqueza de especies de mamíferos en las zonas neotropicales (Nowak 1991; Fenton *et al.* 1992). Además, comprenden un amplio espectro trófico lo que los hace primordiales en procesos como la regeneración debido a su participación en la dispersión de semillas (Whittaker & Jones 1994; Kelm, Wiesner & Helversen 2008), polinización (Lobo, Quesada & Stoner 2005) y control de las poblaciones de artrópodos y quizás de algunos vertebrados pequeños (Kalka & Kalko 2005; Williams-Guillén, Perfecto & Vandermeer 2008). Se ha demostrado que la fragmentación del paisaje modifica la disponibilidad de sitios para percha y refugio además de las zonas de forrajeo de los murciélagos, lo que propicia la reducción de sus poblaciones (Fenton *et al.* 1992; Cosson *et al.* 1999; Medellín, Equihua & Amin 2000). Sin embargo, estos efectos negativos pueden atenuarse cuando existe conectividad entre fragmentos mediante corredores lineales, que actúan como "trampolines" y permiten el desplazamiento e intercambio de la fauna entre fragmentos (Estrada & Coates-Estrada 2001). La conectividad ecológica o funcional de un paisaje, se define como la capacidad del territorio para permitir los desplazamientos de los organismos entre parches con recursos (Taylor, Fahrig & Henein

1993). Cuándo la disminución de la movilidad de los organismos es significativa, se produce la subdivisión espacial de las poblaciones naturales, lo que a menudo puede tener un efecto negativo en las especie al encontrase más vulnerable a la fluctuaciones, catástrofes ambientales y a la estocasticidad demográfica, así como a ser más proclives al deterioro genético (Primack 1993).

En varios ecosistemas a diferentes latitudes, se ha encontrado que la presencia de vegetación riparia y cercas vivas favorece a diferentes especies de murciélagos ofreciendo hábitat importante por lo que aumenta la diversidad de especies y la actividad de forrajeo dentro de la matriz agrícola (Fig. 1). Particularmente, trabajos desarrollados en bosques templados, han registrado la importancia de los ríos y vegetación riparia para la comunidad de murciélagos del gremio insectívoro (Racey 1998; Fukui *et al.* 2006; Lloyd *et al.* 2006; Lundy & Montgomery 2010). Por ejemplo, estudios realizados en Europa han identificado relaciones positivas entre la comunidad de murciélagos y los elementos lineales del paisaje. Se ha reportado que los murciélagos utilizan elementos como cercas vivas, vegetación riparia y corredores arbolados como zonas de vuelo en lugar de volar a través de áreas abiertas (Walsh & Harris 1996; Racey 1998; Smith & Racey 2008; Abbott, Sleeman & Harrison 2009) (Fig. 1).

También, se ha observado gran impacto sobre la actividad de forrajeo de murciélagos debido a cambios relativamente pequeños en la estructura y calidad de las zonas de vegetación riparia dentro de paisajes urbanos, además, es posible cuantificar la actividad como medida del impacto de la calidad del hábitat ripario sobre la diversidad en el sistema fluvial completo (Scott *et al.* 2010); por lo que se sugiere que las estrategias de conservación y manejo se centren en el mantenimiento de la complejidad estructural de la vegetación riparia para promover zonas de forrajeo para la mayor cantidad de especies de murciélagos (Ober & Hayes 2008). En paisajes con producción forestal la comunidad de murciélagos favorece, mediante el mantenimiento de senderos y zonas de vegetación riparia como zonas de forrajeo, la regeneración de bosques y el mantenimiento de la diversidad de especies vegetales (Law & Chidel 2002; Lloyd *et al.* 2006).También, se ha observado gran impacto sobre la actividad de forrajeo de murciélagos debido a cambios relativamente pequeños en la estructura y calidad de las zonas de vegetación riparia dentro de paisajes urbanos, además, es posible cuantificar la actividad como medida del impacto de la calidad del hábitat ripario sobre la diversidad en el sistema fluvial completo (Scott *et al.* 2010); por lo que se sugiere que las estrategias de conservación y manejo se centren en el mantenimiento de la complejidad estructural de la vegetación riparia para promover zonas de forrajeo para la mayor cantidad de especies de murciélagos (Ober & Hayes 2008). En paisajes con producción forestal, la comunidad de murciélagos favorece la regeneración de bosques y el mantenimiento de la diversidad de especies, mediante el mantenimiento de senderos y zonas de vegetación riparia como zonas de forrajeo (Law & Chidel 2002; Lloyd *et al.* 2006)

En los bosques tropicales, elementos del paisaje como cercas vivas, árboles aislados y vegetación riparia dentro de una matriz agropecuaria, rompen con la homogeneidad de las áreas abiertas para el establecimiento de potreros y ayudan a mantener la diversidad de especies de murciélagos, además promueven la conectividad sirviéndoles como trampolines hacia parches aislados de vegetación primaria (Estrada &

Coates-Estrada 2001; Galindo-González & Sosa 2003; Chacón & Harvey 2006). Dentro de paisajes agrícolas en regiones tropicales la presencia de especies de plantas de sucesión secundaria como *Piper, Cecropia* y *Ficus* en vegetación riparia y cercas vivas favorecen la actividad de murciélagos frugívoros y aumentan la abundancia de individuos (Griscom, Kalko & Ashton 2007). Se sugiere que los agropaisajes que mantienen cobertura vegetal heterogénea pueden mantener un ensamblaje diverso de quirópteros (Medina *et al.* 2007).

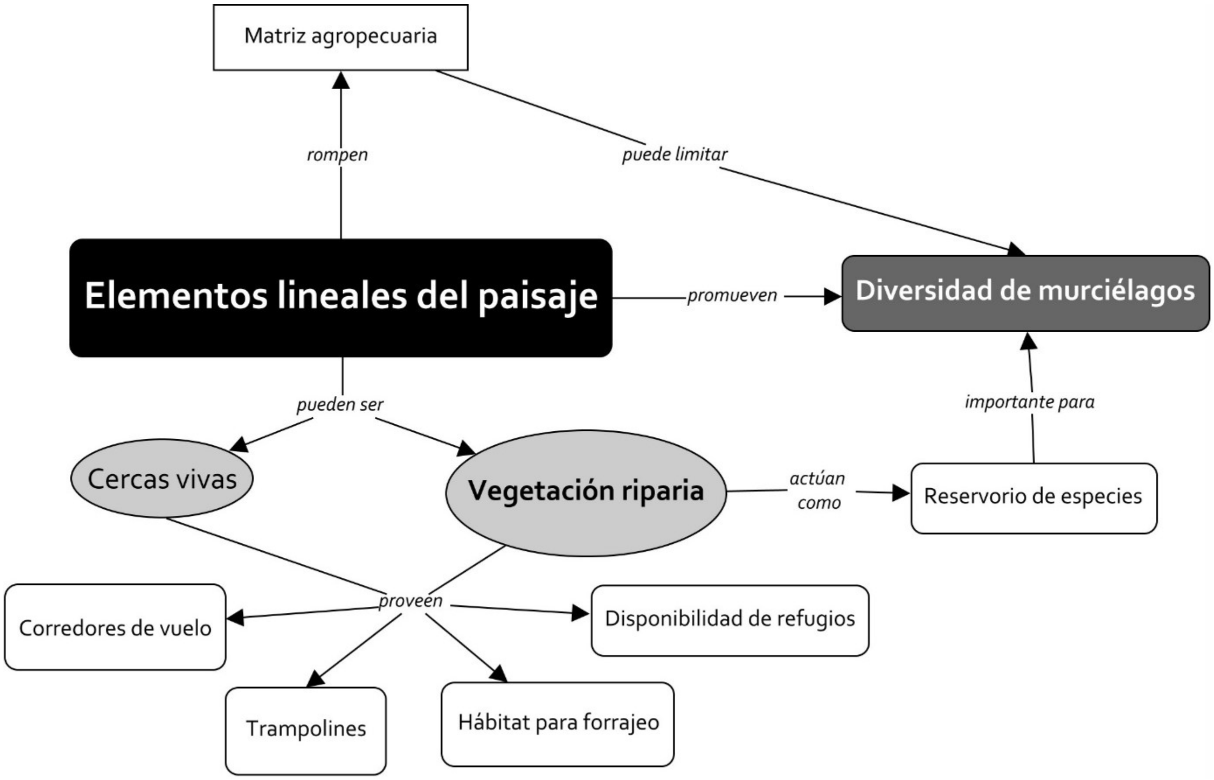

Figura 1. Principales efectos de los elementos lineales de paisajes agropecuarios sobre la comunidad de murciélagos

Perturbación del hábitat y su efecto en las comunidades de murciélagos

La perturbación del hábitat puede modificar la comunidad de murciélagos debido a mortalidad y/o extinciones locales a causa de actividades como deforestación e incendios (efectos directos) y cambios en los patrones demográficos y comportamiento de los quirópteros (efectos indirectos) (Figura 2). La mayoría de los estudios acerca de los efectos que tiene la matriz agropecuaria sobre la comunidad de murciélagos se centran en las respuestas a nivel de especie (inter-específicos) mientras que la potencial importancia de los cambios intra-específicos son ignorados (Lintott *et al.* 2014). Las alteraciones de la distribución espacial de recursos provocadas por la fragmentación de hábitat, resultan en cambios en los patrones demográficos de algunas especies de acuerdo a la plasticidad específica de las mismas (Bender, Contreras, Fahrig 1998; Nupp & Swihart 2000). Se ha observado que las diferencias biológico/metabólicas de machos y hembras de la misma especie ocasiona segregación de uso de hábitat y/o competencia (Lemaître *et al.* 2014; Lintott *et al.* 2014; Beerman *et al.* 2016). A pesar de que los murciélagos no presentan dimorfismo sexual, la mayoría de las especies exhiben una marcada segregación sexual durante la gestación y crianza (Senior, Butlin & Altringham 2005; Sgroi & Wilkins 2010; Encarnação 2012). Por ejemplo, las hembras tienen mayor consumo energético debido a la reproducción (*e.g*. gestación, lactancia) y suelen visitar con menor frecuencia ambientes con recursos alimenticios limitados (Ramos Pereira *et al.* 2009)

Por otra parte, históricamente se ha utilizado la diversidad taxonómica (riqueza de especies presentes en un área dada) como métrica clásica para estimar la biodiversidad

(Petchey & Gaston 2002), sin embargo, la diversidad funcional definido como el valor y rango de los rasgos funcionales de los organismos en un ecosistema dado, refleja interacciones no solamente a nivel de población y comunidad sino que también muestra la relaciones de las especies con el hábitat, proporcionando un espectro más amplio de las interacciones en los ecosistemas (Tilman 2001; Villéger, Mason & Mouillot 2008; Wordley *et al.* 2017). El concepto de filtrado de atributos sugiere que las características del hábitat y los factores ambientales afectan los patrones de biodiversidad actuando como un embudo que favorece los atributos de ciertas especies (Villéger *et al.* 2008). El análisis de diversidad funcional permite medir cuáles atributos son filtrados por el hábitat, lo cual proporciona información sobre las variables abióticas que permiten la presencia de ciertas especies en un hábitat determinado (Meyer *et al.* 2008; Hanspach *et al.* 2012; Farneda *et al.* 2015).Por otra parte, comparado con la diversidad taxonómica, la diversidad funcional refleja interacciones no solamente a nivel de población y comunidad sino que también muestra la relaciones de las especies con el hábitat, proporcionando un espectro más amplio de las interacciones en los ecosistemas (Villéger *et al.* 2008; Wordley *et al.* 2017). El concepto de filtrado de atributos sugiere que las características del hábitat y los factores ambientales afectan los patrones de biodiversidad actuando como un embudo que favorece los atributos de ciertas especies (Villéger *et al.* 2008). El análisis de diversidad funcional permite medir cuáles atributos son filtrados por el hábitat, lo cual proporciona información sobre las variables abióticas que permiten la presencia de ciertas especies en un hábitat determinado (Meyer *et al.* 2008; Hanspach *et al.* 2012; Farneda *et al.* 2015).

Entender las relaciones entre las características ecológicas y la sensibilidad de las especies a los diferentes tipos de hábitat puede generar importantes predicciones acerca de cuáles especies tienen mayor probabilidad de permanencia (Jennings & Pocock 2009). Dada la matriz agropecuaria actual en Mesoamérica, las zonas de vegetación riparia pueden representar un importante refugio para una gran variedad de taxa y procesos ecosistémicos. Es por esto que el presente trabajo pretende incluir las características inter e intraespecíficas que determinan la relación de la comunidad de murciélagos con el hábitat fragmentado en la región de la selva Lacandona en Chiapas, México. Obtener información de la utilización de las zonas de vegetación riparia por los murciélagos hábitats fragmentados y su repercusión en la dinámica del ecosistema es esencial para el desarrollo de programas de conservación y restauración de ecosistemas riparios y evitar el deterioro de las poblaciones y de la diversidad de especies de quirópteros.

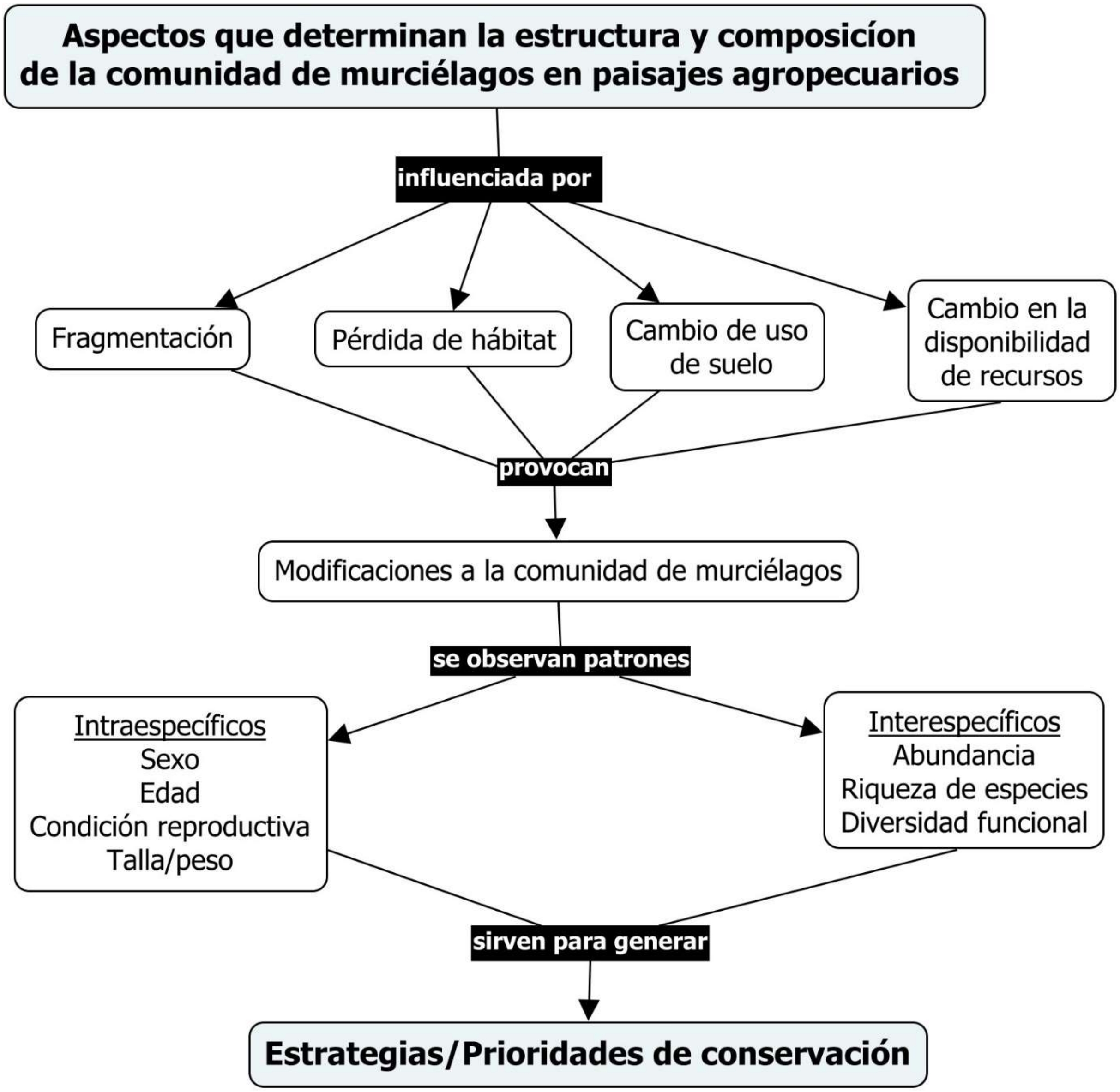

Figura 2. Relación de los factores externos e internos que modifican la estructura de la comunidad de murciélagos.

El presente trabajo de investigación tiene como **objetivo general** documentar la importancia de las zonas de vegetación riparia para las comunidades de murciélagos y determinar qué variables ligadas a la estructura de la vegetación riparia determinan la estructura y composición de la comunidad de murciélagos en un paisaje agropecuario en la región de la selva Lacandona, México.

Como **hipótesis general** se plantea que la comunidad de murciélagos presente en paisajes agropecuarios con distintas coberturas de vegetación se enfrentan a una serie de cambios en la disponibilidad de hábitat, recursos y en la estructura y composición del paisaje, para hacer frente a dichos cambios en las condiciones bióticas y abióticas, muestran adaptaciones. Algunas de estas adaptaciones se reflejan en la variación de la abundancia, diversidad de gremios tróficos y de grupos funcionales, además de la estructura de sexos y edades. Específicamente la vegetación riparia dentro de paisajes agropecuarios posee características estructurales de la vegetación más complejas en comparación con el resto de la matriz, lo que le confiere mayor concentración de recursos alimenticios (e. g. insectos y frutos), y un aumento en la disponibilidad de refugios. Por lo anterior expresado, se espera que la vegetación riparia presente mayor abundancia y riqueza de especies y mayor tasa de captura de hembras. Se espera también que la complejidad estructural de la vegetación explique la variación en la diversidad funciona y en los sitios de pastizal de encuentre la menor diversidad funcional y aumenten la cantidad de atributos funcionales que están siendo filtrados

El **capítulo I** se centra en conocer la influencia del bosque ripario en la distribución, riqueza y densidad de murciélagos filostómidos en un paisaje agropecuario en el bosque tropical húmedo de México. Para esto, evaluamos los siguientes aspectos 1) atributos de la comunidad de murciélagos (*e. g.*, composición de especies y densidad) tanto en hábitat ripario como no ripario; 2) la relación de la complejidad estructural de la vegetación con la composición de especies; y 3) la distribución de especies, géneros y subfamilias en los diferentes tipos de hábitat con la finalidad de identificar posibles taxones indicadores.

En el **capítulo II** se compararon las tasas de captura de hembras y machos de las seis especies más abundantes de la comunidad de murciélagos en los diferentes tipos de hábitat, con la finalidad de identificar los cambios en la estructura social de la comunidad de murciélagos, documentando si existe preferencia por hembras y machos asociada al hábitat ripario y a atributos específicos de la vegetación en una matriz agropecuaria del trópico mexicano.

El **capítulo III** utiliza un enfoque funcional empleando los atributos de importancia ecológica para los murciélagos y evaluando los componentes de la diversidad funcional, con el objetivo de evaluar los cambios en la diversidad funcional de la comunidad de murciélagos para los diferentes tipos de hábitat. Además determinar que rasgos funcionales están siendo filtrados por los diferentes tipos de hábitat y poder identificar los atributos que afectan la sensibilidad de las especies a la actividad agropecuaria.

Finalmente en la D**iscusión General** se presenta una síntesis sobre los principales resultados obtenidos del trabajo de investigación. Con base en esto se proponen algunas acciones de manejo dirigidas hacia los bosques riparios que pretenden promover y conservar la diversidad de murciélagos en paisajes agropecuarios a largo plazo.

LITERATURA CITADA

Abbott, I.M., Sleeman, D.P. & Harrison, S. (2009) Bat activity affected by sewage effluent in Irish rivers. *Biological Conservation*, **142**, 2904–2914.

Adams, R.A. & Hayes, M.A. (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, **77**, 1115–1121.

Aguiar, L.M.S., Bernard, E. & Machado, R.B. (2014) Habitat use and movements of Glossophaga soricina and Lonchophylla dekeyseri (Chiroptera�: Phyllostomidae) in a Neotropical savannah. *Zoologia*, **31**, 223–229.

Altringham, J.D. (2011) *Bats: From Evolution to Conservation*, 2nd ed. Oxford University Press, Oxford.

Alvarez, T. & Sánchez-Casas, N. (1999) Diferenciación alimentaria entre los sexos de Glossophaga soricina (Chiroptera: Phyllostomidae) en México. *Revista de Biologia Tropical*, **47**, 1129–1136.

Arita, H.T. & Fenton, M.B. (1997) Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology and Evolution*, **12**, 53–58.

Arita, H.T. & Santos-del-Prado, K. (1999) Conservation Biology of Nectar-Feeding Bats in Mexico. *Journal of Mammalogy*, **80**, 31–41.

Arnone, I.S., Trajano, E., Pulchério-Leite, A. & Passos, F.C. (2016) Long-distance movement by a great fruit-eating bat, Artibeus lituratus (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica*, **16**, 1–6.

Barclay, R.M.R. (1989) The effect of reproductive condition on the foraging behavior of female hoary bats, Lasirurus cinereus. *Behavioral Ecology and Sociobiology*, **24**, 31–37.

Barlow, K.E. (1997) The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology*, **243**, 597–609.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2014) Fitting linear mixed-effects models using lme4 Douglas. *Journal of Statistical Software*, 1–51.

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2016) Sexual segregation when foraging in an extremely social killer whale population. *Behavioral Ecology and Sociobiology*, **70**, 189–198.

Bender, D. J., Contreras, T. A., Fahrig, L. (1998) Habitat Loss and Population Decline: a Meta-Analysis of the Patch Size Effect. *Ecology*, **79**, 517–533.

Bernard, E. & Fenton, M.B. (2002) Species diversity of bats (Mammalia: Chiroptera) in forest fragments , primar ...

Bhagwat, S.A., Willis, K.J., Birks, H.J.B. & Whittaker, R.J. (2008) Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution*, **23**, 261–267.

Bianconi, G. V, Mikich, S.B. & Pedro, W.A. (2006) Movements of bats (Mammalia , Chiroptera) in Movements Chiropteroptera) Atlantic For est remnants in southern Brazil Forest remnants southern Brazil. *Revista Brasileira de Zoologia*, **23**, 1199–1206.

van Breugel, M., Martínez-Ramos, M., Bongers, F., Martinez-Ramos, M. & Bongers, F. (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, **22**, 663–674.

Broders, H.G., Forbes, G.J., Woodley, S. & Thompson, I.D. (2006) Range extent and stand selection for roosting and foraging in forest-dwelling Northern Long-eared Bats and Little Brown Bats in the Greater Fundy ecosystem, New Brunswick. *Journal of Wildlife Management*, **70**, 1174–1184.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Castro-Luna, A.A., Sosa, V.J. & Castillo-Campos, G. (2007) Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, **10**, 219–228.

Chacón, M. & Harvey, C.A. (2006) Live fences and landscape connectivity in a neotropical agricultural landscape. *Agroforestry Systems*, **68**, 15–26.

Charles-Dominique, P. (1991) Feeding strategy and activity budget of the frugivorous bat Carollia perspicillata (Chiroptera: Phyllostomidae) in French Guiana. *Journal of Tropical Ecology*, **7**, 243.

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, **21**, 523–533.

Comisión Federal de Electricidad. (2006) *División Hidrométrica Sureste.* Estación Lacantún, Marqués de Comillas, Chiapas, México.

CONAFOR. (2016) *Manual de Mejores Prácticas de Manejo Forestal Para La Conservación de La Biodiversidad En Ecosistemas Tropicales de La Región Sureste de México*. Ciudad de México.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A Trait-Based Test for Habitat Filtering: Convex Hull Volume. , **87**, 1465–1471.

Cosson, J.F., Pons, J.M. & Masson, D. (1999) Effects of Forest Fragmentation on Frugivorous and Nectarivorous Bats in French Guiana. , 515–534.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Denzinger, A. & Schnitzler, H.U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, **4 JUL**, 1–15.

Diamond, G.F. & Diamond, J.M. (2014) Bats and Mines: Evaluating Townsend's Big-Eared

Bat (Corynorhinus townsendii) Maternity Colony Behavioral Response to Gating. *Western North American Naturalist VO - 74*, **74**, 416.

Dietz, M., Kalko, E.K. V & Encarnação, J.A. (2006) Small scale distribution patterns of female and male Daubenton's bats (Myotis daubentonii). *Acta Chiropterologica*, **8**, 403–415.

Dirzo, R. & Raven, P.H. (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, **28**, 137–167.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, **23**, 849–860.

Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S. & Hamer, K.C. (2014) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation*, **17**, 163–173.

Encarnação, J.A. (2012) Spatiotemporal pattern of local sexual segregation in a tree-dwelling temperate bat Myotis daubentonii. *Journal of Ethology*, **30**, 271–278.

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

Estrada, A. & Coates-Estrada, R. (2002) Bats in continous forest, forest fragments and in an agricultural mosiac habitat island at Los Tuxtlas, Mexico. *Biodiversity and*

Conservation, **103**, 237–245.

Evelyn, M.J. & Stiles, D. a. (2003) Roosting requirements of two frugivorous bats (Sturnira lilium and Arbiteus intermedius) in fragmented Neotropical forest. *Biotropica*, **35**, 405–418.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C., Chazdon, R.L. & Sanchun, A. (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, **8**, 034017.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, **52**, 1381–1391.

Fenton, A.M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K., Syme, D.M. & Adkins, B. (1992) Phyllostomid Bats (Chiroptera : Phyllostomidae) as Indicators of Habitat Disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Frank, H.K., Mendenhall, C.D., Judson, S.D., Daily, G.C. & Hadly, E.A. (2016) Anthropogenic impacts on Costa Rican bat parasitism are sex specific. *Ecology and Evolution*, **6**, 4898–4909.

Freudmann, A., Mollik, P., Tschapka, M. & Schulze, C.H. (2015) Impacts of oil palm agriculture on phyllostomid bat assemblages. *Biodiversity and Conservation*, **24**, 3583–3599.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, **75**, 1252–1258.

Galindo-González, J. (1998) Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. *Acta Zoologica Mexicana*, 57–74.

Galindo-González, J. & Sosa, V.J. (2003) Frugivorous Bats in Isolated Trees and Riparian Vegetation Associated With Human-Made Pastures in a Fragmented Tropical Landscape. *The Southwestern Naturalist*, **48**, 579–589.

Garcia-Martínez, M.A., Escobar-Sarria, F., Pez-Barrera, F.L., Castano-Meneses, G. & Lez, J.E.V.G. (2015) Value of Riparian Vegetation Remnants for Leaf-Litter Ants (Hymenoptera: Formicidae) in a Human-Dominated Landscape in Central Veracruz, Mexico. *Environmental Entomology*, **44**, 1488–1497.

García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez, A.E. & Ávila-Gómez, E.S. (2016) Deforestation Impacts on Bat Functional

Diversity in Tropical Landscapes. *Plos One*, **11**, e0166765.

Gorresen, P.M. & Willig, M.R. (2004) Landscape Responses of Bats To Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*, **85**, 688–697.

Grau, H.R. & Aide, M. (2008) Globalization and land-use transitions in Latin America. *Ecology and Society*, **13**.

Griscom, H.P., Kalko, E.K. V & Ashton, M.S. (2007) Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica*, **39**, 278–282.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed : evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii ? , 540–548.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: A case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842–850.

Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñóz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., Navas, A., Saenz, J., Sánchez, D., Medina, A., Vilchez, S., Hernández, B., Perez, A., Ruiz, F., López, F., Lang, I. & Sinclair, F.L. (2005) Contribution of live fences to the ecological integrity of agricultural landscapes. *Agriculture, Ecosystems and Environment*, **111**, 200–230.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation\t. *Biodiversity and Conservation*, **13**, 207–251.

Henry, M. & Kalko, E.K. V. (2007) Froraging Strategy and Breeding Constraints of Rhynophyla Pumilio (PHYLLOSTOMIDAE) in the Amazon Lowlands. *Journal of Mammalogy*, **88**, 81–93.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) *Global Status Survey and Conservation Action Plan: Microchiropteran Bats*.

INE. (2000) *Programa de Manejo Reserva de La Biósfera Montes Azulez, México.* México.

Instituto Nacional de Ecología. (2000) *Programa de Manejo de La Reserva de La Biosfera Montes Azules*, 1a. Enkidu Editores, S.A. de C.V., México, D.F.

Istvanko, D.R., Risch, T.S. & Rolland, V. (2016) Sex-specific foraging habits and roost characteristics of Nycticeius humeralis in north-central Arkansas. *Journal of Mammalogy*, **97**, 1–9.

Jennings, N.V., Parson, S., Barlow, K.E. & Gannon, M.R. (2004) Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterologica*, **6**, 75–90.

Jennings, N. & Pocock, M.J.O. (2009) Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conservation Biology*, **23**, 1195–1203.

Jobin, B., Bélanger, L., Boutin, C. & Maisonneuve, C. (2004) Conservation value of agricultural riparian strips in the Boyer River watershed, Québec (Canada). *Agriculture, Ecosystems and Environment*, **103**, 413–423.

De Jong, B.H.J., Ochoa-Goana, S., Castillo-Santiago, M.A., Ramirez-Marcial, N. & Cairns, M.A. (2000) Carbon flux and patterns of land-use/land-cover change in het Selva Lacandona, Mexico. *A Journal of the Human Environment*, **29**, 504–511.

Jong, D. & Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13**_ _, 275–280.

Jung, K., Kalko, E.K. V & Von Helversen, O. (2007) Echolocation calls in Central American emballonurid bats: Signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.

Kalka, M. & Kalko, E.K. V. (2005) Gleaning bats as underestimated predators of herbivorous insects: diet of Micronycteris microtis (Phyllostomidae) in Panama. *Journal of Tropical Ecology*, **22**, 1.

Kalko, E.K. V & Handley, C.O. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.

Keen, R. & Hitchcock, H.H.B. (1980) Survival and longevity of the little brown bat (Myotis lucifugus) in southeastern Ontario. *Journal of Mammalogy*, **61**, 1–7.

Kelm, D.H., Wiesner, K.R. & Helversen, O. Von. (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conservation Biology*, **22**, 733–741.

Klingbeil, B.T. & Willig, M.R. (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest Brian. *Journal of Applied Ecology*, **46**, 203–213.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, **119**, 1654–1664.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kurta, A. & Matson, J.O.. (1980) Disproportionate Sex Ratio in the Big Brown Bat (Eptesicus fuscus). , **104**, 367–369.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015a) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015b) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**, 903–913.

de la Peña-Cuéllar, E., Stoner, K.E., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2012) Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. *Biodiversity and Conservation*, **21**, 1381–1397.

de la Torre, J.A., Núñez, J.M. & Medellín, R.A. (2017) Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. *Biological Conservation*, **206**, 270–282.

Lande, R. (1987) Extinction Thresholds in Demographic Models of Territorial Populations. *The American Naturalist*, **130**, 624–635.

Laurance, W.F. (1991) Society for Conservation Biology Ecological Correlates of Extinction Proneness in Australian Tropical Rain Forest Mammals. *Conservation Biology*, **5**, 79–89.

Laurance, W., Bierregaard, R. & Moritz, C. (1997) *Tropical Forest Remnants : Ecology, Management, and Conservation of Fragmented Communities*. University Of Chicago Press.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, **16**, 605–618.

Law, B. & Chidel, M. (2002) Tracks and Riparian Zones Facilitate the Use of Australian Regrowth Forest by Insectivorous Bats. *The Journal of Applied Ecology*, **39**, 605–617.

Lebrija-trejos, E., Pérez-garcía, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by : Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly. *Ecology*, **91**, 386–398.

Lemaître, J.-F., Gaillard, J.-M., Pemberton, J.M., Clutton-Brock, T.H. & Nussey, D.H. (2014) Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer. *Proceedings. Biological sciences / The Royal Society*, **281**, 20140792-.

Lenth, R.V. (2014) lsmeans: Least-square means.

Lintott, P.R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R.J., Olley, L. & Park, K.J. (2014) City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal society open science*, **1**, 1–8.

Lloyd, A., Law, B. & Goldingay, R. (2006) Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation*, **129**, 207–220.

Lobo, J.A., Quesada, M. & Stoner, K.E. (2005) Effects of pollination by bats on the mating system of Ceiba pentandra (Bombacaceae) populations in two tropical life zones in Costa Rica. *American Journal of Botany*, **92**, 370–376.

Lundy, M. & Montgomery, I. (2010) Summer habitat associations of bats between riparian landscapes and within riparian areas. *European Journal of Wildlife Research*, **56**, 385–394.

Martínez-Ramos, M. & García-Orth, X. (2007) Sucesión ecológica y restauración de las selvas húmedas. *Bol. Soc. Bot. Méx*, **80**.

Mayaux, P., Holmgren, P., Achard, F., Eva, H.D., Stibig, H.-J.J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*,

360, 373–84.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesk, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.

McCracken, G.F. & Wilkinson, G.S. (2000) Bat Mating Systems. *Reproductive Biology of Bats*, pp. 321–362.

Mcgill, J. & Kalko, V. (2015) Climate , habitat , and species interactions at different scales determine the structure of a Neotropical bat community Author (s): Sergio Estrada-Villegas , Brian J . McGill and Elisabeth K . V . Kalko Published by : Ecological Society of America Stabl. , **93**, 1183–1193.

Medellin, R. a. (1994) Mammal Diversity and Conservation in the Selva-Lacandona, Chiapas, Mexico. *Conservation Biology*, **8**, 780–799.

Medellín, R. a, Equihua, M. & Amin, M. a. (2000) Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests\rDiversidad y Abundancia de Murciélagos como Indicadores de Perturbaciones en Selvas Húmedas Neotropicales. *Conservation Biology*, **14**, 1666–1675.

Medellín, R.A., Equihua, M. & Amin, M.A. (2011) *Identificación de Los Murciélagos de México: Clave de Campo*. México, D.F.

Medina, A., Harvey, C. a, Sánchez, D., Vílchez, S. & Hernández, B. (2007) Bat diversity and movement in a Neotropical agricultural landscape. *Biotropica*, **39**, 120–128.

Meli, P., Ruiz, L., Aguilar, R., Rabasa, A., Rey-Benayas, J.M. & Carabias, J. (2017) Bosques ribereños del trópico húmedo de México: Un caso de estudio and aspectos críticos para una restauración exitosa. *Madera Bosques*, **23**, 181–193.

de Mello, M.A.R. & Fernandez, F.A.S. (2000) Reproductive ecology of the bat Carollia perspicillata (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest. *International Journal of Mammalian Biology*, **65**, 340–349.

Meyer, C.F.J., Fr??nd, J., Lizano, W.P. & Kalko, E.K. V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.

Meyer, C.F.J. & Kalko, E.K. V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.

Miller, K., Chang, E. & Johnson, N. (2001) *Defining Common Ground for the Mesoamerican Biological Corridor*.

Montoya Gómez, G., Hernández Ruiz, J.F., Velasco Pérez, A., Reygadas, L. & Ramos Maza, T. (2006) Organización comunitaria para la conservación forestal: estudio de caso en la Selva Lacandona de Chiapas, México. *Papeles de población*, **14**, 11.

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. , 149–158.

Morrison, D.W. (1978) Lunar phobia in a neotropical fruit bat, Artibevs jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852–855.

Mouillot, D., Graham, N.A.J., Vill??ger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Muench, C. & Martínez-Ramos, M. (2016) Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico. *Tropical Conservation Science*, **9**, 178–202.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecological Applications*, **3**, 209–212.

Nardone, V., Cistrone, L., Di Salvo, I., Ariano, A., Migliozzi, A., Allegrini, C., Ancillotto, L., Fulco, A. & Russo, D. (2015) How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat Myotis daubentonii. *PLoS ONE*, **10**, 1–15.

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **316**, 335–427.

Nowak, R. (1991) *Walker's Mammals of the World*. Johns Hopkins Univ Pr.

Nupp, T. & Swihart, R. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512–526.

Ober, H.K. & Hayes, J.P. (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, **256**, 1124–1132.

Ortega, J. & Arita, H.T. (1999) Structure and Social dynamics of harem groups in Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, **80**, 1173–1185.

Ortega, J. & Maldonado, J.E. (2006) Female interactions in harem groups of the Jamaican fruit-eating bat, Artibeus jamaicensis (Chiroptera : Phyllostomidae). *Acta Chiropterologica*, **8**, 485–495.

Ortiz-Ramírez, D., Lorenzo, C., Naranjo, E. & León-Paniagua, L. (2006) Selección de refugios por tres especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en la Selva Lacandona, Chiapas, México. *Revista Mexicana de Biodiversidad*, **77**, 261–270.

Perry, R.W., Carter, S.A. & Thill, R.E. (2010) Temporal Patterns in Capture Rate and Sex Ratio of Forest Bats in Arkansas. *American Midland Naturalist*, **164**, 270–282.

Perry, R.W., Thill, R.E. & Carter, S.A. (2007) Sex-specific roost selection by adult red bats in a diverse forested landscape. *Forest Ecology and Management*, **253**, 48–55.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Pinto, N. & Keitt, T.H. (2008) Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, **117**, 1725–1731.

Presley, S.J., Willig, M.R., Wunderle, J.M. & Saldanha, L.N. (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology*, **45**, 14–25.

Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates Sunderland, Massachusetts.

Racey, P.A. (1998) The importance of the riparian environment as a habitat for British bats. *Symposia of the Zoological Society of London*, pp. 69–91. London: The Society, 1960-1999.

Racey, P.A. & Speakman, J.R. (1987) The energy costs of pregnancy and lactation in heterothermic bats. *Symposia of the zoological society of London*, pp. 107–125.

Ramos Pereira, M.J., Marques, J.T. & Palmeirim, J.M. (2010) Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in amazonian forests. *Biotropica*, **42**, 680–687.

Ramos Pereira, M.J., Marques, J.T., Santana, J., Santos, C.D., Valsecchi, J., De Queiroz, H.L., Beja, P. & Palmeirim, J.M. (2009) Structuring of Amazonian bat assemblages: The roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, **78**, 1163–1171.

Rocha, R., Ferreira, D.F., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B., Palmeirim, J.M. & Meyer, C.F.J. (2017) Does sex matter ? Gender-specific responses to forest fragmentation in Neotropical bats. *Biotropica*, 1–10.

Russo, D., Cistrone, L., Garonna, A.P. & Jones, G. (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodiversity and Conservation*, **19**, 2501–2515.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Jani, A., Katz, G., Soykan, C., Watts, J., Welter, J., Ecology, S., Jan, N. & Heffernan, J.I.M. (2005) Riparian Zones Increase Regional Species Richness by Harboring Different , Not More , Species. *Ecology*, **86**, 56–62.

Safi, K., König, B. & Kerth, G. (2007) Sex differences in population genetics, home range size and habitat use of the parti-colored bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biological Conservation*, **137**, 28–36.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321–1333.

Scott, S.J., McLaren, G., Jones, G. & Harris, S. (2010) The impact of riparian habitat quality on the foraging and activity of pipistrelle bats (Pipistrellus spp.). *Journal of Zoology*, **280**, 371–378.

Seaman, B.S. & Schulze, C.H. (2010) The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. *Biological Conservation*, **143**, 391–398.

Senior, P., Butlin, R.K. & Altringham, J.D. (2005) Sex and segregation in temperate bats.

Proceedings. Biological sciences / The Royal Society, **272**, 2467–73.

Sgroi, M.P. & Wilkins, K.T. (2010) Roosting Behavior of the Mexican Free-Tailed Bat (Tadarida Brasiliensis) in a Highway Overpass. *Western North American NaturaHst63*, **63**, 366–373.

Smith, P.G. & Racey, P.A. (2008) Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *Journal of Zoology*, **275**, 314–322.

Sosa, M., De Ascencao, A. & Soriano, P. (1996) Dieta y patrón reproductivo de Rhogessa minutilla (Chiroptera: Vespertilionidae) en una zona árida de Los Andes de Venezuela. *Revista de Biología Tropical*, **44**, 867–875.

Soule, M.E. & Gilpin, M.E. (1991) The teory of wildlife corridor capability. *Nature Conservation 2: The Role of Corridors* (eds D.A. Saunders & R.J. Hobbs), pp. 3–8. Surrey Beatty and Sons, Chipping Norton, Australia, New South Wales, Australia.

StrauB, A., Reeve, E., Randrianiaina, R.-D., Vences, M. & Glos, J. (2010) The world 's richest tadpole communities show functional redundancy and low functional diversity : ecological data on ecological data on Madagascar 's stream-dwelling amphibian larvae. *BMC Ecology*, **10**, 1–10.

Taylor, P.D., Fahrig, L. & Henein. (1993) Connectivity is a Vital Element of Landscape Structure. *Oikos*, **68**, 571–573.

Tilman, D. (2001) Functional Diversity. *Encyclopedia of Biodiversity*, pp. 587–596.

van Toor, M.L., Jaberg, C. & Safi, K. (2011) Integrating sex-specific habitat use for

conservation using habitat suitability models. *Animal Conservation*, **14**, 512–520.

Turner, I.M. (1996) Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Society*, **33**, 200–209.

La Val, R. (2017) Banding Returns and Activity Periods of Some Costa Rican Bats. *The Southwestern Naturalist*, **15**, 1–10.

Vandermeer, J. & Perfecto, I. (2007) The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, **21**, 274–277.

Villéger, Mason & Mouillot. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Ramos Miranda, J., Flores Hernández, D. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological applications*, **20**, 1512–1522.

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

Vleut, I., Levy-Tacher, S.I., Galindo-González, J., de Boer, W.F. & Ramírez-Marcial, N. (2012) Tropical rain-forest matrix quality affects bat assemblage structure in secondary forest patches. *Journal of Mammalogy*, **93**, 1469–1479.

Walsh, A.L. & Harris, S. (1996) Foraging Habitat Preferences of Vespertilionid Bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Warkentin, I.G., Greenberg, R. & Ortiz, J.S. (1995) Songbird use of Gallety Woodlands in

Recently Cleared and Older Settled Landscapes of the Selva Lacandona, Chiapas, Mexico. *Conservation Biology*, **9**, 1095–1106.

Wearmouth, V.J. & Sims, D.W. (2008) Sexual Segregation in Marine Fish , Reptiles , Birds and Mammals : Behaviour Patterns , Mechanisms and Conservation Implications., pp. 108–170.

Weller, T.J., Cryan, P.M. & O'Shea, T.J. (2009) Broadening the focus of bat conservation and research in the USA for the 21st century. *Endangered Species Research*, **8**, 129–145.

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245–258.

Williams-Guillén, K. & Perfecto, I. (2010) Effects of agricultural intensification on the bat assemblage in a coffee landscape in Chiapas, Mexico. *Biotropica*, **42**, 605–613.

Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008) Bats limit insects in a neotropical agroforestry system. *Science (New York, N.Y.)*, **320**, 70.

Willig, M., Presley, S.J., Bloch, C.P., Yanoviak, S.P., Díaz, M.M., Arias Chauca, L., Pacheco, V. & Weaver, S.C. (2007) Phyllostomid Bats of Lowland Amazonia: Effects of Habitat Alteration on Abundance. *Biotropica*, **39**, 737–746.

Wordley, C.F.R., Sankaran, M., Mudappa, D. & Altringham, J.D. (2017) Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biological Conservation*, **210**, 48–55.

Zarazúa-Carbajal, M., Avila-Cabadilla, L.D., Alvarez-Añorve, M.Y., Benítez-Malvido, J. & Stoner, K.E. (2017) Importance of riparian habitat for frugivorous bats in a tropical dry forest in western Mexico. *Journal of Tropical Ecology*, **33**, 74–82.

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J. & Martínez-Ramos, M. (2015) Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, **18**, 443–455.

CAPÍTULO I

STRUCTURE AND DIVERSITY OF PHYLLOSTOMID BAT ASSEMBLAGES ON RIPARIAN CORRIDORS IN A HUMAN-DOMINATED TROPICAL LANDSCAPE

Ecology and Evolution

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Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape

Erika de la Peña-Cuéllar[1], Julieta Benítez-Malvido[1], Luis Daniel Avila-Cabadilla[2], Miguel Martínez-Ramos[1] & Alejandro Estrada[3]

[1]Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Michoacán, México
[2]Escuela Nacional de Estudios Superiores, Universidad Nacional Autónoma de México, Morelia, Michoacán, México
[3]Estacion de Biología Tropical "Los Tuxtlas", Instituto de Biología, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

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Agricultural matrix, corridors, diversity, frugivores, indicator taxa.

Correspondence
Erika de la Peña-Cuéllar, Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Apartado Postal 27-3 (Xangari), Morelia, Michoacán 58190, México.
Tel:+52 443-322-2777; Fax: +52 443-322-2719;
E-mail: erikapc@cieco.unam.mx

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Abstract

Tropical forests around the world have been lost, mainly because of agricultural activities. Linear elements like riparian vegetation in fragmented tropical landscapes help maintain the native flora and fauna. Information about the role of riparian corridors as a reservoir of bat species, however, is scanty. We assessed the value of riparian corridors on the conservation of phyllostomid bat assemblage in an agricultural landscape of southern Mexico. For 2 years (2011–2013), mist-netting at ground level was carried out twice during the dry season (December to May) and twice during the wet season (June to November) in different habitats: (1) riparian corridors in mature forest, (2) riparian corridors in pasture, (3) continuous forest away from riparian vegetation, and (4) open pastures. Each habitat was replicated three times. To determine the influence of vegetation structure on bat assemblages, all trees ($\geq$10 cm dbh) were sampled in all habitats. Overall, 1752 individuals belonging to 28 species of Phyllostomidae were captured with Sternodermatinae being the most rich and abundant subfamily. Riparian corridors in mature forest and pastures had the greatest species richness and shared 65% of all species. Open pastures had the lowest richness and abundance of bats with no Phyllostominae species recorded. Six of the 18 species recorded could be considered as habitat indicators. There was a positive relationship between bat species composition and tree basal area. Our findings suggest that contrary to our expectations, bats with generalist habits and naturally abundant could be useful detector taxa of habitat modification, rather than bats strongly associated with undisturbed forest. Also in human-dominated landscapes, the maintenance of habitat elements such as large trees in riparian corridors can serve as reservoirs for bat species, especially for those that are strongly associated with undisturbed forest.

Introduction

Habitat loss and fragmentation are considered the most serious threats to biodiversity and the main cause of the current extinction crisis (Laurance and Bierregaard 1997). In tropical regions, many biodiversity hot spots have been converted to agricultural lands (Myers et al. 2000; Achard et al. 2002). In many of these landscapes, the presence of vegetation along streams is a common feature and is relatively resistant to agricultural practices and small-scale land use changes (Lundy and Montgomery 2010). Riparian habitats provide some of the most diverse and complex terrestrial habitats (Naiman et al. 1993). Especially, in fragmented landscapes, riparian vegetation contrasts with adjacent grassland areas as it provides the following landscape elements for the native biota: habitat for many species, corridors for flying and terrestrial animals, connectivity between forest fragments and for fostering network dispersion (Naiman et al. 2000; Estrada and Coates-Estrada 2001). In particular, bird species composition and density differ considerably between riparian vegetation and the surrounding agricultural matrix (Warkentin et al. 1995; Seaman and Schulze 2010). Similarly, bats use riparian vegetation as flyways during foraging activities, reducing the distance that they need to travel from and to their refuges (Daniel et al. 2008).

Intensification of agricultural practices in the tropics is likely to threaten the persistence of some bat species; nonetheless, the presence of landscape elements like live fences, isolated trees, and riparian vegetation disrupts the homogeneity of pastures and has been shown to be important in the maintenance of bat diversity (Harvey et al. 2006; Griscom et al. 2007; Medina et al. 2007). Riparian habitats provide flyways and foraging areas for bats, serving as stepping stones to isolated patches of primary vegetation. In addition, riparian zones offer important sources of water and food for bats (Estrada and Coates-Estrada 2001; Galindo-González and Sosa 2003).

Bats are widely studied because they play a crucial role in the ecosystem functioning as pollinators, seed dispersal agents and controllers of invertebrate and small vertebrate populations (Muscarella and Fleming 2007; Kalka et al. 2008; Kunz et al. 2011). Particularly in the Neotropics, bats are considered an important component of mammal biodiversity accounting for over 50% of the species (Medelln 1994). The response of bats to habitat loss in the Neotropics is ambiguous, compared to the Stenodermatinae (frugivore bats), and the Phyllostominae bats are very sensitive to disturbance and tend to decrease in degraded and fragmented habitats because of their limited range sizes, specialized resource needs (food and roosting), and because of their avoidance of open pastures (Kalko et al. 1999; Medellín et al. 2000; Schulze et al. 2000; Castro-Luna et al. 2007a; de la Peña-Cuéllar et al. 2012; García-Morales et al. 2013). We selected the Phyllostomidae family because it is the most species rich and functionally diverse bat family in the Neotropics. Furthermore, because of the broad spectrum of biological interactions in which they are involved, phyllostomids have been recognized as useful indicators of habitat quality (Fenton et al. 1992; Medellín et al. 2000; Jones et al. 2009).

In human-impacted landscapes, information about the importance of riparian vegetation in maintaining bat species diversity is crucial for understanding bat behavioral and ecological flexibility. In this framework, we recorded the richness and abundance of phyllostomid bats present in different habitat types within an agricultural matrix to determine the following: (1) bat assemblages attributes (i.e., species composition and species density) in riparian and nonriparian habitats; (2) the extent to which the structural complexity of the vegetation explains bat species composition; and (3) the distribution of species, genera and subfamilies in the different habitats in order to identify indicator taxa.

Methods

Study area and sampling sites

The study was conducted in the tropical rain forest region of Lacandona, Chiapas, Mexico. The original vegetation consists of semideciduous and lowland tropical rain forests. Mean annual temperature is 24°C, and average annual rainfall is 3000 mm with June to October as the wettest months (551 mm per month) and February to April as the driest months (<100 mm per month) (Breugel et al. 2006; CFE 2006). Deforestation of the region began in the 1970s, resulting in the reduction of closed forest from 95% in 1976 to 56% in 1996 (de Jong et al. 2000); only 36% of closed forest remains today (Carabias et al. 2008). The main practices of the region consist of grazing pastures, maize and other crops, and patches of secondary and old-growth forests (de Jong et al. 2000).

We sampled four different habitats: (1) riparian sites within mature continuous forest (RM); (2) riparian sites in open pastures (RP); (3) mature continuous forest away from riparian vegetation (MF); and (4) open pastures (P). Each habitat type was replicated three times, and sites were at least 1.5 km away from each other. Streams were all permanent (although with variable amounts of running water throughout the year); stream width varied from two to eight meters. Study sites in pastures were located in the fragmented landscape of the Marqués de Comillas municipality, on the south side of the Lacantún River. Mature continuous forest sites were located in the 330,000 ha Montes Azules Biosphere Reserve (MABR) on the north side of the river (16°04′N–90°45′ W; Fig. 1) (INE 2000).

Bat and vegetation sampling

Bat sampling was performed twice during the dry season (December to May) and two times during the wet season (June to November) for three consecutive years (2011, 2012, and 2013). Eighteen nights were sampled at RM, RP, and P habitats, and sixteen nights were sampled at the MF habitat. Bats were surveyed at all sites using the same standardized method. Five nets (12 m long × 2.6 m high) were set at ground level and were opened at dusk for four consecutive hours, which corresponds to the peak foraging time for most phyllostomid species (La Val 1970). The nets were arranged following three configurations located roughly 50 m apart: (1) one individual net and two pairs of nets were placed in the “L” position (two nets connected perpendicularly); (2) in the riparian habitats nets were located parallel and diagonally across the stream depending on site characteristics, in the MF habitat nets were placed in natural corridors that represented flyways for bats; and 3) in P, nets were located in open spaces devoid of vegetation. Bat sampling avoids nights with a full moon or heavy rain (Morrison 1978). Captured individuals were temporarily stored in cloth bags and identified to species following Medellín et al. (2011). We used Koopman’s classification (1993) for bat

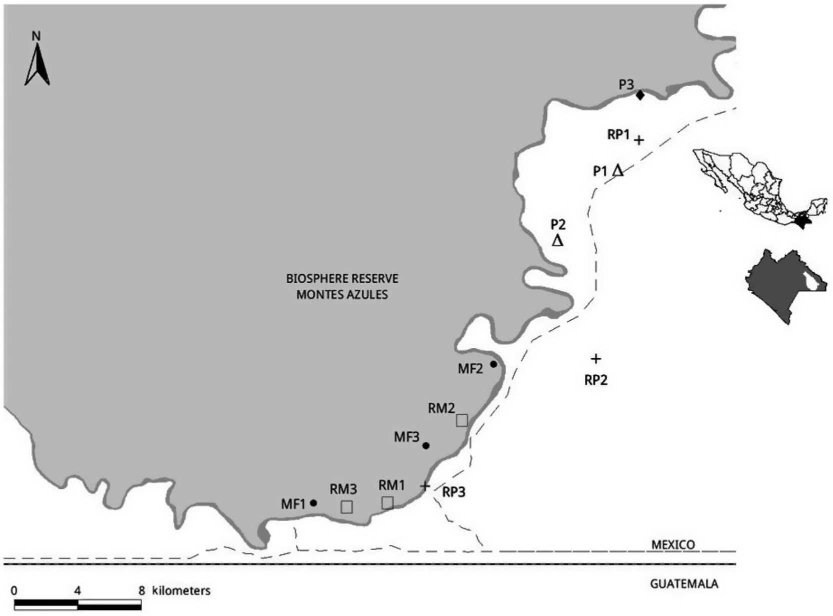

Figure 1. Study area and bat sampling sites at the Lacandona forest, Chiapas, Mexico.

families, subfamilies and genera. For species and feeding guilds, we followed Timm and La Val (1998) classification (i.e., aerial insectivores, carnivores, gleaning insectivores, frugivores, nectarivores, and sanguivores).

Tree sampling was carried out once at each habitat to determine the influence of vegetation structure on bat assemblages; we recorded all trees ≥10 cm dbh within a 0.1 ha (20 × 50 m) plot (Gentry 1982). Plots were located along streams in RM and RP habitats and randomly located in MF and P habitats. We considered the following vegetation attributes: number of individuals (NI), number of species (NS), total basal area (BA), and height (H).

Statistical analyses

Bat sampling completeness

We assessed the completeness of the bat survey by calculating the percentage of estimated species richness that was effectively covered by our samples. To ensure a good representation of bat richness, species richness was estimated by computing the average of the following indices: ICE, Chao2 and Bootstrap (Colwell et al. 2004). Ninety percent of completeness was considered to be a satisfactory level of sampling efficiency (Moreno and Halffter 2001).

We used a Mantel test with 999 permutations to determine whether bat assemblages closer together were more similar than those farther apart (Mantel 1967). We computed the correlation between the matrix representing the Euclidean distance among sites (represented in UTM units) and the matrix of Bray–Curtis indices representing ecological distances. These analyses were performed in R (R Development Core Team 2009) with the vegan package (Oksanen et al. 2011).

Bat assemblages

We built rank-abundance (dominance-diversity) plots for each habitat; these graphs have been suggested as an alternative to diversity indexes when comparing communities in different habitats (Feinsinger 2001). Individual-based rarefaction curves were constructed to compare species richness among habitats (EstimateS software, version 7.5, Copyright R. K. Colwell: http://viceroy.eeb.uconn.edu/estimates). The 95% confidence intervals of the moment-based estimator for species richness (sobs Mao Tau) were used to determine significant differences among habitats (Colwell et al. 2004).

To evaluate dissimilarity patterns among phyllostomid assemblages we used nonmetric multidimensional scaling (NMDS) based on Bray–Curtis similarity. The NMDS is one of the most appropriate ordination methods in community ecology (McCune and Grace 2002) as it can properly handle nonlinear species responses (Oksanen 2010), high beta-diversity and data not adjusted to a particular underlying model (i.e., multivariate normality), which are common in community dataset (McCune and Grace 2002). We used the stress value to evaluate the ordination. Low stress values indicate that the distances between objects in space ordination are similar to the distances between objects in the original space, defined by n-dimensions (in this case, the species considered in the matrix). The lower the stress value, the more reliable the results achieved by the ordination.

Phyllostomid bats as indicator taxa

We evaluated if phyllostomid taxa (subfamily, genus and species) were associated with particular habitats, and therefore considered as indicators of such habitats. Indicator taxa are characteristic of a particular habitat whereas detector taxa exhibit different degrees of preferences for different habitat types and consequently are useful in indicating habitat change. For this purpose, we performed the "indicator value analysis" (Dufrene and Legendre 1997). This method assigns an indicator value (IV) to each taxon, in each habitat, based on the taxon's relative frequency of occurrence (fidelity) and relative abundance (specificity). We then selected the maximum IV (IV_{max}) for each taxon and identified the corresponding habitat. The IV_{max} statistical significance was evaluated through a Monte Carlo test based on 1000 iterations. Following Castro-Luna et al. (2007b), and Avila-Cabadilla (2011), we considered as detectors all taxa with an $IV_{max} \geq 0.5$ and considered as indicators those taxa in which IV_{max} was statistically significant. These analyses were carried out in the R package labdsv, version 1.4-1.

Phyllostomids and site attributes

We examined correlations between phyllostomid response (abundance, species composition) and all the explanatory variables (season, habitat and tree basal area) using a generalized linear mixed model (GLMM). The GLMM is an extension of generalized linear models (GLMs) that include both fixed and random effects. In our models, we considered as fixed effects the season, habitat and tree basal area and as a random effect the sampling nights. In this way, we are accounting for the correlation structure caused by repeated sampling night on the same sites. For each model, we calculated Akaike's information criterion corrected for small sample size (AIC_c) following Burnham and Anderson (2002). This approach allowed us to select the most plausible models from a set of models. The set of models considered for every response variable, at each scale, included the null model (without explanatory power) and other models that considered each explanatory variable independently. We compared the model using Δ_i, which is the difference of AICc between a given model and the best (lowest AIC_c) model. We also calculated the AIC weights (w_i) for each model. The *wi* represents the weight of the evidence that a certain model is the best model given the data and the set of candidate models. The 95% confidence set of the best models was defined by summing the w_i, from the largest to the smallest, until the sum is = 0.95. Only models with an AIC_c lower than the null model were considered to define the 95% confidence set of plausible models. All previous analyses were performed with R program (R Development Core Team 2009).

Results

We completed 70 nights of capture effort, 34 during the dry season, and 36 during the rainy season, resulting in a total capture effort of 180 net hours in RM, RP, and P, and 140 net hours in MF habitats. Overall, 1752 individuals belonging to 28 species of Phyllostomidae were captured. The Stenodermatinae was the richest and most abundant subfamily with 16 species (57.1% of all species) and 1598 individuals (91.2% of all captures). The completeness values were above 85% for all habitats, which is considered appropriate to characterize the phyllostomid bat assemblages (Table 1).

The individual-based rarefaction curves (Fig. 2) showed that we sampled all species occurring in RM and RP habitats. Captures in all habitats were dominated by five species: *Sturnira lilium* (30.1%), *Artibeus lituratus* (22.9%), *A. jamaicensis* (11.4%), *Uroderma bilobatum* (9.6%), and *Glossophaga soricina* (6.1%), which together represented 80.4% of all captures (Fig. 2). Bat composition did not show a significant spatial correlation according to the Mantel test ($R = 0.057$, $P = 0.27$).

Bat assemblages and guilds

Species richness declined from 23 species in RM, to 21 in RP, to 20 in MF and 14 species in P, resulting in a total of 28 species (Fig. 3). Habitats shared 10 species. The RM habitat presented three exclusive species; in addition, the RP had two exclusive species and the MF one exclusive species, while open pastures had none. Species of the subfamily Phyllostominae were absent from open pastures (Table 1).

Frugivores accounted for the greatest percentage of both captured species and individuals (59.2% of species and 90.3% of individuals), followed by gleaning insectivores (18.5% of species and 0.7% of individuals) and nectarivores (11.1% of species and 7.7% of individuals). Sanguivores were represented by *Desmodus rotundus* with 11 individuals and *Diphylla ecaudata* with two individuals; in addition, carnivores were represented only by *Trachos cirrhosus* (Table 1). The number of bat guilds per habitat type declined from five in the RM and the MF, to four in RP, and three guilds in P (Fig. 4).

Table 1. Number of bats captured by species in different habitat types at Lacandona, Chiapas, Mexico. Bat guilds are as follows: F, frugivores; GI, gleaning insectivores; N, nectarivores; C, carnivores; and S, sanguivores.

FAMILY Subfamily *Species*	Guild	Habitats Riparian mature (RM)	 Riparian pasture (RP)	 Mature forest (MF)	 Pasture (P)	 Total
PHYLLOSTOMIDAE						
Carolliinae						
Carollia perspicillata	F^{s}	20 (1.11)	34 (1.8)	5 (0.31)	1 (0.05)	60
Carollia sowelli	F^{s}	9 (0.5)	6 (0.33)	8 (0.5)	2 (0.11)	25
Desmodontinae						
Desmodus rotundus	S	1 (0.05)	8 (0.44)	1 (0.06)	4 (0.22)	14
Diphylla ecaudata	S	0	1 (0.05)	1 (0.06)	0	2
Glossophaginae						
Choeroniscus godmani	N^{s}	2 (0.11)	0	1 (0.06)	0	3
Glossophaga soricina	N^{s}	6 (0.33)	80 (4.44)	2 (0.12)	20 (1.11)	108
Hylonycteris underwoodi	N^{s}	0	0	4 (0.25)	0	4
Lichonycteris obscura	N^{s}	1 (0.07)	0	0	0	1
Phyllostominae						
Lampronycteris brachyotis	GI^{s}	1 (0.05)	0	0	0	1
Lonchorhina aurita	GI^{s}	2 (0.11)	0	0	0	2
Mimon crenulatum	GI^{n}	0	7 (0.38)	0	0	7
Phyllostomus discolor	GI^{s}	0	1 (0.05)	0	0	1
Trachops cirrhosus	C^{s}	2 (0.11)	0	1 (0.06)	0	3
Tonatia saurophila	GI^{s}	3 (0.16)	2 (0.11)	3 (0.18)	0	8
Stenodermatinae						
Artibeus jamaicensis	F^{n}	72 (4)	59 (3.27)	41 (2.56)	29 (1.61)	201
Artibeus lituratus	F^{n}	113 (6.27)	190 (10.55)	25 (1.56)	74 (4.11)	402
Artibeus phaeotis	F^{n}	8 (0.44)	11 (0.61)	0	6 (0.33)	25
Artibeus toltecus	F^{n}	1 (0.05)	0	2 (0.12)	0	3
Artibeus watsoni	F^{n}	3 (0.16)	8 (0.44)	4 (0.25)	1 (0.05)	16
Centurio senex	F^{n}	1 (0.05)	1 (0.05)	2 (0.12)	1 (0.05)	5
Chiroderma salvini	F^{n}	2 (0.11)	3 (0.16)	2 (0.12)	1 (0.05)	8
Chiroderma villosum	F^{n}	0	3 (0.16)	1 (0.06)	0	4
Platyrrhinus helleri	F^{n}	24 (1.33)	47 (2.61)	2 (0.12)	9 (0.5)	82
Sturnira lilium	F^{s}	68 (3.77)	315 (17.5)	27 (1.68)	119 (6.61)	529
Sturnira ludovici	F^{s}	1 (0.05)	1 (0.05)	0	0	2
Uroderma bilobatum	F^{n}	48 (2.66)	92 (5.11)	0	29 (1.61)	169
Vampyresa thyone	F^{n}	7 (0.38)	5 (0.27)	1 (0.06)	3 (0.16)	16
Vampyrodes caraccioli	F^{n}	39 (2.16)	11 (0.611)	1 (0.06)	0	51
Total abundance		434	885	134	299	1752
Samples		18	18	16	18	70
Richness		23	21	20	14	28
Completeness(%)[1]		87	92	92	89	

Parentheses indicate the relative abundance (bats captured per night sampling) from 18 nights of sampling for RM, RP, and P, and 16 nights of sampling for MF.

Feeding strategy based on Soriano (2000); ^{n}=Nomadic and ^{s}=Sedentary.

[1] Based on the average of the following indices: ICE, Chao2 and Bootstrap.

Bats as indicator taxa

Six of the 18 species recorded could be considered as habitat indicators (Table 2). The subfamilies Glossophaginae and Stenodermatinae were tightly associated with RP; however, at the genus level *Glossophaga* was mostly associated with MF, and *Sturnira* was tightly associated with RP.

We identified twice as many detector taxa as indicator taxa (Table 2). The subfamily Desmodontinae was associated with RP. We found *Lonchorhina* and *Vampyrodes* were associated with RM, and *Mimon*, *Platyrrhinus* and *Uroderma* were associated with RP. Finally, most of the detector species were associated with RP (*Carollia perspicillata*, *Mimon crenulatum*, *Platyrrhinus helleri*, and *U. bilobatum*), and only two species were

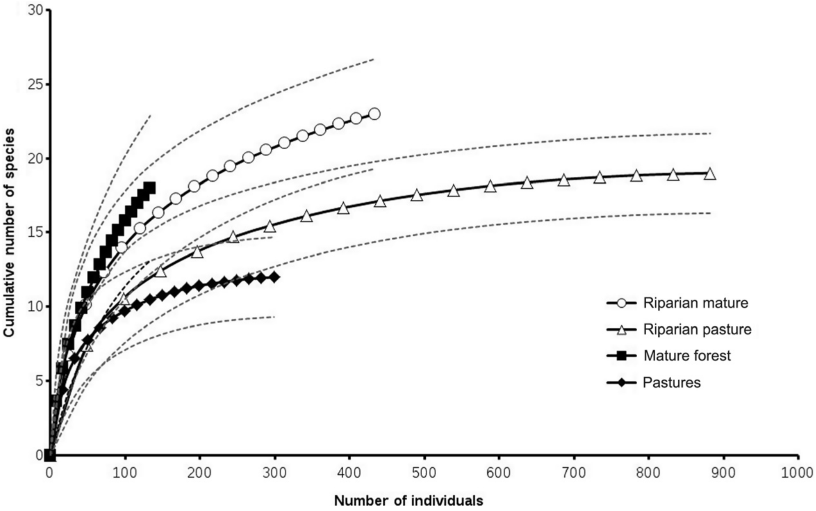

Figure 2. Individual-based rarefaction curves of bat species within different habitat types at the Lacandona forest. Dotted lines delineate 95% of confidence intervals.

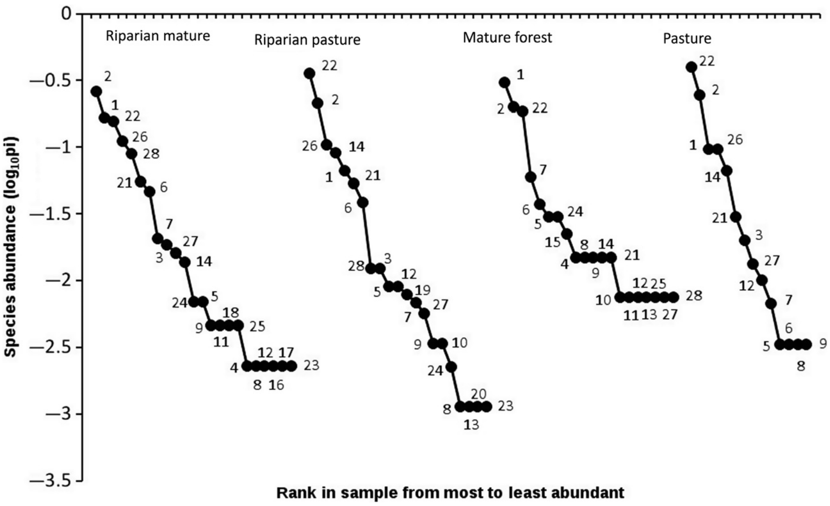

Figure 3. Rank-abundance (dominance-diversity) curves of bat species at Lacandona forest. Numbers represent the species captured. 1: *Artibeus jamaicensis*, 2: *A. lituratus*, 3: *A. phaeotis*, 4: *A. toltecus*, 5: *A. watsoni*, 6: *Carollia perspicillata*, 7: *C. sowelli*, 8: *Centurio senex*, 9: *Chiroderma salvini*, 10: *C. villosum*, 11: *Choeroniscus godmani*, 12: *Desmodus rotundus*, 13: *Diphylla ecaudata*, 14: *Glossophaga soricina*, 15: *Hylonicteris underwoodi*, 16: *Lampronycteris brachyotis*, 17: *Lichonycteris obscura*, 18: *Lonchorhina aurita*, 19: *Mimon crenulatum*, 20: *Phyllostomus discolor*, 21: *Platyrrhinus helleri*, 22: *Sturnira lilium*, 23: *S. ludovici*, 24: *Tonatia saurophila*, 25: *Trachops cirrhosus*, 26: *Uroderma bilobatum*, 27: *Vampyressa thyone*, and 28: *Vampyrodes caraccioli*.

associated with RM (*Lonchorhina aurita* and *Vampyrodes caraccioli*).

Response to habitat attributes

Three axes were considered in the NMDS ordination (Fig. 4, stress = 2.3). We only used scores from axes 1 and 2 for the construction of the biplot. Axis 1 of the plot separated riparian and nonriparian habitats. Riparian pasture and RM habitat are closer together, showing more similarity in species composition than MF and P, which are strongly separated (Fig. 4).

The assemblage dissimilarities represented by NMDS (Fig. 4) were significantly associated with the type of habitat and total basal area of the vegetation. Phyllostominae species such as *M. crenulatum*, *P. discolor*, *Lampronycteris brachyotis*, and *T. saurophila* were associated with the sites with the greater basal area (Table 3). Sites with high basal area were the riparian habitats: RM with 25639.51 m^2/0.1 ha and RP with 20,285.77 m^2/0.1 ha. On the other hand, whereas in nonriparian habitats basal area was 8561.03 m^2/0.1 ha in P and 6241.88 m^2/0.1 ha in RM. Also, the variation in bat abundance was positively associated with the rainy season (Table 3).

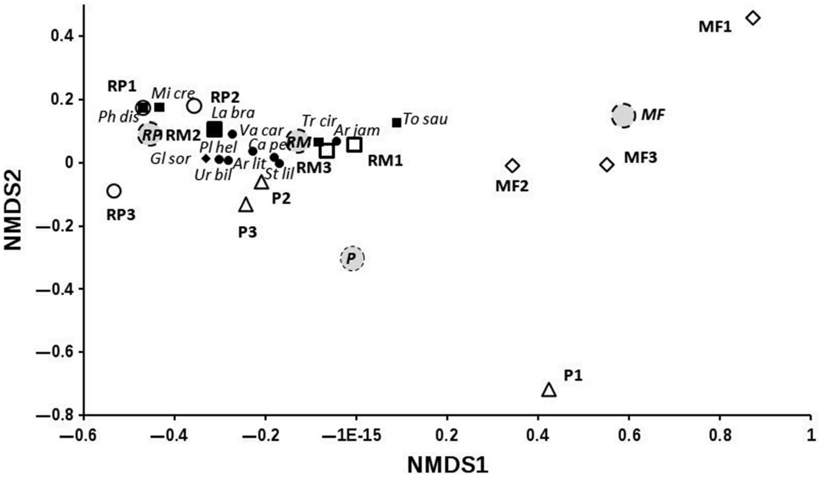

Figure 4. NMDS ordination based on species composition and bat abundance data at the Lacandona forest, where RM, riparian mature; RP, riparian pasture; MF, mature forest; P, open pasture.

Table 2. Bat taxa with a significant indicator value (IV) in the Lacandona, Chiapas, Mexico.

Taxonomic level	Taxon	Habitat	IV	*P*-value	Category
Subfamily	Glossophaginae	RP	0.682	**0.048**	I
	Stenodermatinae	RP	0.500	**0.025**	I
	Desmodontinae	RP	0.548	0.271	D
Genus	Glossophaga	MF	0.739	**0.038**	I
	Lonchorhina	RM	0.666	0.192	D
	Mimon	RP	0.666	0.170	D
	Platyrrhinus	RP	0.573	0.321	D
	Sturnira	RP	0.593	**0.016**	I
	Uroderma	RP	0.544	0.087	D
	Vampyrodes	RM	0.761	0.212	D
Species	*C. perspicillata*	RP	0.559	0.215	D
	G. soricina	RP	0.739	**0.036**	I
	L. aurita	RM	0.666	0.186	D
	M. crenulatum	RP	0.666	0.183	D
	P. helleri	RP	0.573	0.337	D
	S. lilium	RP	0.593	**0.019**	I
	U. bilobatum	RP	0.544	0.089	D
	V. caraccioli	RM	0.761	0.222	D

RM, riparian mature; RP, riparian pasture; MF, mature forest; P, open pasture; D, detector taxon; I, indicator taxon.
Significant *P*-values (<0.05) appear in bold.

Discussion

Our results suggest differences in species richness and abundance of phyllostomid bats between riparian and nonriparian habitats. This suggests that riparian corridors in agricultural landscapes allow the persistence of sensitive phyllostomines, which demonstrates the importance of maintaining different vegetation cover types to conserve bat biodiversity in areas under agricultural land use (Medina et al. 2007; Williams-Guillén and Perfecto 2010).

Bat assemblages

There was a clear association of riparian habitats with greater richness and abundance of bat species (Seaman and Schulze 2010). The high species richness and number of individuals recorded in a riparian habitat corroborates their significance as flyways corridors within fragmented landscapes (Limpens and Kapteyn 1991). Riparian corridors offer a great diversity of chiropterophilic and chiropterochoric resources (Sánchez-Merlo et al. 2005) and provide roosting sites, commuting habitats, water, and refuge from adverse climatic conditions and predators (Estrada and Coates-Estrada 2002; Galindo-González and Sosa 2003).

We found more nomadic bats (Stenodermatinae) in anthropogenic habitats as they frequently move among forest remnants probably searching for food, which increases their capture probability (Table 1 Soriano (2000)). This suggests that Stenodermatinae but especially

Table 3. Confidence set of plausible models (95%) explaining the variation in response variables.

Response variable	Model	K	logLik	AIC_c	Δ_i	w_i
Night data analyses						
Abundance	Season	3	450.82	910.64	0.00	0.81
	Habitat + Season	6	442.39	913.58	2.93	0.19
	Habitat	5	500.12	1020.24	109.59	0.00
Site data analyses						
Species composition	Habitat	5	2.12	15.75	0.00	0.56
	$V_{\text{basal area}}$	3	4.35	17.70	1.94	0.21

K, number of estimated parameters; logLik, log-likelihood; AIC_c, sample-sized adjusted Akaike information criterion; Δ_i, Akaike differences; and w_i, Akaike weights. Response variables: species abundances, species rarified at lowest number of captures, species composition, and guild composition. Explanatory variables are the following: habitat, V_{spcomp}, using scores of NMDS axis 1; V_{height}, average height of trees at each site; $V_{\text{basal area}}$, total basal area at each site; $V_{\text{abundance}}$, total number of trees; V_{rich}, number or species.

Artibeus and *Sturnira* may facilitate forest regeneration in open pastures through seed dispersal (García-Morales et al. 2012). Nonetheless, *V. caraccioli* (Stenodermatinae) was caught exclusively in undisturbed forest, and *C. perspicillata* (Carolliinae) was caught mainly in riparian pasture habitat, supporting the idea that sedentary bats seldom leave mature forests (Soriano 2000). In this context, open pastures generate impermeability, because they seem to limit the movement of frugivorous bats restraining seed-flux between fragments and their matrix process that is crucial in the recovery in old fields (Cortés-Delgado and Pérez-Torres 2011).

The most abundant species in pastures were *A. lituratus*, *C. perspicillata,* and *S. lilium*. These species are common and may be less susceptible to habitat disturbance because of their generalist diet, and their probability of arriving to modified areas is higher compared to rare species. Species such as *Uroderma bilobatum* was associated with all habitat types reflecting its capacity to consume fruits from primary and secondary forests (Gorresen and Willig 2004).

Habitat disturbance and bat guilds

Frugivores were the best represented trophic guild in all habitats. The feeding habits of the Phyllostomid frugivorous species make them highly tolerant to human-disturbed habitats, and they can easily recolonize disturbed areas (Avila-Cabadilla et al. 2009). We found a higher abundance of some frugivorous species (*A. lituratus*, *P. hellery*, *S. lilium,* and *U. bilobatum*) in RP than in the other habitats. In the case of *A. lituratus*, the guild of large fig-eating bats (genus *Artibeus*) showed greater tolerance to fragmentation than other frugivorous phyllostomids, because of its foraging strategy and capacity for flying long distances (Cosson et al. 1999; Avila-Cabadilla et al. 2012). In contrast, gleaning insectivores and carnivores (Phyllostominae) preferred mature forest instead of human-disturbed habitats (García-Morales et al. 2013). In our study, gleaning insectivores and carnivores were absent from open pastures, perhaps as a consequence of food scarcity, shelter, and roost resources (Medellín et al.2000; Schulze et al. 2000; Gorresen and Willig 2004; de la Peña-Cuéllar et al. 2012). Gleaning insectivores were present, however, in RP, supporting our hypothesis that these habitats offer good sites for lurking and hunting for prey (Gorresen and Willig 2004; García-Morales et al. 2013).

Bats as indicator taxa

Taxonomic level analysis demonstrates that in the study area phyllostomid bats are poor ecological indicators (Castro-Luna et al. 2007b). Contrary to other findings (Fenton et al.1992; Medellín et al. 2000) that suggest the Phyllostominae subfamily is an ecological indicator of habitat modification because of strong association with preserved forest, our results suggest that generalist abundant species like the subfamilies Glossopaginae and Stenodermatinae may be better as ecological indicators. Frugivorous bats like Stenodermatinae, which can fly over large distances and visit different vegetation types (Estrada and Coates-Estrada 2002), could be useful detector taxa for studies aimed at evaluating different degrees of disturbance, rather than highly specialized taxa in which populations decline rapidly under environmental changes (Mcgeoch et al. 2002; Castro-Luna et al. 2007b).

Nectarivorous *G. soricina* and frugivorous *S. lilium* can be both considered as indicator taxa of habitat change in RP. These species can forage in areas with a simple vegetation structure but with high abundance of chiropterophilic and chiropterocoric species, in particular, *S. lilium* that usually feeds on understory shrubs and pioneer tree species (Marinho-Filho 1991).

Habitat attributes

Despite the relatively stable climatic conditions throughout the year in tropical rain forests, the availability of resources varies seasonally, and our results suggest that bats could be forced to make adjustments in their foraging strategy to cope with seasonal variations of resources availability such as food and roosts (Ramos-Pereira et al. 2010). Frugivores diet varies over the year and throughout their geographic ranges as the abundance and availability of fruit species change (Bonaccorso 1979). Seasonal variation could be a cause of variation in resource abundance and diversity, reproductive constraints and forest fragmentation, intensifying the severity of seasonal changes in source availability, furthermore, this variation could be a cause of shifts in foraging strategy that may not be needed in unfragmented landscapes (Klingbeil and Willig 2010).

The positive relationship between species composition and basal area of trees can be explained by the preference of some bat species for roosting in large trees. Large trees provide more potential roost sites because there is a close relationship between tree size and the number of natural cavities (Evelyn and Stiles 2003; Ortiz-Ramírez et al. 2006).

Conservation implications

Our results suggest that more efforts are needed to preserve riparian corridors in order to conserve Neotropical bats in human-dominated landscapes. Specifically, increasing matrix heterogeneity at larger spatial scales through the retention and protection of riparian forests is important (Akasaka et al. 2012). In human-dominated landscapes, riparian vegetation is highly threatened by agricultural practices, cattle concentration, extraction of firewood and timber. This suggests that conservation strategies should provide incentives for landowners to conserve and restore riparian vegetation in their properties (Harvey et al. 2006). Maintaining diverse populations of bats in human-dominated landscapes can benefit agricultural practices via seed dispersal and pollination services and by limiting arthropod populations (Perfecto and Vandermeer 2008; Williams-Guillén et al. 2008). Additionally, management programs in human-dominated landscapes should also focus on the quality of the remaining riparian vegetation as a suitable breeding habitat for bats and other animals (Bolívar-Cimé et al. 2013).

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Conflict of Interest

None declared.

References

Achard, F., H. D. Eva, H. J. Stibig, P. Mayaux, J. Gallego, T. Richards, et al. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002.

Akasaka, T., M. Akasaka, and F. Nakamura. 2012. Scale-independent significance of river and riparian zones on three sympatric Myotis species in an agricultural landscape. Biol. Conserv. 145:15–23.

Avila-Cabadilla, L. D. 2011. Diversidad de murciélagos filostómidos en estadios sucesionales de bosques neotropicales secos. PhD thesis, Universidad Nacional Autónoma de México, México.

Avila-Cabadilla, L. D., K. E. Stoner, M. Henry, and M. Y. Álvarez-Añorve. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. For. Ecol. Manage. 258:986–996.

Avila-Cabadilla, L. D., G. A. Sanchez-Azofeifa, K. E. Stoner, M. Y. Alvarez-Añorve, M. Quesada, and C. A. Portillo-Quintero. 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forest. PLoS ONE 7:e35228.

Bolívar-Cimé, B., J. Laborde, C. MacSwiney, C. Muñóz-Robles, and J. Tun-Garrido. 2013. Response of phytophagous bats to patch quality and landscape attributes in fragmented tropical semi-deciduous forest. Acta Chiropt. 15:399–409.

Bonaccorso, F. J. 1979. Foraging and reproductive ecology in a panamanian bat community. Bull. Florida State Mus. Biol. Sci. 24:357–409.

Breugel, M. V., M. Martínez-Ramos, and F. Bongers. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. J. Trop. Ecol. 22:663–674.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.

Carabias, J., G. Hernández, and P. Meli. 2008. Análisis comparativo de la deforestación de los ejidos de Marqués de Comillas, y determinación de corredores biológicos que conecten los fragmentos de selva de los ejidos con la Reserva de la Biosfera Montes Azules. Informe Final de Proyecto, INE, México.

Castro-Luna, A., V. J. Sosa, and G. Castillo-Campos. 2007a. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. Anim. Conserv. 10:219–228.

Castro-Luna, A., V. J. Sosa, and G. Castillo-Campos. 2007b. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. Acta Chiropt. 9:219–228.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating and comparing incidence-based species accumulation curves. Ecology 85:2717–2727.

Comisión Federal de Electricidad. 2006. División Hidrométrica Sureste. Estación Lacantún, Marqués de Comillas, Chiapas, México.

Cortés-Delgado, N., and J. Pérez-Torres. 2011. Habitat edge context and the distribution of phyllostomid bats in the Andean forest and anthropogenic matrix in the Central Andes of Colombia. Biodivers. Conserv. 20:987–999.

Cosson, J. F., J. M. Pons, and D. Masson. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. J. Trop. Ecol. 15:515–534.

Daniel, S., C. Korine, and B. Pinshow. 2008. Central-place foraging in nursing, arthropo-gleaning bats. Can. J. Zool. 86:623–626.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species, the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345–366.

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

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

Evelyn, M. J., and D. A. Stiles. 2003. Roosting requirements of two frugivorous bats (*Sturnira lilium* and *Artibeus intermedius*) in fragmented neotropical forest. Biotropica 35:405–418.

Feinsinger, P. 2001. Designing field studies for biodiversity conservation. Island Press, Washington, DC.

Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Orbist, et al. 1992. Phyllostomid bats (Chiroptera:Phyllostomidae) as indicators of habitat disruption in the neotropics. Biotropica 24:440–446.

Galindo-González, J., and V. J. Sosa. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. Southwest. Nat. 48:579–589.

García-Morales, R., L. Chapa-Vargas, J. Galindo-González, and E. I. Badano. 2012. Seed dispersal among three different vegetation communities in the Huasteca region, Mexico, analyzed from bat feces. Acta Chiropt. 14:357–367.

García-Morales, R., E. I. Badano, and C. Moreno. 2013. Response of neotropical bat assemblages to human land use. Conserv. Biol. 27:1096–1106.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Mo. Bot. Gard. 69:557–593.

Gorresen, P. M., and M. R. Willig. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. J. Mammal. 85:688–697.

Griscom, H. P., E. K. V. Kalko, and M. S. Ashton. 2007. Frugivory by small vertebrates within a deforested, dry tropical region of central America. Biotropica 39:278–282.

Harvey, C. A., A. Medina, D. Merlo-Sánchez, S. Vílchez, B. Hernández, J. C. Saenz, et al. 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecol. Appl. 16:1986–1999.

INE. 2000. Programa de Manejo Reserva de la Biósfera Montes Azules, México. Dirección de Publicaciones de la Dirección Ejecutiva de Participación Social, Enlace y Comunicación, Instituto Nacional de Ecología, México. 256 pp.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endanger. Species Res. 8:1–23.

de Jong, B. H. J., S. Ochoa-Gaona, M. A. Castillo-Santiago, N. Ramírez-Marcial, and M. A. Cairns. 2000. Carbon flux and patterns of land-use/land cover change in the selva Lacandona, Mexico. Ambio 29:504–511.

Kalka, M., A. R. Smith, and K. V. E. Kalko. 2008. Bats limit arthropods and herbivory in a tropical forest. Science 320:71.

Kalko, E. K. V., D. Friemel, C. O. Handley Jr, and H. U. Schnitzler. 1999. Roosting and foraging behavior of two neotropical gleaning bats, Tonatia silvicola and Trachops cirrhosus (Phyllostomidae). Biotropica 31:344–353.

Klingbeil, B. T., and M. R. Willig. 2010. Seasonal differences in population ensemble and community-level responses of bats to landscape structure in Amazonia. Oikos 119:1654–1664.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137–232 *in* D. E. Wilson and D. M. Reeder, eds. Mammal species of the world. Smithsonian Institution Press, Washington, DC.

Kunz, T. H., E. B. de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Year in Ecology and Conservation Biology. Ostfeld, R. S Schlesinger W. H., NewYork.

La Val, R. K. 1970. Banding returns and activity periods of some Costa Rican bats. Southwest. Nat. 15:1–10.

Laurance, W., and R. O. Jr Bierregaard. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago, IL.

Limpens, H., and K. Kapteyn. 1991. Bats, their behavior and linear landscape elements. Myotis 29:39–48.

Lundy, M., and I. Montgomery. 2010. Summer habitat associations of bats between riparian landscapes and within riparian areas. Eur. J. Wildl. Res. 56:385–394.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

Marinho-Filho, J. S. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. J. Trop. Ecol. 7:59–67.

Mcgeoch, M. A., B. J. VanRensburg, and B. Antoinette. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystems. J. Appl. Ecol. 39:661–672.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, OR. 300 pp.

Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. Conserv. Biol. 14:1666–1675.

Medellín, R. A., H. T. Arita, and O. Sánchez. 2011. Identificación de los murciélagos de México: clave de campo. Asociación Mexicana de Mastozoología, México, DF.

Medellín, R. A. 1994. Mammal diversity and conservation in the selva Lacandona, Chiapas, Mexico. Conserv. Biol. 8:780–799.

Medina, A., C. A. Harvey, D. S. Merlo, S. Vílchez, and B. Hernández. 2007. Bat diversity and movement in an agricultural landscape in Matiguas, Nicaragua. Biotropica 39:120–128.

Moreno, C. E., and G. Halffter. 2001. Assessing the completeness of bat biodiversity inventories using species accumulation curves. J. Appl. Ecol. 37:149–158.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera:Phyllostomidae). Anim. Behav. 26:852–855.

Muscarella, R., and T. H. Fleming. 2007. The role of frugivorous bats in tropical forest succession. Biol. Rev. 82:573–590.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3:209–212.

Naiman, R. J., R. E. Bilby, and P. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. Bioscience 50:996–1011.

Oksanen, J., F. Guillaume, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, et al. 2011. Vegan: Community ecology package version 1.17-6 http://CRAN.R-project.org/package=vegan.

Oksanen, J. Multivariate analysis of ecological communities in R: vegan tutorial. 2010. Available at: http://cc.oulu.fi/~jarioksa/softhelp/vegan.html. (accessed 25 January).

Ortiz-Ramírez, D., C. Lorenzo, E. Naranjo, and L. León-Paniagua. 2006. Selección de refugios por tres especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en la Selva Lacandona, Chiapas, México. Rev. Mex. Biodivers. 77:261–270.

de la Peña-Cuéllar, E., K. E. Stoner, L. D. Avila-Cabadilla, M. Martínez-Ramos, and A. Estrada. 2012. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. Biodivers. Conserv. 21:1381–1397.

Perfecto, I., and J. Vandermeer. 2008. Biodiversity conservation in tropical agroecosystems. Ann. N. Y. Acad. Sci. 1134:173–200.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ramos-Pereira, M. J., J. T. Marques, and J. M. Palmeirim. 2010. Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forest. Biotropica 42:680–687.

Sánchez-Merlo, D., C. A. Harvey, A. Grijalva, A. Medina, S. Vilchez, and B. Hernández. 2005. Diversidad, composición y estructura de la vegetación en un paisaje ganadero en Matiguás, Nicaragua. Rev. Biol. Trop. 53:387–414.

Schulze, M. D., N. E. Seavy, and D. F. Whitacre. 2000. A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Peten, Guatemala. Biotropica 32:174–184.

Seaman, B. S., and C. H. Schulze. 2010. The importance of gallery forest in the tropical lowlands of Costa Rica for understorey forest birds. Biol. Conserv. 143:391–398.

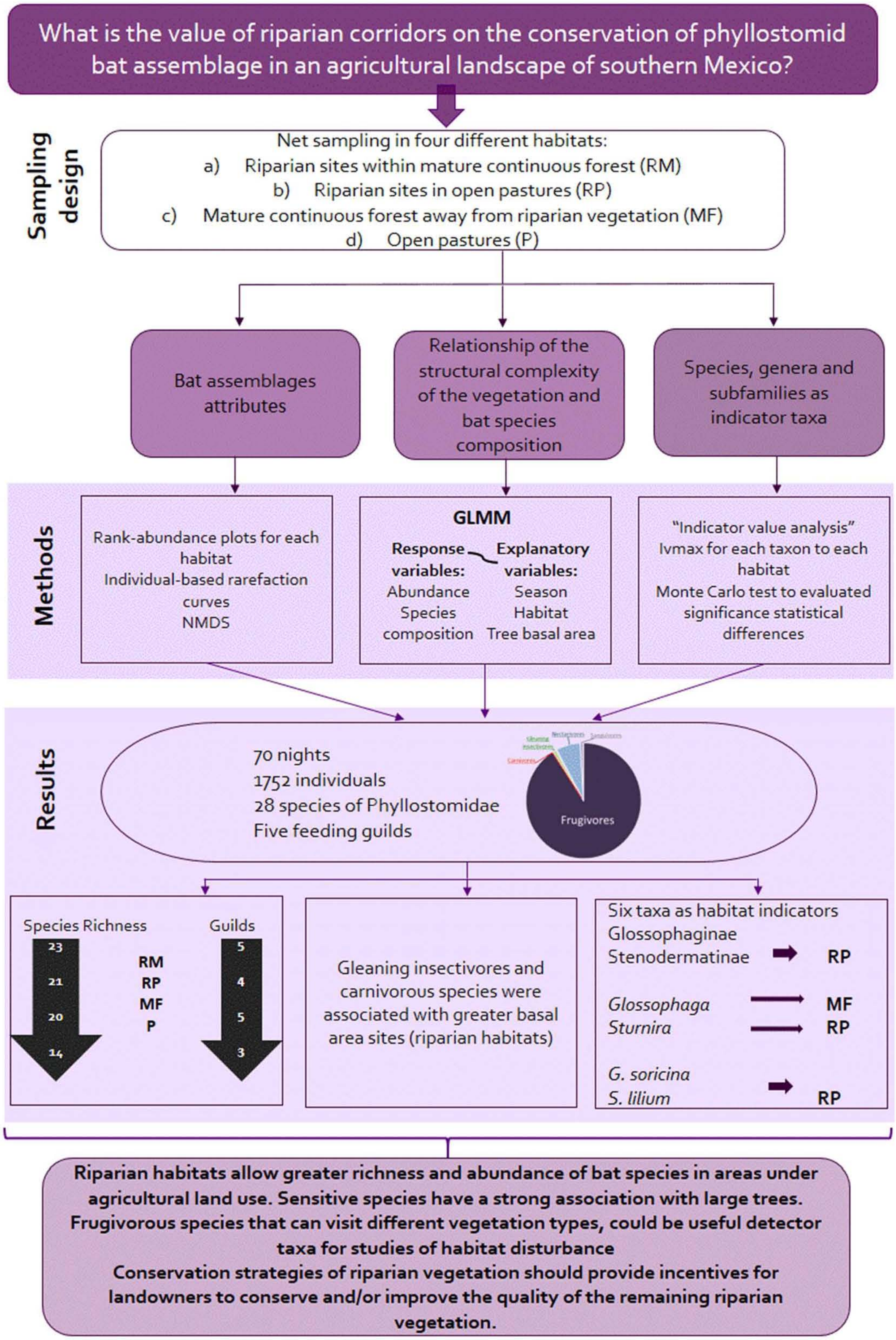
Soriano, P. J. 2000. Functional structure of bat communities in tropical rainforests & Andean cloud forests. Ecotropicos 13:1–20.

Timm, R. M., and R. K. La Val. 1998. A field key to the bats of Costa Rica. Occas. Publ. Ser. Univ. Kan 22:1–32.

Warkentin, I. G., R. Greenberg, and J. Salgado-Ortiz. 1995. Songbird use of gallery woodlands in recently cleared an older settled landscapes of the Selva Lacandona, Chiapas, Mexico. Conserv. Biol. 9:1095–1106.

Williams-Guillén, K., and I. Perfecto. 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. Biotropica 42:605–613.

Williams-Guillén, K., I. Perfecto, and J. Vandermeer. 2008. Bats limit insects in a neotropical agroforestry system. Science 320:70.



What is the value of riparian corridors on the conservation of phyllostomid bat assemblage in an agricultural landscape of southern Mexico?

Net sampling in four different habitats:

a) Riparian sites within mature continuous forest (RM)
b) Riparian sites in open pastures (RP)
c) Mature continuous forest away from riparian vegetation (MF)
d) Open pastures (P)

Bat assemblages attributes

Relationship of the structural complexity of the vegetation and bat species composition

Species, genera and subfamilies as indicator taxa

Rank-abundance plots for each habitat
Individual-based rarefaction curves
NMDS

GLMM

Response variables:	**Explanatory variables:**
Abundance	Season
Species composition	Habitat
	Tree basal area

"Indicator value analysis"
Ivmax for each taxon to each habitat
Monte Carlo test to evaluated significance statistical differences

70 nights
1752 individuals
28 species of Phyllostomidae
Five feeding guilds

Gleaning insectivores and carnivorous species were associated with greater basal area sites (riparian habitats)

Six taxa as habitat indicators
Glossophaginae
Stenodermatinae → **RP**

Glossophaga → **MF**
Sturnira → **RP**

G. soricina
S. lilium → **RP**

Riparian habitats allow greater richness and abundance of bat species in areas under agricultural land use. Sensitive species have a strong association with large trees. Frugivorous species that can visit different vegetation types, could be useful detector taxa for studies of habitat disturbance
Conservation strategies of riparian vegetation should provide incentives for landowners to conserve and/or improve the quality of the remaining riparian vegetation.

Figure 1. . Diagram of chapter I summary

CAPÍTULO II

SEX-SPECIFIC PATTERNS OF PHYLLOSTOMID BATS IN A HUMAN DOMINATED TROPICAL LANDSCAPE

Sex-specific patterns of phyllostomid bats in a human dominated tropical landscape

Erika de la Peña-Cuéllar*[a], Julieta Benítez-Malvido[a],

[a] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional
Autónoma de México. Morelia, Michoacán, México

*Corresponding author: erikapc@cieco.unam.mx

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Abstract

To accurately assess the impacts of forest disturbance on native animal populations and communities it is essential to understand what drives species patterns within a human-dominated tropical landscape. Animal species exhibit sex-specific patterns as an adaptation to their habitats however adaptability to a human-dominated landscape is commonly explored without considering intraspecific differences. Biological differences of males and females lead to a sexual segregation in habitat use. Here, we explored sex-specific responses to the presence of riparian corridors in continuous forest and cattle pastures using six common species of phyllostomid bats: *Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina* and *Platyrrhinus helleri*. We further explored the responses of bats to vegetation attributes and seasonality. We found that capture rates were significantly skewed towards females, and that riparian corridors in pastures were the habitat with the highest female capture rates. Females of *A. lituratus* exhibit a strong relationship with habitat quality, and also *G. soricina* females is significantly and positively correlated to height and high basal area of trees, supporting the idea that females of both species might depend on local temporal foliage roosts that can provide energetic and thermal requirements to leave the young while foraging. We found that seasonality was particularly important for *A. lituratus* and *S. lilium* females, this might reside on the differences in abundance or diversity of food resources between the wet and dry seasons, resulting in shortened flights during the exploration for food and roost sources, whereas during the dry season when food resources are often scarce, females tend to increase foraging movements into resource rich secondary forest areas.

The results indicate a sexual bias response in bats, leading to important implications for our understanding of bat adaptability to habitat modification. The high energetic demands of female associated to reproduction could leads to increased foraging movements into riparian corridors. The maintenance of vegetation characteristics in riparian corridors associated to the presence of females can guarantee a dynamic and long-term conservation of the bat community.

Keywords: forest disturbance, intraspecific differences, phyllostomid bats, reproduction´s energetic demand, riparian, sex–ratio.

INTRODUCTION

The configuration of tropical landscapes is highly dynamic as a consequence of changes of land use and cover (Mayaux *et al.* 2005; Fagan *et al.* 2013). A common feature in tropical agricultural landscapes is the relict natural vegetation along streams which can persist even when being exposed to long term agricultural practices and small-scale land use changes (Lundy & Montgomery 2010). Habitat disturbance can alter the spatial arrangement of critical resources for animals within a given landscape, potentially resulting in distinct demographic patterns (e.g. sex-ratio, abundance, age classes, etc.) among habitat patches. The degree to which habitat disturbance alters the demography of animal populations however, should vary as a function of the behavioral plasticity of individual species (Bender, D. J., Contreras, T. A., Fahrig 1998; Nupp & Swihart 2000).

Males and females of the same species may differ in several aspects of their biology (e.g., sexual dimorphism, different thermoregulatory strategies), which may result in sexual segregations in habitat use (Lintott *et al.* 2014) and/or competition between the sexes (Lemaître *et al.* 2014; Beerman *et al.* 2016; Benítez-Malvido et al. 2016). Sexual segregation can be broadly categorized into two types: habitat segregation and social segregation Habitat segregation occurs where the sexes differ in their use of the physical environment, whilst social segregation in the tendency for a species to form single-sex groups. (Wearmouth & Sims 2008)

One hypotheses postulated to explain habitat segregation suggests that inherent sexual differences in reproductive strategies (i.e. reproductive energy demands, breeding period and predation risk (Dietz, Kalko & Encarnação 2006; Nardone *et al.* 2015; Beerman *et* *al.* 2016; Benítez-Malvido et al 2016) result in females trade off food quality of the habitat in favour of safety to their offspring (Wearmouth & Sims 2008).

Most studies on the effects of human-modified landscapes on bat communities have focused at the species level responses, while the potential importance of intra-specific differences are often ignored (Lintott *et al.* 2014). Bats are an ideal taxon in studies under the sexual segregation context, since sexual dimorphism in bats is rare but sexual segregation is widespread (Senior *et al.* 2005). Seasonal and maternity sexual segregation has been documented in many bat species (Sgroi & Wilkins 2010; Encarnação 2012; Diamond & Diamond 2014). Many female species of tropical bats roost in groups in resource-rich habitats with other females and few to no males (harem groups) (Ortega & Arita 1999; McCracken & Wilkinson 2000; Altringham 2011). Particularly due to reproductive and parental costs, females have higher energy requirements, so they are less abundant in habitats with limited food resources (Racey & Speakman 1987; Ramos Pereira, Marques & Palmeirim 2010). Given that males and females of the same bat species may have seasonal distributions, different reproductive strategies, and select roosts with different characteristics, sexes should be considered separately whenever possible in the study of bats (Broders *et al.* 2006; Safi, König & Kerth 2007; Weller, Cryan & O'Shea 2009). The importance of fine-scale spatiotemporal and demographically precise data is unquestioned for conservation strategies (van Toor, Jaberg & Safi 2011).

Because one of the major threats that bat communities face is habitat destruction, understanding the consequences of human impact for their conservation is important in sustainable management programs in modified landscapes (Hutson, Mickleburgh & Racey

2001; Russo *et al.* 2010). Information on the abundance and sex ratios of bat populations throughout the year is important for understanding their ecology, critical periods of time and critical habitats (Perry, Carter & Thill 2010). Therefore, obtaining sex-specific information on the behavior and habitat needs of bats should be one of the primary goals in conservation efforts (Weller *et al.* 2009; Perry *et al.* 2010). In order to understand the mechanisms by which some bat species are affected by habitat perturbation, it is necessary to determine not only if habitat disturbance affects life-history parameters, but also if habitat disturbance generates changes in their social structure. In this study we assessed six common species of phyllostomid bats to identify sex-specific patterns in bat communities within a human-dominated landscape. Our study provides insight into the importance of habitat type on sex ratio and on sex distribution throughout different tropical habitat types. The objective of this study was to determine whether or not bat sex is associated to riparian habitat in a human dominated landscape in Southern Mexico. We hypothesized that sex specific differences in habitat use will be detected mainly because of the reproductive energetic demands in females (i.e., pregnancy and lactation). At the local scale, vegetation attributes may affect female abundance, because females are frequently restricted to high-quality habitats for foraging (Lintott *et al.* 2014). We expected that due to the increase fruit availability in riparian vegetation (Naiman *et al.* 1993), capture rate of females would be higher in riparian habitats. Because one of the major threats that bat communities face is habitat destruction, understanding the consequences of human impact for their conservation is important in sustainable management programs in modified landscapes (Hutson *et al.* 2001; Russo *et al.* 2010). Information on the abundance and sex ratios of bat populations throughout the year is important for understanding their ecology, critical periods of time and critical habitats (Perry *et al.* 2010). Obtaining sex-specific information on the behavior and habitat needs of bats should be one of the primary goals in conservation efforts (Weller *et al.* 2009; Perry *et al.* 2010). In order to understand the mechanisms by which some bat species are affected by habitat perturbation, it is necessary to determine not only if habitat disturbance affects life-history parameters, but also if habitat disturbance generates changes in their social structure. We assessed six common species of phyllostomid bats to identify sex-specific patterns in bat communities within a human-dominated landscape. Our study provides insight into the importance of habitat type on sex ratio and on sex distribution throughout different tropical habitat types. The objectives of this study were to determine whether or not bat sex is associated to riparian habitat in a human dominated landscape in Southern Mexico. We hypothesized that sex specific differences in habitat use will be caused by the reproductive energetic demands in females (i.e., pregnancy and lactation). At the local scale, vegetation attributes may affect female abundance, because females are frequently restricted to high-quality habitats for foraging (Lintott *et al.* 2014). We expected that due to the increase fruit availability in riparian vegetation (Naiman *et al.* 1993), capture rate of female would be higher in riparian habitats.

METHODS

Study area and sites

The study was performed in the tropical region of Lacandona, south of the state of Chiapas, Mexico. The original vegetation consists mainly on lowland tropical rain forests.

Deforestation of the region began in the 1970s, resulting in the reduction of old-growth continuous forest from 95% in 1976 to 56% in 1996 (De Jong *et al.* 2000); only 36% of the original old-growth continuous forest remains today (Carabias, Hernández & Meli 2008). Currently, the main land-use practices in the region consist of cattle pastures, the cultivation of maize and other crops, and patches of secondary and old-growth forests (De Jong *et al.* 2000; Zermeño-Hernández *et al.* 2015). The region has a mean annual temperature of 24°C; average annual rainfall is 3000 mm with June to October as the wettest months (551 mm month^{-1}) and February to April as the driest months (<100 mm month^{-1}) (CFE 2006; Van Breugel, Martínez-Ramos & Bongers 2006).The study was performed in the tropical region of Lacandona, south of the state of Chiapas, Mexico. The original vegetation consists mainly on lowland tropical rain forests. Deforestation of the region began in the 1970s, resulting in the reduction of old-growth continuous forest from 95% in 1976 to 56% in 1996 (De Jong *et al.* 2000); only 36% of the original old-growth continuous forest remains today (Carabias, Hernández & Meli 2008). Currently, the main land-use practices in the region consist of cattle pastures, the cultivation of maize and other crops, and patches of secondary and old-growth forests (De Jong *et al.* 2000; Zermeño-Hernández *et al.* 2015). The region has a mean annual temperature of 24°C, and average annual rainfall is 3000 mm with June to October as the wettest months (551 mm month) and February to April as the driest months (<100 mm month) (CFE 2006; Van Breugel, Martínez-Ramos & Bongers 2006).

Four different habitat types were selected for this study including the following: (i) riparian habitat within old-growth continuous forest (RC); (ii) riparian habitat in active cattle pastures (RP); (iii) old-growth continuous forest away from riparian vegetation (CF); and (iv) active cattle pastures (P) away from riparian vegetation. Each habitat type was replicated three times and study sites were at least 1.5 km away from each other (Fig. 1). Streams were all permanent (although with variable amounts of running water throughout the year) while stream width varied from two to eight meters. Study sites in pastures were located in the fragmented landscape of the Marqués de Comillas municipality, on the south side of the Lacantún River. Old-growth continuous forest sites were located in the 330, 000 ha Montes Azules Biosphere Reserve (MABR) on the north side of the river (16°04′N to 90°45′ W; INE 2000, Fig. 1).

Bat sampling

Sampling of bats was conducted twice during the dry season (December to May) and twice during the wet season (June to November) for three years (2011, 2012, and 2013), using a standardized method of four nights per site. Five nets (12 m long x 2.6 m high) were set at ground level and were opened at dusk (1800 - 1830) for four consecutive hours, which corresponds to peak foraging time for most phyllostomid species (La Val 2017). The bat sampling nets were arranged according to habitat type: 1) in the riparian habitats (including continuous forest and pastures), nets were located parallel and/or diagonally across the stream, depending on site characteristics; 2) in continuous forest nets were positioned across natural flying corridors;3) in pastures nets were located in open spaces devoid of vegetation. In all sites we searched for similar physical characteristics that allow the same mist net arrangement, this is one individual net and two pairs of nets in an "L" position (two nets connected perpendicularly), also nets were located roughly 50 m apart. Nights with a full moon or heavy rain were avoided during the bat sampling in order to prevent variation in capture success associated with these conditions (Morrison 1978). Captured individuals were temporarily stored in cloth bags and identified to species following Medellín, Equihua & Amin (2011). For all captured bats, we determined sex by inspecting genitalia (Racey 1988) In females, we diagnosed pregnancy by palpation (Racey 1988), and lactation by the occurrence of enlarged nipples surrounded by a hairless skin area and by extruding milk with a gentle finger pressure on the nipple base. Sex ratio was calculated as the ratio of males to females in each area (Russo 2010).

Vegetation structure

Vegetation structure of each sampling site was carried out once to determine the influence of vegetation structure on sex abundances; for each habitat we recorded all trees ≥ 10 cm dbh within a 0.1 ha (20 × 50 m) plot (Gentry 1982). Transects were located along streams in riparian continuous forest and riparian pasture habitats and randomly located in continuous forest and pasture habitats. We considered the following vegetation attributes: number of individuals (NI), number of species (NS), total basal area (BA), and tree height (H). We performed nonmetric multidimensional scaling analyses (NMDS) to obtain a continuous synthetic variable summarizing dissimilarity patterns among vegetation structures. The scores of axis 1 were used as an explanatory variable for evaluating differential sex response to vegetation structure.

Data Analyses

Data analyses were performed considering only the six most abundant bat species: *Artibeus jamaicensis*, *Artibeus lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga* *soricina* and *Platyrrhinus helleri*. Firstly, we compared capture rates for each sex among habitats by using a standardized capture rate (captures/1000 mist net hour) that compensated for differences in number of nets, size of nets and length of times nets were open (Perry *et al.* 2010). We compared capture rates using analysis of variance on ranks (ANOVA). Secondly, we fitted a general linear mixed model (GLMM) with binomial error distribution and logit link to determine the influence of vegetation traits on male and female abundance. In order to assess the relative effects of the explanatory variables on males in comparison to females, the model was run with the proportion of females to males per night (n = 70) as the response variable, with "site" as a random factor (Lintott *et al.* 2014). We considered the following explanatory variables: habitat type; Vba, total tree basal area; Vab, total number of trees; Vrich , number of trees species; Vh , average height of trees; Vspcomp , scores of NMDS axis 1. For each model, we calculated Akaike's information criterion (AICc) corrected for small sample size following Burnham and Anderson (2002). This approach allowed us to select the most plausible models from a set of models. Only models with an AICc lower than the null model were considered to define the 95% confidence set of plausible models. All analyses were performed with R v. 1.0.136 (R Core Team 2016).

RESULTS

Proportion of sexes

Over 70 nights, 34 during the dry season and 36 during the rainy season, we captured a total of 1752 individuals belonging to 28 species of the Phyllostomidae family (de la Peña-Cuellar, et al. 2015). For the analyses however, we considered only 1365 individuals (78 % of all captures) belonging to the six most abundant species (*Artibeus jamaicensis* (11%), *Artibeus lituratus* (23%), *Sturnira lilium* (30%), *Carollia perspicillata* (3%), *Glossophaga soricina* (6%) and *Platyrrhinus helleri* (5%), which were also present in all habitats. Overall, 43 % of the sampled individuals from the six bat species considered were males, while 57 % were females. The capture rates were significantly skewed towards females (F = 5.282, P < 0.001) (Fig. 2). Riparian pasture, was the habitat with the highest female capture rates (433 indv, 2.14 capture rate), followed by riparian continuous forest (152, 0.75) and pasture (141, 0.69) and continuous forest was the habitat with the lowest female capture rates (50, 0.28) (Fig. 2).

Vegetation attributes

The vegetation of riparian habitats (RM y RP) showed a higher structural complexity than M and P. Despite of the fact that RM contained more trees than RP, they showed similar average canopy height (13.63 m and 13.12 m in RM and RP, respectively), whereas in MF tree height was 10.6 m and in OP 9.7 m, the lowest recorded . On the other hand, whereas in non-riparian old-growth habitat basal area was 8561.03 m^2/0.1ha and, 6241.88 m2/0.1 ha in pasture, riparian old-growth forest accounted 25,639.51 m^2/0.1 ha and riparian pasture 20,285.77 m^2/0.1ha (Table 1).

Sex ratio and habitat traits

Seasonality and habitat type were the best explanatory variables describing the presence of females for *A. jamaicensis*; while for of *S. lilium*, vegetation structure and seasonality appeared as the most important variables explaining the presence of females. In the case of *G. soricina* we found that the presence of females was positively related to vegetation structure including total basal area and average tree height (Table 2).

DISCUSSION

Overall, the results showed differences in the susceptibility of males and females to cope with habitat disturbance. The sex ratio was skewed towards females, which is an expected pattern for the harem species (*A. jamaicensis* and *A. lituratus*) (de Mello & Fernandez 2000). Furthermore, the results provide insights into the relative importance of different habitats for a specific sex. Except for Mature Forest, overall capture rates of females were greater than those of males; this pattern might imply that females of some bat species may increase their activity (e. g., foraging and/or drinking) during lactation when energy and water requirements increase (Barclay 1989; Adams & Hayes 2008).

Unlike males, females need to return at night to the maternity roost to nurse their young which probably limits female foraging areas and restricts foraging females to the profitable areas located in the proximity of their roosts (van Toor *et al.* 2011). In contrast, males may have greater survival than females (Keen & Hitchcock 1980; Kurta & Matson 1980), because males are not subject to the additional energetic pressures associated with pregnancy and lactation. We found that capture rates in pastures were predominately towards females. The prevalence of females may be related to the high energy demanding of flying in cluttered habitat than flying in more open areas (Grodzinski *et al.* 2009), due to the elevated energetic costs associated with higher vegetation complexity might represent a particularly high burden for females during pregnancy and while nursing, males otherwise prefer sites with greater vegetation cover possibly related to roost defense (Henry & Kalko 2007; Rocha *et al.* 2017).

Sex ratio and habitat quality

We did not find significant differences in the sex ratio for *A. jamaicensis*, *C. perspicillata* and *P. helleri* suggesting that males and females use habitats similarly. In contrast, according to our hypothesis, we found that females of *A. lituratus* exhibit a strong relationship with habitat quality. *Artibeus lituratus* is the largest species of Stenodermatinae, and as in other mammals, larger species could be more sensitive to human habitat perturbation (Lande 1987). Nevertheless, the high number of females reflect selective foraging in a resource rich environment and higher roost availability in forested habitats. Even though *Artibeus* species may cross inhospitable matrix areas in fragmented landscapes, covering different vegetation types and flying distances ranging from 5 to 10 km (Galindo-González 1998), females of *A. lituratus* might locally depend on temporal foliage roosts, and prefer larger trees within the dense and shaded vegetation of mature forest that can provide energetic and thermal requirements to leave the young while foraging (Evelyn & Stiles 2003; Bianconi, Mikich & Pedro 2006; Arnone *et al.* 2016). For the same study area *A. lituratus* has shown to select roosts with high humidity located in trees with the greatest basal areas (Ortiz-Ramírez *et al.* 2006).

Sex ratio and seasonality

The importance of seasonality for *A. lituratus* and *S. lilium* females might reside on the differences in abundance or diversity of food resources between the wet and dry seasons. Seasonal fluctuations in rainfall influence phenology of fruiting plants and affects productivity in tropical forests (Janzen 1967). In tropical regions, usually the rainy season corresponds to greatest fruit abundance and the dry season with fewer food resources (Smythe 1986). Food abundance due to seasonality can result in shortened flights during the exploration for food and roost sources, whereas during the dry season when food resources are often scarce, females tend to increase foraging movements into resource rich secondary forest areas to compensate for the elevated energetic burden associated with pregnancy and milk production (Rocha et al. 2017). This increases the importance of vegetation characteristics associated to the reproduction's energetic demand (pregnancy, lactation, roost defense) (Charles-Dominique 1991; Klingbeil & Willig 2010).

Furthermore, some studies have argued that Glossophaginae are resilient to land use change (Willig *et al.* 2007). Our data indicate that the presence of *G. soricina* females is significantly and positively correlated to vegetation attributes such as tree height and basal area, supporting the idea that the species is an habitat specialist (Aguiar, Bernard & Machado 2014).The association between females of *G. soricina* with large trees could be due to the fact that large trees can provide a greater availability of roosts and foraging opportunities (Evelyn & Stiles 2003; Ortiz-Ramírez *et al.* 2006). There is evidence showing food differentiation between the sexes for individuals of *G*. *soricina* in the same area where females preferred a food item (plant) different from males (Alvarez & Sánchez-Casas 1999). Supporting the idea that during pregnancy and breeding season females feed on the nearest available resource and males fly larger distances to other feeding areas (Sosa, De Ascencao & Soriano 1996). This foraging behavior might reduce the activity of *G. soricina* to habitats with high resource availability which limits their activity to small home ranges and increases the susceptibility to local extinction (Arita & Santos-del-Prado 1999).

Implications for conservation and future research

Our results show that in addition to trait filtering, responses of Neotropical bat communities associated to riparian habitat within a human dominated matrix are sex-specific. The understanding of changes in sex ratio may help to a better understanding of the pervasive consequences of forest loss, fragmentation, and habitat deterioration. Sex-specific studies are critical to habitat managers because practices used to promote habitat conditions favorable for females may not be equally beneficial to males and the opposite (Perry, Thill & Carter 2007). Our results suggests that the structural complexity of the vegetation and large trees influence the presence of females of *G. soricina*. In these sense management efforts should promote a riparian vegetation cover with large basal area of trees that has shown to be important for the conservation of the entire bat community. Even though our analysis was restricted to six common bat species, we assumed that the maintenance of habitats that favor habitat generalist species should also benefit bat species that are more habitat specialized (Istvanko, Risch & Rolland 2016; Rocha *et al.* 2017). Therefore, we encourage the inclusion of species of sensitive trophic guilds (gleaning insectivores and carnivores) and particularly roosting habits emphasizing adequate protection of females in conservation plans. Conservation actions towards female protection are particularly important due to their high level of parental investment associated with rearing pups (Istvanko *et al.* 2016). The management decisions that do not guarantee the protection of the habitat frequently used by female bats would likely have detrimental long term consequences on their reproduction, jeopardizing the dynamics and long-term persistence (van Toor *et al.* 2011; Frank *et al.* 2016).

In human dominated landscapes, pastures cannot sustain the same species richness of bats as old-growth forest and riparian vegetation (de la Peña-Cuéllar *et al.* 2015a). Moreover, pastures seem to have a large effect on bat population dynamics, which cause detrimental effects on the ecosystem services provided by bats and in the recovery of degraded areas. Additional research is needed to directly examine the effects of pregnancy and lactation on habitat selection by bats. We encourage radio-tracking studies that can show specific habitat use of males and females (roost and foraging areas) and if there exists temporally segregation between sexes; this could provide information about how different habitats have an impact in the demography of bat populations.

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References

Abbott, I.M., Sleeman, D.P. & Harrison, S. (2009) Bat activity affected by sewage effluent in Irish rivers. *Biological Conservation*, **142**, 2904–2914.

Adams, R.A. & Hayes, M.A. (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, **77**, 1115–1121.

Aguiar, L.M.S., Bernard, E. & Machado, R.B. (2014) Habitat use and movements of Glossophaga soricina and Lonchophylla dekeyseri (Chiroptera : Phyllostomidae) in a Neotropical savannah. *Zoologia*, **31**, 223–229.

Altringham, J.D. (2011) *Bats: From Evolution to Conservation*, 2nd ed. Oxford University Press, Oxford.

Alvarez, T. & Sánchez-Casas, N. (1999) Diferenciación alimentaria entre los sexos de Glossophaga soricina (Chiroptera: Phyllostomidae) en México. *Revista de Biologia Tropical*, **47**, 1129–1136.

Arita, H.T. & Fenton, M.B. (1997) Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology and Evolution*, **12**, 53–58.

Arita, H.T. & Santos-del-Prado, K. (1999) Conservation Biology of Nectar-Feeding Bats in Mexico. *Journal of Mammalogy*, **80**, 31–41.

Arnone, I.S., Trajano, E., Pulchério-Leite, A. & Passos, F.C. (2016) Long-distance movement by a great fruit-eating bat, Artibeus lituratus (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica*, **16**, 1–6.

Barclay, R.M.R. (1989) The effect of reproductive condition on the foraging behavior of female hoary bats, Lasirurus cinereus. *Behavioral Ecology and Sociobiology*, **24**, 31–37.

Barlow, K.E. (1997) The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology*, **243**, 597–609.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2014) Fitting linear mixed-effects models using lme4 Douglas. *Journal of Statistical Software*, 1–51.

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2016) Sexual segregation when foraging in an extremely social killer whale population. *Behavioral Ecology and Sociobiology*, **70**, 189–198.

Bender, D. J., Contreras, T. A., Fahrig, L. (1998) Habitat Loss and Population Decline : a Meta-Analysis of the Patch Size Effect. *Ecology*, **79**, 517–533.

Bernard, E. & Fenton, M.B. (2002) Species diversity of bats (Mammalia : Chiroptera) in forest fragments , primar ...

Bhagwat, S.A., Willis, K.J., Birks, H.J.B. & Whittaker, R.J. (2008) Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution*, **23**, 261–267.

Bianconi, G. V, Mikich, S.B. & Pedro, W.A. (2006) Movements of bats (Mammalia , Chiroptera) in Movements Chiropteroptera) Atlantic For est remnants in southern Brazil Forest remnants southern Brazil. *Revista Brasileira de Zoologia*, **23**, 1199–1206.

van Breugel, M., Martínez-Ramos, M., Bongers, F., Martinez-Ramos, M. & Bongers, F. (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, **22**, 663–674.

Broders, H.G., Forbes, G.J., Woodley, S. & Thompson, I.D. (2006) Range extent and stand selection for roosting and foraging in forest-dwelling Northern Long-eared Bats and Little Brown Bats in the Greater Fundy ecosystem, New Brunswick. *Journal of Wildlife Management*, **70**, 1174–1184.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Castro-Luna, A.A., Sosa, V.J. & Castillo-Campos, G. (2007) Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, **10**, 219–228.

Chacón, M. & Harvey, C.A. (2006) Live fences and landscape connectivity in a neotropical agricultural landscape. *Agroforestry Systems*, **68**, 15–26.

Charles-Dominique, P. (1991) Feeding strategy and activity budget of the frugivorous bat Carollia perspicillata (Chiroptera: Phyllostomidae) in French Guiana. *Journal of Tropical Ecology*, **7**, 243.

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, **21**, 523–533.

Comisión Federal de Electricidad. (2006) *División Hidrométrica Sureste.* Estación Lacantún, Marqués de Comillas, Chiapas, México.

CONAFOR. (2016) *Manual de Mejores Prácticas de Manejo Forestal Para La Conservación de*

La Biodiversidad En Ecosistemas Tropicales de La Región Sureste de México. Ciudad de México.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A Trait-Based Test for Habitat Filtering : Convex Hull Volume. , **87**, 1465–1471.

Cosson, J.F., Pons, J.M. & Masson, D. (1999) Effects of Forest Fragmentation on Frugivorous and Nectarivorous Bats in French Guiana. , 515–534.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Denzinger, A. & Schnitzler, H.U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, **4 JUL**, 1–15.

Diamond, G.F. & Diamond, J.M. (2014) Bats and Mines: Evaluating Townsend's Big-Eared Bat (Corynorhinus townsendii) Maternity Colony Behavioral Response to Gating. *Western North American Naturalist VO - 74*, **74**, 416.

Dietz, M., Kalko, E.K. V & Encarnação, J.A. (2006) Small scale distribution patterns of female and male Daubenton's bats (Myotis daubentonii). *Acta Chiropterologica*, **8**, 403–415.

Dirzo, R. & Raven, P.H. (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, **28**, 137–167.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, **23**, 849–860.

Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S. & Hamer, K.C. (2014) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation*, **17**, 163–173.

Encarnação, J.A. (2012) Spatiotemporal pattern of local sexual segregation in a tree-dwelling temperate bat Myotis daubentonii. *Journal of Ethology*, **30**, 271–278.

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

Estrada, A. & Coates-Estrada, R. (2002) Bats in continous forest, forest fragments and in an agricultural mosiac habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, **103**, 237–245.

Evelyn, M.J. & Stiles, D. a. (2003) Roosting requirements of two frugivorous bats (Sturnira lilium and Arbiteus intermedius) in fragmented Neotropical forest. *Biotropica*, **35**, 405–418.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C., Chazdon, R.L. & Sanchun, A. (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, **8**, 034017.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, **52**, 1381–1391.

Fenton, A.M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K., Syme, D.M. & Adkins, B. (1992) Phyllostomid Bats (Chiroptera : Phyllostomidae) as Indicators of Habitat Disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Frank, H.K., Mendenhall, C.D., Judson, S.D., Daily, G.C. & Hadly, E.A. (2016) Anthropogenic impacts on Costa Rican bat parasitism are sex specific. *Ecology and Evolution*, **6**, 4898–4909.

Freudmann, A., Mollik, P., Tschapka, M. & Schulze, C.H. (2015) Impacts of oil palm agriculture on phyllostomid bat assemblages. *Biodiversity and Conservation*, **24**, 3583–3599.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, **75**, 1252–1258.

Galindo-González, J. (1998) Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. *Acta Zoologica Mexicana*, 57–74.

Galindo-González, J. & Sosa, V.J. (2003) Frugivorous Bats in Isolated Trees and Riparian Vegetation Associated With Human-Made Pastures in a Fragmented Tropical Landscape. *The Southwestern Naturalist*, **48**, 579–589.

Garcia-Martínez, M.A., Escobar-Sarria, F., Pez-Barrera, F.L., Castano-Meneses, G. & Lez, J.E.V.G. (2015) Value of Riparian Vegetation Remnants for Leaf-Litter Ants (Hymenoptera: Formicidae) in a Human-Dominated Landscape in Central Veracruz, Mexico. *Environmental Entomology*, **44**, 1488–1497.

García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez, A.E. & Ávila-Gómez, E.S. (2016) Deforestation Impacts on Bat Functional Diversity in Tropical Landscapes. *Plos One*, **11**, e0166765.

Gorresen, P.M. & Willig, M.R. (2004) Landscape Responses of Bats To Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*, **85**, 688–697.

Grau, H.R. & Aide, M. (2008) Globalization and land-use transitions in Latin America. *Ecology and Society*, **13**.

Griscom, H.P., Kalko, E.K. V & Ashton, M.S. (2007) Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica*, **39**, 278–282.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed : evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii ? , 540–548.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: A case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842–850.

Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñóz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., Navas, A., Saenz, J., Sánchez, D., Medina, A., Vilchez, S., Hernández, B., Perez, A., Ruiz, F., López, F., Lang, I. & Sinclair, F.L. (2005) Contribution of live fences to the ecological integrity of agricultural landscapes.

Agriculture, Ecosystems and Environment, **111**, 200–230.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation\t. *Biodiversity and Conservation*, **13**, 207–251.

Henry, M. & Kalko, E.K. V. (2007) Froraging Strategy and Breeding Constraints of Rhynophyla Pumilio (PHYLLOSTOMIDAE) in the Amazon Lowlands. *Journal of Mammalogy*, **88**, 81–93.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) *Global Status Survey and Conservation Action Plan: Microchiropteran Bats*.

INE. (2000) *Programa de Manejo Reserva de La Biósfera Montes Azulez, México.* México.

Instituto Nacional de Ecología. (2000) *Programa de Manejo de La Reserva de La Biosfera Montes Azules*, 1a. Enkidu Editores, S.A. de C.V., México, D.F.

Istvanko, D.R., Risch, T.S. & Rolland, V. (2016) Sex-specific foraging habits and roost characteristics of Nycticeius humeralis in north-central Arkansas. *Journal of Mammalogy*, **97**, 1–9.

Jennings, N.V., Parson, S., Barlow, K.E. & Gannon, M.R. (2004) Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterologica*, **6**, 75–90.

Jennings, N. & Pocock, M.J.O. (2009) Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conservation Biology*, **23**, 1195–1203.

Jobin, B., Bélanger, L., Boutin, C. & Maisonneuve, C. (2004) Conservation value of agricultural riparian strips in the Boyer River watershed, Québec (Canada). *Agriculture, Ecosystems and Environment*, **103**, 413–423.

De Jong, B.H.J., Ochoa-Goana, S., Castillo-Santiago, M.A., Ramirez-Marcial, N. & Cairns, M.A. (2000) Carbon flux and patterns of land-use/land-cover change in het Selva Lacandona, Mexico. *A Journal of the Human Environment*, **29**, 504–511.

Jong, D. & Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13**_ _, 275–280.

Jung, K., Kalko, E.K. V & Von Helversen, O. (2007) Echolocation calls in Central American emballonurid bats: Signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.

Kalka, M. & Kalko, E.K. V. (2005) Gleaning bats as underestimated predators of herbivorous insects: diet of Micronycteris microtis (Phyllostomidae) in Panama. *Journal of Tropical Ecology*, **22**, 1.

Kalko, E.K. V & Handley, C.O. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.

Keen, R. & Hitchcock, H.H.B. (1980) Survival and longevity of the little brown bat (Myotis lucifugus) in southeastern Ontario. *Journal of Mammalogy*, **61**, 1–7.

Kelm, D.H., Wiesner, K.R. & Helversen, O. Von. (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conservation Biology*, **22**, 733–741.

Klingbeil, B.T. & Willig, M.R. (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest Brian. *Journal of Applied Ecology*, **46**, 203–213.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, **119**, 1654–1664.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kurta, A. & Matson, J.O.. (1980) Disproportionate Sex Ratio in the Big Brown Bat (Eptesicus fuscus). , **104**, 367–369.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015a) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015b) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**, 903–913.

de la Peña-Cuéllar, E., Stoner, K.E., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2012) Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. *Biodiversity and Conservation*, **21**, 1381–1397.

de la Torre, J.A., Núñez, J.M. & Medellín, R.A. (2017) Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. *Biological Conservation*, **206**, 270–282.

Lande, R. (1987) Extinction Thresholds in Demographic Models of Territorial Populations. *The American Naturalist*, **130**, 624–635.

Laurance, W.F. (1991) Society for Conservation Biology Ecological Correlates of Extinction Proneness in Australian Tropical Rain Forest Mammals. *Conservation Biology*, **5**, 79–89.

Laurance, W., Bierregaard, R. & Moritz, C. (1997) *Tropical Forest Remnants : Ecology, Management, and Conservation of Fragmented Communities*. University Of Chicago Press.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, **16**, 605–618.

Law, B. & Chidel, M. (2002) Tracks and Riparian Zones Facilitate the Use of Australian Regrowth Forest by Insectivorous Bats. *The Journal of Applied Ecology*, **39**, 605–617.

Lebrija-trejos, E., Pérez-garcía, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by : Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly. *Ecology*, **91**, 386–398.

Lemaître, J.-F., Gaillard, J.-M., Pemberton, J.M., Clutton-Brock, T.H. & Nussey, D.H. (2014) Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer. *Proceedings. Biological sciences / The Royal Society*, **281**, 20140792-.

Lenth, R.V. (2014) lsmeans: Least-square means.

Lintott, P.R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R.J., Olley, L. & Park, K.J. (2014) City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal society open science*, **1**, 1–8.

Lloyd, A., Law, B. & Goldingay, R. (2006) Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation*, **129**, 207–220.

Lobo, J.A., Quesada, M. & Stoner, K.E. (2005) Effects of pollination by bats on the mating system of Ceiba pentandra (Bombacaceae) populations in two tropical life zones in Costa Rica. *American Journal of Botany*, **92**, 370–376.

Lundy, M. & Montgomery, I. (2010) Summer habitat associations of bats between riparian landscapes and within riparian areas. *European Journal of Wildlife Research*, **56**, 385–394.

Martínez-Ramos, M. & García-Orth, X. (2007) Sucesión ecológica y restauración de las selvas húmedas. *Bol. Soc. Bot. Méx*, **80**.

Mayaux, P., Holmgren, P., Achard, F., Eva, H.D., Stibig, H.-J.J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **360**, 373–84.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesk, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.

McCracken, G.F. & Wilkinson, G.S. (2000) Bat Mating Systems. *Reproductive Biology of Bats*, pp. 321–362.

Mcgill, J. & Kalko, V. (2015) Climate , habitat , and species interactions at different scales determine the structure of a Neotropical bat community Author (s): Sergio Estrada-Villegas , Brian J . McGill and Elisabeth K . V . Kalko Published by : Ecological Society of America Stabl. , **93**, 1183–1193.

Medellin, R. a. (1994) Mammal Diversity and Conservation in the Selva-Lacandona, Chiapas, Mexico. *Conservation Biology*, **8**, 780–799.

Medellín, R. a, Equihua, M. & Amin, M. a. (2000) Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests\rDiversidad y Abundancia de Murciélagos como Indicadores de Perturbaciones en Selvas Húmedas Neotropicales. *Conservation Biology*, **14**, 1666–1675.

Medellín, R.A., Equihua, M. & Amin, M.A. (2011) *Identificación de Los Murciélagos de México: Clave de Campo*. México, D.F.

Medina, A., Harvey, C. a, Sánchez, D., Vílchez, S. & Hernández, B. (2007) Bat diversity and movement in a Neotropical agricultural landscape. *Biotropica*, **39**, 120–128.

Meli, P., Ruiz, L., Aguilar, R., Rabasa, A., Rey-Benayas, J.M. & Carabias, J. (2017) Bosques ribereños del trópico húmedo de México: Un caso de estudio and aspectos críticos para una restauración exitosa. *Madera Bosques*, **23**, 181–193.

de Mello, M.A.R. & Fernandez, F.A.S. (2000) Reproductive ecology of the bat Carollia perspicillata (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest. *International Journal of Mammalian Biology*, **65**, 340–349.

Meyer, C.F.J., Fr??nd, J., Lizano, W.P. & Kalko, E.K. V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.

Meyer, C.F.J. & Kalko, E.K. V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.

Miller, K., Chang, E. & Johnson, N. (2001) *Defining Common Ground for the Mesoamerican Biological Corridor*.

Montoya Gómez, G., Hernández Ruiz, J.F., Velasco Pérez, A., Reygadas, L. & Ramos Maza, T. (2006) Organización comunitaria para la conservación forestal: estudio de caso en la Selva Lacandona de Chiapas, México. *Papeles de población*, **14**, 11.

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. , 149–158.

Morrison, D.W. (1978) Lunar phobia in a neotropical fruit bat, Artibevs jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852–855.

Mouillot, D., Graham, N.A.J., Vill??ger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Muench, C. & Martínez-Ramos, M. (2016) Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico. *Tropical Conservation Science*, **9**, 178–202.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecological Applications*, **3**, 209–212.

Nardone, V., Cistrone, L., Di Salvo, I., Ariano, A., Migliozzi, A., Allegrini, C., Ancillotto, L., Fulco, A. & Russo, D. (2015) How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat Myotis daubentonii. *PLoS ONE*, **10**, 1–15.

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **316**, 335–427.

Nowak, R. (1991) *Walker's Mammals of the World*. Johns Hopkins Univ Pr.

Nupp, T. & Swihart, R. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512–526.

Ober, H.K. & Hayes, J.P. (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, **256**, 1124–1132.

Ortega, J. & Arita, H.T. (1999) Structure and Social dynamics of harem groups in Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, **80**, 1173–1185.

Ortega, J. & Maldonado, J.E. (2006) Female interactions in harem groups of the Jamaican fruit-eating bat, Artibeus jamaicensis (Chiroptera : Phyllostomidae). *Acta Chiropterologica*, **8**, 485–495.

Ortiz-Ramírez, D., Lorenzo, C., Naranjo, E. & León-Paniagua, L. (2006) Selección de refugios por tres especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en la Selva Lacandona, Chiapas, México. *Revista Mexicana de Biodiversidad*, **77**, 261–270.

Perry, R.W., Carter, S.A. & Thill, R.E. (2010) Temporal Patterns in Capture Rate and Sex Ratio of Forest Bats in Arkansas. *American Midland Naturalist*, **164**, 270–282.

Perry, R.W., Thill, R.E. & Carter, S.A. (2007) Sex-specific roost selection by adult red bats in a diverse forested landscape. *Forest Ecology and Management*, **253**, 48–55.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Pinto, N. & Keitt, T.H. (2008) Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, **117**, 1725–1731.

Presley, S.J., Willig, M.R., Wunderle, J.M. & Saldanha, L.N. (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology*, **45**, 14–25.

Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates Sunderland, Massachusetts.

Racey, P.A. (1998) The importance of the riparian environment as a habitat for British bats. *Symposia of the Zoological Society of London*, pp. 69–91. London: The Society, 1960-1999.

Racey, P.A. & Speakman, J.R. (1987) The energy costs of pregnancy and lactation in heterothermic bats. *Symposia of the zoological society of London*, pp. 107–125.

Ramos Pereira, M.J., Marques, J.T. & Palmeirim, J.M. (2010) Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in amazonian forests. *Biotropica*, **42**, 680–687.

Ramos Pereira, M.J., Marques, J.T., Santana, J., Santos, C.D., Valsecchi, J., De Queiroz, H.L., Beja, P. & Palmeirim, J.M. (2009) Structuring of Amazonian bat assemblages: The roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, **78**, 1163–1171.

Rocha, R., Ferreira, D.F., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B., Palmeirim, J.M. & Meyer, C.F.J. (2017) Does sex matter ? Gender-specific responses to forest fragmentation in Neotropical bats. *Biotropica*, 1–10.

Russo, D., Cistrone, L., Garonna, A.P. & Jones, G. (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodiversity and Conservation*, **19**, 2501–2515.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Jani, A., Katz, G., Soykan, C., Watts, J., Welter, J., Ecology, S., Jan, N. & Heffernan, J.I.M. (2005) Riparian Zones Increase Regional Species Richness by Harboring Different , Not More , Species. *Ecology*, **86**, 56–62.

Safi, K., König, B. & Kerth, G. (2007) Sex differences in population genetics, home range size and habitat use of the parti-colored bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biological Conservation*, **137**, 28–36.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321–1333.

Scott, S.J., McLaren, G., Jones, G. & Harris, S. (2010) The impact of riparian habitat quality on the foraging and activity of pipistrelle bats (Pipistrellus spp.). *Journal of Zoology*, **280**, 371–378.

Seaman, B.S. & Schulze, C.H. (2010) The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. *Biological Conservation*, **143**, 391–

398.

Senior, P., Butlin, R.K. & Altringham, J.D. (2005) Sex and segregation in temperate bats. *Proceedings. Biological sciences / The Royal Society*, **272**, 2467–73.

Sgroi, M.P. & Wilkins, K.T. (2010) Roosting Behavior of the Mexican Free-Tailed Bat (Tadarida Brasiliensis) in a Highway Overpass. *Western North American NaturaHst63*, **63**, 366–373.

Smith, P.G. & Racey, P.A. (2008) Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *Journal of Zoology*, **275**, 314–322.

Sosa, M., De Ascencao, A. & Soriano, P. (1996) Dieta y patrón reproductivo de Rhogessa minutilla (Chiroptera: Vespertilionidae) en una zona árida de Los Andes de Venezuela. *Revista de Biología Tropical*, **44**, 867–875.

Soule, M.E. & Gilpin, M.E. (1991) The teory of wildlife corridor capability. *Nature Conservation 2: The Role of Corridors* (eds D.A. Saunders & R.J. Hobbs), pp. 3–8. Surrey Beatty and Sons, Chipping Norton, Australia, New South Wales, Australia.

StrauB, A., Reeve, E., Randrianiaina, R.-D., Vences, M. & Glos, J. (2010) The world 's richest tadpole communities show functional redundancy and low functional diversity : ecological data on ecological data on Madagascar 's stream-dwelling amphibian larvae. *BMC Ecology*, **10**, 1–10.

Taylor, P.D., Fahrig, L. & Henein. (1993) Connectivity is a Vital Element of Landscape Structure. *Oikos*, **68**, 571–573.

Tilman, D. (2001) Functional Diversity. *Encyclopedia of Biodiversity*, pp. 587–596.

van Toor, M.L., Jaberg, C. & Safi, K. (2011) Integrating sex-specific habitat use for

conservation using habitat suitability models. *Animal Conservation*, **14**, 512–520.

Turner, I.M. (1996) Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Society*, **33**, 200–209.

La Val, R. (2017) Banding Returns and Activity Periods of Some Costa Rican Bats. *The Southwestern Naturalist*, **15**, 1–10.

Vandermeer, J. & Perfecto, I. (2007) The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, **21**, 274–277.

Villéger, Mason & Mouillot. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Ramos Miranda, J., Flores Hernández, D. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological applications*, **20**, 1512–1522.

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

Vleut, I., Levy-Tacher, S.I., Galindo-González, J., de Boer, W.F. & Ramírez-Marcial, N. (2012) Tropical rain-forest matrix quality affects bat assemblage structure in secondary forest patches. *Journal of Mammalogy*, **93**, 1469–1479.

Walsh, A.L. & Harris, S. (1996) Foraging Habitat Preferences of Vespertilionid Bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Warkentin, I.G., Greenberg, R. & Ortiz, J.S. (1995) Songbird use of Gallety Woodlands in Recently Cleared and Older Settled Landscapes of the Selva Lacandona, Chiapas, Mexico. *Conservation Biology*, **9**, 1095–1106.

Wearmouth, V.J. & Sims, D.W. (2008) Sexual Segregation in Marine Fish , Reptiles , Birds and Mammals : Behaviour Patterns , Mechanisms and Conservation Implications., pp. 108–170.

Weller, T.J., Cryan, P.M. & O'Shea, T.J. (2009) Broadening the focus of bat conservation and research in the USA for the 21st century. *Endangered Species Research*, **8**, 129–145.

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245–258.

Williams-Guillén, K. & Perfecto, I. (2010) Effects of agricultural intensification on the bat assemblage in a coffee landscape in Chiapas, Mexico. *Biotropica*, **42**, 605–613.

Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008) Bats limit insects in a neotropical agroforestry system. *Science (New York, N.Y.)*, **320**, 70.

Willig, M., Presley, S.J., Bloch, C.P., Yanoviak, S.P., Díaz, M.M., Arias Chauca, L., Pacheco, V. & Weaver, S.C. (2007) Phyllostomid Bats of Lowland Amazonia: Effects of Habitat Alteration on Abundance. *Biotropica*, **39**, 737–746.

Wordley, C.F.R., Sankaran, M., Mudappa, D. & Altringham, J.D. (2017) Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biological Conservation*, **210**, 48–55.

Zarazúa-Carbajal, M., Avila-Cabadilla, L.D., Alvarez-Añorve, M.Y., Benítez-Malvido, J. & Stoner, K.E. (2017) Importance of riparian habitat for frugivorous bats in a tropical dry forest in western Mexico. *Journal of Tropical Ecology*, **33**, 74–82.

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J. & Martínez-

Ramos, M. (2015) Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, **18**, 443–455.

Table 1. Tree community attributes in four different habitat types in a rain forest, Chiapas, Mexico. The values are data of ten 50 × 2 m transects (0.1 ha) in each habitat. Only trees with diameter at breast height > 10 cm were measured.

Vegetation attributes	**Riparian vegetation in old-growth forest**	**Riparian vegetation in pasture**	**Old-growth forest**	**Pasture**
Number of individuals	182	101	55	37
Number of species	46	46	29	17
Total basal AREA (m^2ha^{-1})	25639.51	20285.77	8561.030	6241.88
Tree height (m)	13.63	13.12	10.69	6.6

Table 2. Results of Akaike information criterion (AIC)-based model selection, assessing the association between the proportion of bat females and the explanatory variables including season and vegetation attributes. Confidence set of plausible models (95 %) explaining the variation in response variables. Only highest ranked models explaining gender variation for each species are shown.

BAT SPECIES	***FACTOR***	***K***	***logLik***	***AICc***	***Δi***	***wi***
Artibeus lituratus	Season	3	-72.49	151.35	0.00	1
	Habitat	3	-89.39	185.15	33.80	0
Sturnira lilium	*Vegetation structure*	*3*	*-86.88*	*180.12*	*0.00*	*0.88*
	Season	*3*	*-89.03*	*184.42*	*4.30*	*0.98*
Glossophaga soricina	*Total tree basal area*	*3*	*-26.45*	*59.27*	*0.00*	*0.63*
	Average height of trees	*3*	*-28.23*	*62.82*	*3.55*	*0.74*

K, number of estimated parameters; logLik, log-likelihood; AIC*c*, sampled-sized adjusted Akaike information criterion; Δ*i*, Akaike differences; and *wi*, Akaike weights. Response variable: proportion of females to males per night. Explanatory variables: Habitat, Season (rainy, dry), Vegetation structure (using scores of NMDS axis), Total basal area at each site, Average height of trees at each site.

Figure 1. Study area and bat sampling sites at the Lacandona rain forest, Chiapas, Mexico. The map shows the distribution of the habitat types used to sample bat species: riparian vegetation in mature forest (RM), riparian vegetation in pasture (RP), mature forest (MF), Pasture (P).

Figure 2. Capture rate (bats/mist net hour) of males and females of the six species across different habitat types at the Lacandona rain forest in the dry and rainy seasons.

Figure 3. Diagram of chapter II summary.

Figure 1

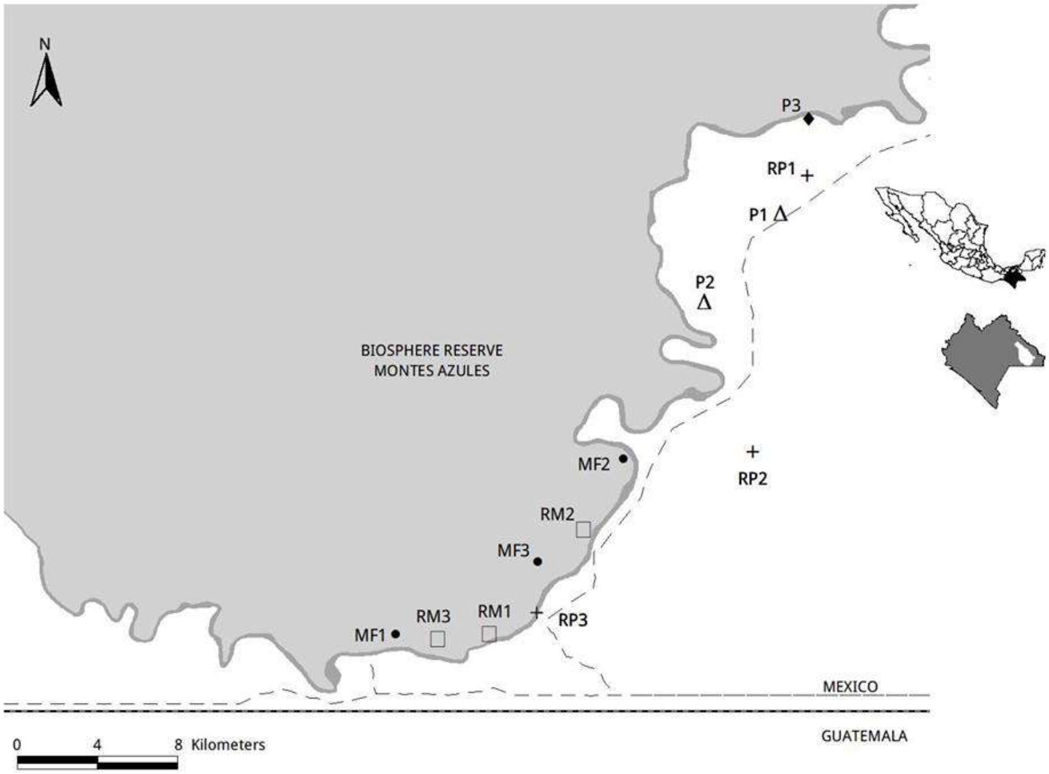

N
P3
RP1
P1
P2
BIOSPHERE RESERVE
MONTES AZULES
MF2
RP2
RM2
MF3
RM1
RM3
MF1
RP3
MEXICO
GUATEMALA
0
4
8 Kilometers

Figure 2

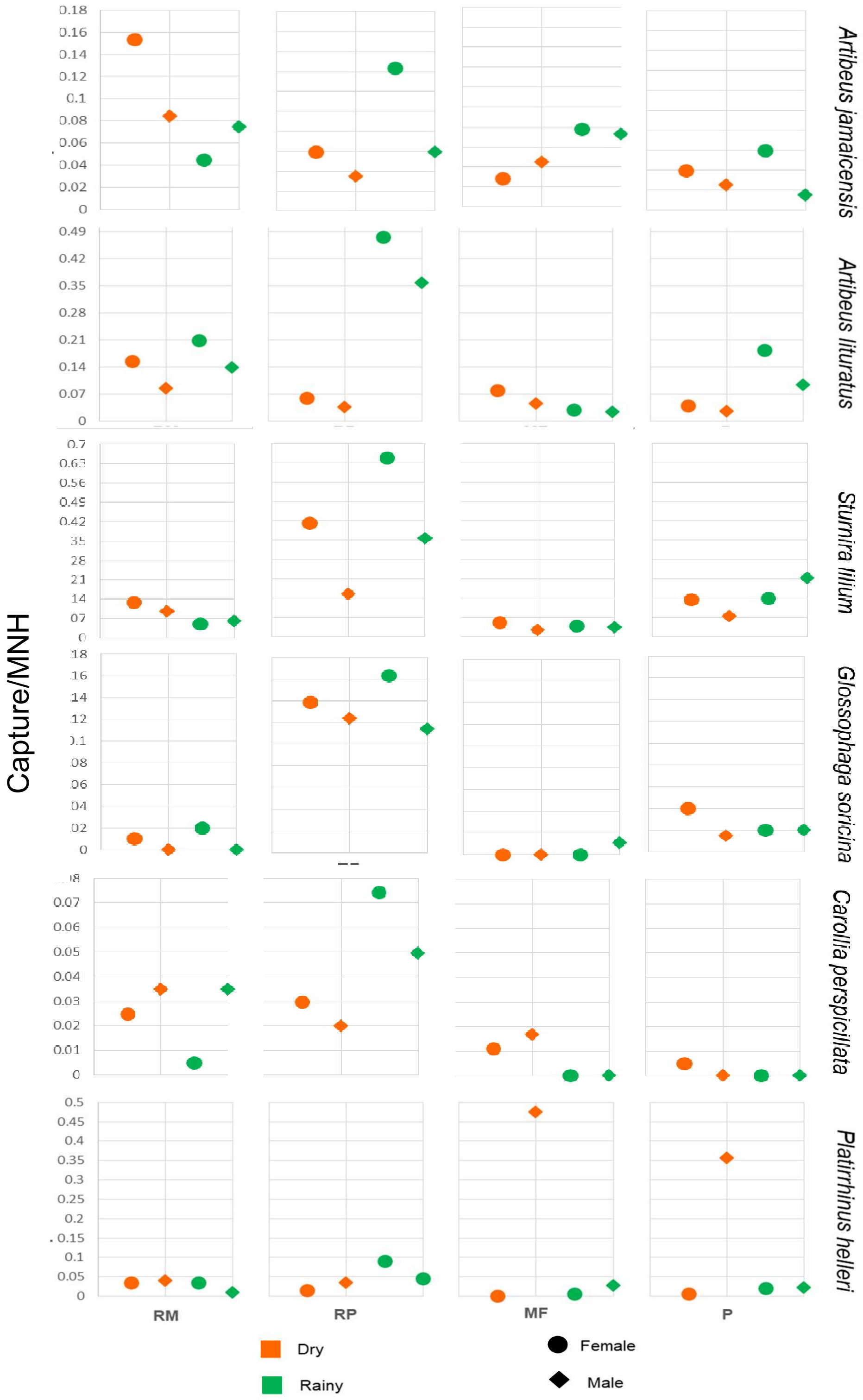
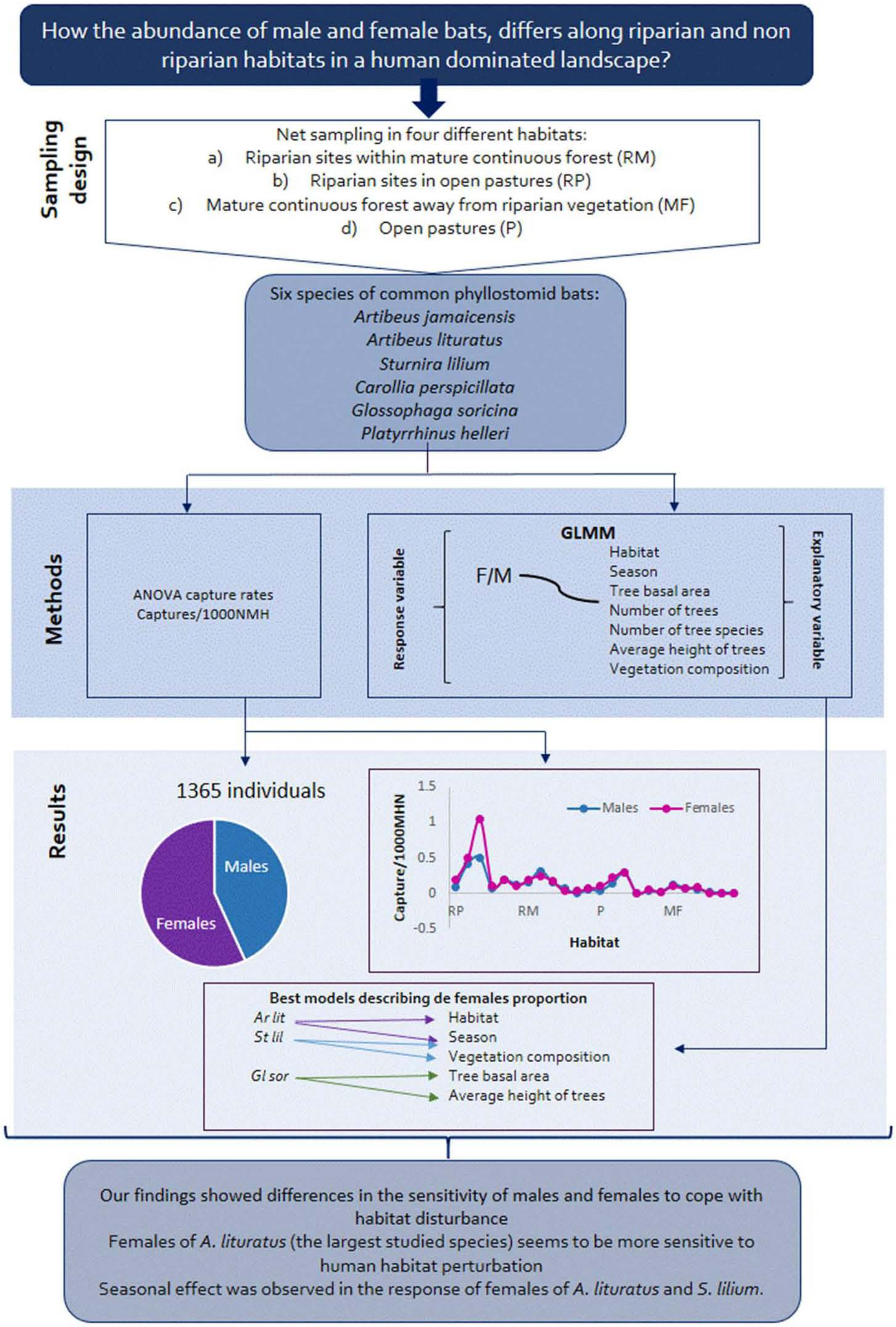

Capture/MNH
Artibeus jamaicensis
Artibeus lituratus
Sturnira lilium
Glossophaga soricina
Carollia perspicillata
Platirrhinus helleri
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
0.49
0.42
0.35
0.28
0.21
0.14
0.07
0
0.7
0.63
0.56
0.49
0.42
35
28
21
14
07
0
18
16
14
12
0.1
08
06
04
02
0
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
RM
RP
MF
P
Dry
Rainy
Female
Male

Figure. 3


How the abundance of male and female bats, differs along riparian and non riparian habitats in a human dominated landscape?
Sampling design
Net sampling in four different habitats:
a) Riparian sites within mature continuous forest (RM)
b) Riparian sites in open pastures (RP)
c) Mature continuous forest away from riparian vegetation (MF)
d) Open pastures (P)
Six species of common phyllostomid bats:
Artibeus jamaicensis
Artibeus lituratus
Sturnira lilium
Carollia perspicillata
Glossophaga soricina
Platyrrhinus helleri
Methods
ANOVA capture rates
Captures/1000NMH
GLMM
Response variable
F/M
Habitat
Season
Tree basal area
Number of trees
Number of tree species
Average height of trees
Vegetation composition
Explanatory variable
Results
1365 individuals
Males
Females
Capture/1000MHN
1.5
1
0.5
0
-0.5
RP
RM
P
MF
Habitat
Males
Females
Best models describing de females proportion
Ar lit
St lil
Gl sor
Habitat
Season
Vegetation composition
Tree basal area
Average height of trees
Our findings showed differences in the sensitivity of males and females to cope with habitat disturbance
Females of A. lituratus (the largest studied species) seems to be more sensitive to human habitat perturbation
Seasonal effect was observed in the response of females of A. lituratus and S. lilium.

CAPÍTULO III

BAT FUNCTIONAL DIVERSITY AND TRAIT FILTERING IN A TROPICAL AGRICULTURAL LANDSCAPE

Bat functional diversity and trait filtering in a tropical agricultural landscape

Erika de la Peña-Cuéllar[1], Gabriela Rodríguez-Barrera[2], John D. Altringham[2], Julieta Benítez-Malvido[1]

[1]Instituto de Investigaciones en Ecosistema y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

[2]School of Biology, University of Leeds, Leeds, United Kingdom

Corresponding author: erikapc@cieco.unam.mx

Preparado para: **Functional Ecology**

Abstract

Land use change and deforestation have negative implications for Neotropical bat species, populations and communities. Compared to taxonomic species richness the use of traits to explore functional diversity can provide a broader spectrum of ecosystem interactions. Based on bat species functional traits we analyzed bat responses to habitat modification within an agricultural landscape in the south of Mexico. For three years we recorded bat species within mature continuous forest with and without riparian vegetation and within open pastures with and without riparian vegetation. We measured the following traits in bats: skull form, forearm length and frequency of echolocation calls. Furthermore, we also determined functional evenness, divergence and specialization of the bat community. Overall, results show that relative to mature forest habitats, bats in pastures had smaller skulls, shorter forearms and species echolocated with higher frequency calls. Furthermore, bats in mature forests had higher functional evenness, divergence and specialization, with mature forest habitats providing refuge for species with the more extreme traits. Finally, riparian vegetation presented greater species richness, abundance and variety of bat functional traits. Our results support the suggestion that it is essential to include large mature forest tracks in tropical agricultural landscapes in order to conserve highly specialist bat species that are absent from disturbed habitats.

INTRODUCTION

Major land use changes as a consequence of agricultural expansion can have serious consequences for global biodiversity, through habitat loss and fragmentation (Laurance & Bierregaard 1997; Lindenmayer & Fischer 2006;). Furthermore, habitat loss and fragmentation are highly linked with local extinction rates (Laurance 1991; Turner 1996). Tropical agricultural landscapes usually contain forest fragments of native vegetation, active pasture lands and old-fields, different crops, and strips of riparian vegetation, among other land-uses (Warkentin *et al.* 1995). The maintenance of forest fragments and biodiversity-friendly agroforestry plantations in agricultural landscapes are management practices that can support local biodiversity, help to maintain viable populations of many species and increase resilience to climate change (Vandermeer & Perfecto 2007). A similar effect has been observed when maintaining strips of riparian vegetation in the agricultural landscapes. Landowners frequently maintain riparian vegetation due to the ecological services they provide such as erosion and flood controllers, and as filters of sediments and contaminants. This riparian vegetation remnants are known to be highly dynamic, acting as corridors for animal movement and dispersal as well as for providing food and shelter, with positive impacts to landscape biodiversity (Naiman et al. 1993; Lees & Peres 2007; Gillies & St. Claire 2008; Grey et al. 2014).

In the Neotropics many studies have suggested that bat community abundance and richness are directly affected by land use change (Fenton *et al.* 1992; Medellín *et al.* 2000; Estrada & Coates-Estrada 2002; Gorresen & Willig 2004; Schulze *et al.* 2004; de la Peña-Cuéllar *et al.* 2012). Bats have been suggested as a good model group for the study of functional traits because of their varied trophic guilds and of their important ecological roles as pest controllers, seed dispersers and pollinators (Medellín *et al.* 2000). Most studies on the impacts of human-modified landscapes on bat communities have focused on species richness and abundance (Henle *et al.* 2004), however, the inclusion of trait and functional diversity variables have appeared as important tools to better understand the interactions between animals and their habitats (Violle *et al.* 2007; Duchamp & Swihart 2008; Meyer *et al.* 2008; Cadotte, Carscadden & Mirotchnick 2011; Farneda *et al.* 2015; Mcgill & Kalko 2015; Wordley *et al.* 2017).

In addition, functional diversity enables us to identify the traits being filtered in a particular habitat, compared to simply identifying which species are able to persist (Meyer & Kalko 2008; Hanspach *et al.* 2012; Edwards *et al.* 2014; Farneda *et al.* 2015).The trait filtering concept suggests that habitat characteristics and environmental factors affect biodiversity patterns by acting as a filter that favors certain traits over others (Villéger *et al.* 2008; Lebrija-trejos *et al.* 2010; Mouillot *et al.* 2013). Using bats as models for the study of functional traits provides a good understanding of habitat interactions and disturbance effects (Duchamp & Swihart 2008; Flynn *et al.* 2009; Farneda *et al.* 2015; Wordley *et al.* 2017). Furthermore, utilizing ecologically realistic models like functional diversity analysis could provide a better understanding of how species coexist and would facilitate decision making for conservation purposes (Mayfield *et al.* 2010; Cadotte *et al.* 2011).

It is imperative to understand how species react to habitat disturbance and to comprehend the relationships between these interactions and habitat characteristics so we can implement effective conservation strategies (Bernard & Fenton 2002; Bhagwat *et al.*

2008; Cardoso et al. 2011;Fahrig *et al.* 2011; Mouillot *et al.* 2013). Based on bat functional traits, we used the metrics to assess bat assemblage responses among habitats in an agricultural tropical landscape of southern Mexico. This approach could provide important tools for management decisions on this highly biodiverse region in need of protection (Edwards et al. 2013; Farneda *et al.* 2015; Wordley *et al.* 2017). The aim of this study was to quantify bat functional diversity and trait filtering in riparian and non-riparian habitat within an agricultural-pasture landscape of Chiapas, Mexico, with a focus on understanding the specific effects that habitats have on certain traits.

METHODS

The fieldwork was conducted in the region of Marqués de Comillas south of the Montes Azules Biosphere Reserve (MABR) (16°04' N; 90°45'W approximately) in the Lacandona tropical rain forest in the State of Chiapas, Mexico. The original vegetation of the area consists of lowland tropical rain forest, with mean annual temperature of 24°C and average annual rainfall of 3000 mm (Comisión Federal de Electricidad 2006; van Breugel *et al.* 2006). In Mexico, the Lacandon Forest is the largest remnant of tropical rain forest, constituting the most diverse ecosystem and sustaining the only Mexican populations of many species (Medellin 1994). Land use change in the region began in the 1970s resulting in large scale deforestation and reducing the total area of mature forest from 95% land cover in 1976 to 56% in 1996 (Jong & Reid 1998). The main land use practices are agricultural fields of maize and other crops, cattle pastures, and patches of secondary and old-growth forest (De Jong *et al.* 2000). Mature continuous forest sites were located in the 330,000 ha MABR on the north side of the Lacantún River (INE 2000).

Site selection

Twelve sites where permanently established consisting in: three riparian sites within mature continuous forest (RF), three riparian sites in pastures (RP), three mature continuous forest (F), and three open pastures away from riparian vegetation (P). Sites where at least 1.5 km away from each other. Streams were permanent (although with variable water flow through the year); stream width varied from 2 to 8 m. Sites in pastures were located in the Marqués de Comillas municipality, on the south side of the Lacantún River. Mature continuous forest sites were located on the north side of the river, in the Montes Azules Biosphere Reserve (MABR) (330, 000 ha; 16°04´N-90°45´W; Fig. 1).

Bat sampling

For three consecutive years (2011-2013) bat sampling was performed twice in the rainy and twice in the dry season (December to May – dry season and June to November – wet season) (Breugel *et al*. 2006, CFE 2006). Eighteen nights were sampled at riparian forest, riparian pastures, and pasture habitats, and 17 nights at the continuous forest habitat; using the same method. Five mist nets (12 m long, 2.6 m high) were set at ground level and were opened at dusk for four hours, which corresponds to the peak foraging time for most bat species (La Val. 1970). The bat sampling nets were arranged according to habitat type: 1) in the riparian habitats (including continuous forest and pastures), nets were located parallel and/or diagonally across the stream, depending on site characteristics; 2) in continuous forest nets were positioned across natural flying corridors;3) in pastures nets were located in open spaces devoid of vegetation. In all sites we searched for similar physical characteristics that allow the same mist net arrangement, this is one individual net and two pairs of nets in an “L” position (two nets connected perpendicularly), also nets were located roughly 50 m apart. Sampling was not performed on nights with a full moon or heavy rain (Morrison 1978). Captured bats were temporarily stored in individual cloth bags and identified to species following Medellín *et al*. (2011).

Our study included all the families represented in captures (Emballonuridae, Phyllostomidae, Mormoopidae and Vespertilionidae). However only Phyllostomidae and Mormoopidae have numerous understory species that are easily caught with mist nets (Moreno & Halffter 2000). Families of aerial insectivores like Emballonuridae, Molossidae, and Vespertilionidae tend to forage over the canopy so can be underestimated with mist netting and require a complementary sampling method (e.g. canopy mist nets or acoustic bat monitoring) to fully understand the impact of land use change on the functional diversity of bat communities.

Data analysis

Data including ten functional traits (Table 1) were obtained from the literature (references in Table S1) for all the 22 species captured in all sites together with the forearm length measurements of actual captured individuals. A total of 11 traits were obtained from our data and from the literature, all species were listed with their mean trait values (Table 4). All traits are considered to be ecologically relevant and have been used for functional analysis of bats in several studies (Barlow 1997; Duchamp & Swihart 2008; Meyer *et al.* 2008; Hanspach *et al.* 2012; Farneda *et al.* 2015; Wordley *et al.* 2017). The traits are related to size: forearm length (FA); wing morphology; aspect ratio (AR): is a measure of wing shape, calculated as the length from tip to tip (span), divided by the width, front to back (chord) (Altringham 2011); and relative wing loading (RWL); bite force: greatest length of skull (GLS), breadth across molars (BAM) and zygomatic breadth (ZYG); echolocation: frequency of maximum energy (FmaxE) and type of echolocation call (Call Type), pulses of echolocation are described as frequency modulated (FM), constant frequency (CF), quasi-constant frequency (QCF), low constant frequency (LCF), and low frequency modulated, but many, perhaps most, species of bat use combinations of these (Jung, Kalko & Von Helversen 2007; Altringham 2011); trophic level: diet (D); and foraging: space preference (SP): bats foraging in "narrow space" exploit animal prey positioned on or near background objects like vegetation or the ground, or they forage for fruits and flowers which are part of the background. Bats foraging in "edge space" exploit the resource of airborne prey found near the edges of buildings and vegetation, in gaps, or above the ground and water surfaces, and catch their prey in the "aerial" mode (Denzinger & Schnitzler 2013); and foraging preference (FP): "passive gleaning" mode is used by bats that have no chance to find food echo in the dense clutter echoes from the background, so they have to rely on other senses and use food generated cues to find it; on the other hand in the "active gleaning" mode bats are still able to find food, which is either part of the substrate or positioned on substrate, only by echolocation even under challenging clutter conditions. Bats that use the "flutter detecting" mode recognize insect echoes from their long CF-FM signals, which are modulated in the rhythm of the beating wings, and discriminate them from unmodulated clutter echoes; "trawling" foragers fly at low height above water (Denzinger & Schnitzler 2013).

Functional metrics

Functional metrics based on Villéger *et al*. (2008) and Mouillot *et al*. (2013) were calculated. Four components of functional diversity were used: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional specialization (FSpe). These components incorporate species abundances and a measure of position in functional-trait space to describe how much space is filled within a created trait-space using Principal Coordinates Analysis (PCoA), based on the standardization of trait values, so that each trait gets the same weight and no single trait over influences the results. First Gower-distance and PCoA were estimated using the "cluster" package in R (Maechler et al, 2015). Gower-distance calculates functional distances between species and is recommended when using both categorical and continuous traits (Villéger *et al.* 2008). Principal Coordinates Analysis (PCoA), is used to reduce variables to the least correlated ones while still explaining most of the variance and plotting them in a Euclidean multidimensional functional space. Once the functional trait-space is obtained plotting the distances using PCoA, diversity indices were calculated using the "ape" and "geometry" packages in R. Functional richness is a measure of the amount of functional space filled by the species in the community based on the convex hull volume (obtained from PCoA). Functional evenness measures the changes in abundance distributions within the obtained functional space, based on a minimum spanning tree (MST). Functional divergence measures the proportion of abundances of species with the most extreme trait and functional specialization measures abundance of generalist or specialist species increase within the functional space, generalist species with the least extreme traits tend to be in the center and if they have a higher abundance then functional specialization will be lower (Cornwell, Schwilk & Ackerly 2006;

Villéger *et al.* 2008; Mouillot *et al.* 2013). All metrics were calculated using functions provided by Villéger *et al.* (2008). Metric results obtained for functional richness, evenness and specialization were then compared for each habitat using generalized linear models in R. Functional divergence was compared using quasi-generalized linear models in R (Bates *et al*. 2014). All analyses were compared by FDR adjusted pairwise comparisons with ´lsmeans´ package in R (Lenth 2014). Additional measures using sampled nights in each habitat could not be run because in some cases there were not enough species (less than 2) per night in some cases.

Trait analysis

We obtained community weighted means (CWM) of each continuous trait (forearm, aspect ratio, relative wing loading, greatest length of skull, breadth across molars, zygomatic breadth, Fmax) for each habitat using the "FD" package in R (Laliberté *et al*. 2015). The data were used to evaluate differences between each habitat to provide evidence for habitat trait filtering (Cornwell *et al.* 2006; Villéger *et al.* 2010). Traits were tested for collinearity. For instance, zygomatic breadth was correlated to breadth across upper molars (Kendall correlation: $\tau < 0.80$) and greatest length of skull (Kendall correlation: $\tau < 0.72$) so it was removed from further analysis. After zygomatic breadth was removed, functional traits were no longer correlated (Kendall correlation: $\tau < 0.60$). In total 18 analyses were carried out. Differences in habitat types were analyzed using linear models in R (Bates *et al.* 2014) for mean forearm length, mean aspect ratio, mean relative wing loading, mean greatest length of skull, mean breadth across upper molars, mean FmaxE, abundance of bats that use FM multiharmonic (Fmmulti) bat calls, abundance of frugivorous individuals, abundance of narrow-space preference individuals and abundance of passive/active-gleaning foraging individuals. Habitat differences in relation to the abundance of individuals with different insectivore, nectarivorous, sanguivorous and omnivore individuals; abundance of individuals that have an edge-space space preference and abundance of individuals that are aerial, flutter detecting and trawling foragers were analyzed using quasi-generalized linear models due to data over dispersion. All analyses were adjusted by false discovery rate (FDR) pairwise comparisons using the "lsmeans" package in R (Lenth 2014). This controls the number of false positives within the analysis by making p-values larger, limiting the number of false positives in multiple comparisons.

RESULTS

Bat sampling

Overall, a total of 1,688 individuals were captured including 119 in mature forest habitat, 289 in pasture habitat, 367 in riparian mature forest habitat, and 913 in riparian vegetation pasture habitat (Table 2). A total of 22 species: 14 Phyllostomidae species, four Mormoopidae, two Emballonuridae and two Vespertilionidae were captured. Frugivore species accounted for 89 % of all captures and they were the second most dominant feeding guild (32% of all species). The insectivore guild had most species (36 % of all species) but accounted for only 3% of all captures. Nectarivores made up 7 % of the captures.

Functional diversity metrics

The principal coordinate analysis (PCoA) on species traits captured 71% of the distance table variance (Fig. 2). The closest species in space are the most similar. Dimension

1 is positively correlated with *A. jamaicensis*, *A. lituratus*, *C. perspicillata*, *C. villosum*, *P. helleri*, *S. lilium*, *U. bilobatum*, *T. cirrhosus*, *C. godmani*, *G. soricina*, *L. brachyotis*, *D. rotundus*; whereas dimension 2 is positively correlated with *A. jamaicensis, A. lituratus, M. crenulatum, T. cirrhosis, T. saurophila, M. megalophyla, P. parnelli, S. bilineata* and *D. rotundus.*

Functional specialization showed high significant difference for continuous forest ($F_{3,8}$ = 5.859, P=0.020). In contrast, functional richness ($F_{3,8}$ = 0.764, P=0.545), evenness ($F_{3,8}$ = 1.939, P=0.2019) and divergence ($F_{3,8}$ = 1.460, P=0.2966) showed no significant difference among habitats. FEve and FSpe are higher in forest habitats while FRic is higher in riparian habitats. There is a high FDiv in forest and riparian habitats but a low FDiv in pasture habitat (Fig 3, Table 3). FSpe was higher for mature forest (F) than for all pasture habitats. (Supporting information Table S.1).

Functional traits

Functional traits were analyzed individually in order to show how each trait was filtered in each habitat. Significant results were found in community-weighted mean (called mean from here on), forearm length ($F_{3,8}$=5.87, P < 0.02), mean relative wing loading ($F_{3,8}$=7.09, P < 0.01), mean greatest length of skull ($F_{3,8}$=6.57, P < 0.01), mean frequency of maximum energy ($F_{3,8}$=8.52, P < 0.01), number of FM multi-harmonic individuals ($F_{3,8}$=25.94, P < 0.001), frugivores ($F_{3,8}$=26.07, P < 0.001), nectarivores ($F_{3,8}$=7.85, P < 0.01), narrow-space preferences ($F_{3,8}$=23.22, P < 0.001) and passive/active gleaning foragers ($F_{3,8}$=27.38, P < 0.001). Mean forearm length was significantly higher in all forest habitats. Mean relative wing loading was higher in non-forest habitats and increased significantly in the pasture non-riparian (P). Greatest length of skull significantly increased in the forest habitat (F) while frequency of maximum energy decreased significantly. Abundance of: individuals that use FM multiharmonics, nectarivores, and narrow-space preference individuals were significantly low in all but riparian pasture habitats. The abundances of frugivores and passive/active gleaning forager individuals were higher in riparian habitats but only significantly higher than the forest habitat (Fig 4, Supporting Information Table S.2).

DISCUSSION

Functional metrics among habitats

In our study, functional richness (FRic) does not show significant differences among habitats however, functional richness has been reported to be related to the degree of forest cover (Cisneros, Fagan & Willig 2015; García-Morales *et al.* 2016). The bat assemblages of pasture habitat were impoverished compared to riparian habitats, supporting the idea that probably due to a higher availability of feeding resources as well as suitable commuting areas, riparian habitats show higher taxonomic and functional diversity than the surrounding landscape (Zarazúa-Carbajal *et al.* 2017). In some cases differences in species richness may not reflect changes in species composition and the occurrence of trait filtering (Cisneros *et al.* 2015). Despite changes in species richness, functional diversity may remain constant if species that disappear are functionally redundant (StrauB *et al.* 2010). We can infer that those species that establish or remain in riparian pastures provide similar resource-use traits to those of the riparian forest.

Functional divergence (FDiv) showed the highest values in riparian forest and riparian pastures than in non-riparian habitats. Similarly, pasture showed the lowest FDiv values, this is probably because species of riparian habitats show extreme values for some functional traits like aerial insectivorous and gleaning species while pastures exhibit high abundance of Stenodermatinae species which are all similar in functional space (have similar traits) (Villéger *et al.* 2008; Mouillot *et al.* 2013). Riparian habitats within an agricultural matrix can favor the presence of species with extreme traits values associated with unperturbed habitats including the gleaning insectivore *T. saurophila* and the carnivore *T. cirrhosus.*

Functional traits

Our results show that forearm, frequency of maximum energy, greatest length of skull and aspect ratio were the strongest predictors of species responses comparing F to P. Bat size (forearm length) and wing morphology (aspect ratio) were strong determinants of habitat use by Neotropical bats, small frugivorous species are the most common in disturbed habitats (Medellín *et al.* 2000; Castro-Luna, Sosa & Castillo-Campos 2007; Presley *et al.* 2008). Riparian-mature forest and mature forests showed high mean FA (related to size), which can be explained by the higher abundance of *T. saurophila*, *A. jamaicensis*, *A. lituratus* and *D. rotundus.* Several studies in the Neotropics have reported that as fragmentation increases, body size declines, driven mainly by the declines of large gleaning carnivores and the high abundances of small frugivores capable to exploit resources in secondary forest (Meyer & Kalko 2008; de la Peña-Cuéllar *et al.* 2012, 2015a; Farneda *et al.* 2015)

In this study, we recorded bat species with greatest skull measurements in mature forest and riparian-mature forest, such as the carnivorous *T. cirrhosus* (Freeman, 1984; Herrel et al. 2008; Orihuela, 2011; Santana et al. 2012; Dumont et al. 2012). This trophic specialization may be sensitive to agricultural practices; species at the top of the food chain (carnivorous species) are more prone to extinction than those at lower trophic levels (phytophagous) (Henle et al. 2004). In contrast, most of the bat species presented small skulls like *S. lilium*, indicating that frugivorous generalist species usually dominate habitats with high density of understory chiropterocoric plants (Medellín 2000, Pineda et al. 2005, Rex et al. 2008, Freudmann et al. 2015, de la Peña-Cuellar 2015). Pasture and riparian pasture habitats showed the highest range of AR and RWL where insectivorous species with open habitat preferences were common including: *P. parnelli*, *E. fuscus*, *R. naso* and *S. bilineata* (Norberg et al. 1987; Jennings et al. 2004; Meyer et al. 2008; Jung et al. 2007; Marinello & Bernard, 2014). Species adapted to open-habitats have high wing aspect ratios and wing loadings, traits that facilitate rapid, efficient flight in unobstructed airspaces (Norberg & Rayner 1987; Duchamp & Swihart 2008).

Overall, riparian pasture habitat had bat assemblages with similar functional diversity to riparian mature forest habitat, but some trait filtering was observed. Riparian pasture habitat had a higher number of individuals with multi-harmonic calls, more species of nectarivores, and clutter-adapted species (bats foraging in narrow space). We found that pasture species typically echolocated with high frequency of maximum energy calls. Species with higher maximum energy frequencies in the assemblage are frugivorous and are present in high abundances within pastures. High frequency of maximum energy species are adapted to cluttered habitats thus it is most likely that they are found in pastures while commuting to look for food (Farrel & Miller, 2000; Kalko et al. 1996; Thies et al. 1998). However, in the Neotropics call frequencies must be interpreted with care since there is lack of reference call libraries, because most of the call intensity of tropical bats are very low and difficult to record (Arita & Fenton 1997; Jennings *et al.* 2004).

Conservation implications and future studies

We provide further evidence on the importance of a functional diversity approach as a complementary tool to study disturbance effects on bat assemblages in tropical agricultural landscapes. Our results showed the importance of mature forests tracks in tropical agricultural landscapes to conserve highly specialist species that are absent in other habitats. Although riparian pasture showed high levels of diversity and the presence of rare species, this habitat had the lowest values of functional specialization, implying that riparian habitat cannot be considered as a substitute for continuous mature forest. Since species distribution and niche differentiation are based on the complex interactions among several factors including vegetation structure, it is crucial that management of riparian vegetation encourages landowners to maintain forest cover favoring those bat species that do not fly great distances across deforested lands (Kalko & Handley 2001; Vleut *et al.* 2012). Considering functional diversity could provide other ecological perspectives to trait repetition and high species overlapping within communities (Duchamp & Swihart, 2008; Cadotte et al. 2011; Petchey and Gaston, 2006). This study highlights the importance of maintaining large tracks of mature forests in agricultural landscapes for bat conservation, as mature forests have higher functional evenness, divergence and specialization, and provide refuge for many extreme trait bat species. We also suggest that riparian vegetation in human modified landscapes are of important conservation value for bat biodiversity (de la Peña-Cuellar et al. 2015), retaining high levels of functional diversity assuring ecosystem function throughout the ecological services provided by bats including seed dispersal and insect pest population control (Kunz *et al.* 2011)

Literature cited

Abbott, I.M., Sleeman, D.P. & Harrison, S. (2009) Bat activity affected by sewage effluent in Irish rivers. *Biological Conservation*, **142**, 2904–2914.

Adams, R.A. & Hayes, M.A. (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, **77**, 1115–1121.

Aguiar, L.M.S., Bernard, E. & Machado, R.B. (2014) Habitat use and movements of Glossophaga soricina and Lonchophylla dekeyseri (Chiroptera : Phyllostomidae) in a Neotropical savannah. *Zoologia*, **31**, 223–229.

Altringham, J.D. (2011) *Bats: From Evolution to Conservation*, 2nd ed. Oxford University Press, Oxford.

Alvarez, T. & Sánchez-Casas, N. (1999) Diferenciación alimentaria entre los sexos de Glossophaga soricina (Chiroptera: Phyllostomidae) en México. *Revista de Biologia Tropical*, **47**, 1129–1136.

Arita, H.T. & Fenton, M.B. (1997) Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology and Evolution*, **12**, 53–58.

Arita, H.T. & Santos-del-Prado, K. (1999) Conservation Biology of Nectar-Feeding Bats in Mexico. *Journal of Mammalogy*, **80**, 31–41.

Arnone, I.S., Trajano, E., Pulchério-Leite, A. & Passos, F.C. (2016) Long-distance movement by a great fruit-eating bat, Artibeus lituratus (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica*, **16**, 1–6.

Barclay, R.M.R. (1989) The effect of reproductive condition on the foraging behavior of female hoary bats, Lasirurus cinereus. *Behavioral Ecology and Sociobiology*, **24**, 31–37.

Barlow, K.E. (1997) The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology*, **243**, 597–609.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2014) Fitting linear mixed-effects models using lme4 Douglas. *Journal of Statistical Software*, 1–51.

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2016) Sexual segregation when foraging in an extremely social killer whale population. *Behavioral Ecology and Sociobiology*, **70**, 189–198.

Bender, D. J., Contreras, T. A., Fahrig, L. (1998) Habitat Loss and Population Decline : a Meta-Analysis of the Patch Size Effect. *Ecology*, **79**, 517–533.

Bernard, E. & Fenton, M.B. (2002) Species diversity of bats (Mammalia : Chiroptera) in forest fragments , primar ...

Bhagwat, S.A., Willis, K.J., Birks, H.J.B. & Whittaker, R.J. (2008) Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution*, **23**, 261–267.

Bianconi, G. V, Mikich, S.B. & Pedro, W.A. (2006) Movements of bats (Mammalia , Chiroptera) in Movements Chiropteroptera) Atlantic For est remnants in southern Brazil Forest remnants southern Brazil. *Revista Brasileira de Zoologia*, **23**, 1199–1206.

van Breugel, M., Martínez-Ramos, M., Bongers, F., Martinez-Ramos, M. & Bongers, F. (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, **22**, 663–674.

Broders, H.G., Forbes, G.J., Woodley, S. & Thompson, I.D. (2006) Range extent and stand selection for roosting and foraging in forest-dwelling Northern Long-eared Bats and Little Brown Bats in the Greater Fundy ecosystem, New Brunswick. *Journal of Wildlife Management*, **70**, 1174–1184.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Castro-Luna, A.A., Sosa, V.J. & Castillo-Campos, G. (2007) Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, **10**, 219–228.

Chacón, M. & Harvey, C.A. (2006) Live fences and landscape connectivity in a neotropical agricultural landscape. *Agroforestry Systems*, **68**, 15–26.

Charles-Dominique, P. (1991) Feeding strategy and activity budget of the frugivorous bat Carollia perspicillata (Chiroptera: Phyllostomidae) in French Guiana. *Journal of Tropical Ecology*, **7**, 243.

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, **21**, 523–533.

Comisión Federal de Electricidad. (2006) *División Hidrométrica Sureste.* Estación Lacantún, Marqués de Comillas, Chiapas, México.

CONAFOR. (2016) *Manual de Mejores Prácticas de Manejo Forestal Para La Conservación de*

La Biodiversidad En Ecosistemas Tropicales de La Región Sureste de México. Ciudad de México.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A Trait-Based Test for Habitat Filtering : Convex Hull Volume. , **87**, 1465–1471.

Cosson, J.F., Pons, J.M. & Masson, D. (1999) Effects of Forest Fragmentation on Frugivorous and Nectarivorous Bats in French Guiana. , 515–534.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Denzinger, A. & Schnitzler, H.U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, **4 JUL**, 1–15.

Diamond, G.F. & Diamond, J.M. (2014) Bats and Mines: Evaluating Townsend's Big-Eared Bat (Corynorhinus townsendii) Maternity Colony Behavioral Response to Gating. *Western North American Naturalist VO - 74*, **74**, 416.

Dietz, M., Kalko, E.K. V & Encarnação, J.A. (2006) Small scale distribution patterns of female and male Daubenton's bats (Myotis daubentonii). *Acta Chiropterologica*, **8**, 403–415.

Dirzo, R. & Raven, P.H. (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, **28**, 137–167.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, **23**, 849–860.

Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S. & Hamer, K.C. (2014) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation*, **17**, 163–173.

Encarnação, J.A. (2012) Spatiotemporal pattern of local sexual segregation in a tree-dwelling temperate bat Myotis daubentonii. *Journal of Ethology*, **30**, 271–278.

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

Estrada, A. & Coates-Estrada, R. (2002) Bats in continous forest, forest fragments and in an agricultural mosiac habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, **103**, 237–245.

Evelyn, M.J. & Stiles, D. a. (2003) Roosting requirements of two frugivorous bats (Sturnira lilium and Arbiteus intermedius) in fragmented Neotropical forest. *Biotropica*, **35**, 405–418.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C., Chazdon, R.L. & Sanchun, A. (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, **8**, 034017.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, **52**, 1381–1391.

Fenton, A.M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K., Syme, D.M. & Adkins, B. (1992) Phyllostomid Bats (Chiroptera : Phyllostomidae) as Indicators of Habitat Disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Frank, H.K., Mendenhall, C.D., Judson, S.D., Daily, G.C. & Hadly, E.A. (2016) Anthropogenic impacts on Costa Rican bat parasitism are sex specific. *Ecology and Evolution*, **6**, 4898–4909.

Freudmann, A., Mollik, P., Tschapka, M. & Schulze, C.H. (2015) Impacts of oil palm agriculture on phyllostomid bat assemblages. *Biodiversity and Conservation*, **24**, 3583–3599.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, **75**, 1252–1258.

Galindo-González, J. (1998) Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. *Acta Zoologica Mexicana*, 57–74.

Galindo-González, J. & Sosa, V.J. (2003) Frugivorous Bats in Isolated Trees and Riparian Vegetation Associated With Human-Made Pastures in a Fragmented Tropical Landscape. *The Southwestern Naturalist*, **48**, 579–589.

Garcia-Martínez, M.A., Escobar-Sarria, F., Pez-Barrera, F.L., Castano-Meneses, G. & Lez, J.E.V.G. (2015) Value of Riparian Vegetation Remnants for Leaf-Litter Ants (Hymenoptera: Formicidae) in a Human-Dominated Landscape in Central Veracruz, Mexico. *Environmental Entomology*, **44**, 1488–1497.

García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez, A.E. & Ávila-Gómez, E.S. (2016) Deforestation Impacts on Bat Functional Diversity in Tropical Landscapes. *Plos One*, **11**, e0166765.

Gorresen, P.M. & Willig, M.R. (2004) Landscape Responses of Bats To Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*, **85**, 688–697.

Grau, H.R. & Aide, M. (2008) Globalization and land-use transitions in Latin America. *Ecology and Society*, **13**.

Griscom, H.P., Kalko, E.K. V & Ashton, M.S. (2007) Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica*, **39**, 278–282.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed : evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii ? , 540–548.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: A case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842–850.

Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñóz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., Navas, A., Saenz, J., Sánchez, D., Medina, A., Vilchez, S., Hernández, B., Perez, A., Ruiz, F., López, F., Lang, I. & Sinclair, F.L. (2005) Contribution of live fences to the ecological integrity of agricultural landscapes.

Agriculture, Ecosystems and Environment, **111**, 200–230.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation\t. *Biodiversity and Conservation*, **13**, 207–251.

Henry, M. & Kalko, E.K. V. (2007) Froraging Strategy and Breeding Constraints of Rhynophyla Pumilio (PHYLLOSTOMIDAE) in the Amazon Lowlands. *Journal of Mammalogy*, **88**, 81–93.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) *Global Status Survey and Conservation Action Plan: Microchiropteran Bats*.

INE. (2000) *Programa de Manejo Reserva de La Biósfera Montes Azulez, México.* México.

Instituto Nacional de Ecología. (2000) *Programa de Manejo de La Reserva de La Biosfera Montes Azules*, 1a. Enkidu Editores, S.A. de C.V., México, D.F.

Istvanko, D.R., Risch, T.S. & Rolland, V. (2016) Sex-specific foraging habits and roost characteristics of Nycticeius humeralis in north-central Arkansas. *Journal of Mammalogy*, **97**, 1–9.

Jennings, N.V., Parson, S., Barlow, K.E. & Gannon, M.R. (2004) Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterologica*, **6**, 75–90.

Jennings, N. & Pocock, M.J.O. (2009) Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conservation Biology*, **23**, 1195–1203.

Jobin, B., Bélanger, L., Boutin, C. & Maisonneuve, C. (2004) Conservation value of agricultural riparian strips in the Boyer River watershed, Québec (Canada). *Agriculture, Ecosystems and Environment*, **103**, 413–423.

De Jong, B.H.J., Ochoa-Goana, S., Castillo-Santiago, M.A., Ramirez-Marcial, N. & Cairns, M.A. (2000) Carbon flux and patterns of land-use/land-cover change in het Selva Lacandona, Mexico. *A Journal of the Human Environment*, **29**, 504–511.

Jong, D. & Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13_ _**, 275–280.

Jung, K., Kalko, E.K. V & Von Helversen, O. (2007) Echolocation calls in Central American emballonurid bats: Signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.

Kalka, M. & Kalko, E.K. V. (2005) Gleaning bats as underestimated predators of herbivorous insects: diet of Micronycteris microtis (Phyllostomidae) in Panama. *Journal of Tropical Ecology*, **22**, 1.

Kalko, E.K. V & Handley, C.O. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.

Keen, R. & Hitchcock, H.H.B. (1980) Survival and longevity of the little brown bat (Myotis lucifugus) in southeastern Ontario. *Journal of Mammalogy*, **61**, 1–7.

Kelm, D.H., Wiesner, K.R. & Helversen, O. Von. (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conservation Biology*, **22**, 733–741.

Klingbeil, B.T. & Willig, M.R. (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest Brian. *Journal of Applied Ecology*, **46**, 203–213.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, **119**, 1654–1664.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kurta, A. & Matson, J.O.. (1980) Disproportionate Sex Ratio in the Big Brown Bat (Eptesicus fuscus). , **104**, 367–369.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015a) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015b) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**, 903–913.

de la Peña-Cuéllar, E., Stoner, K.E., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2012) Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. *Biodiversity and Conservation*, **21**, 1381–1397.

de la Torre, J.A., Núñez, J.M. & Medellín, R.A. (2017) Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. *Biological Conservation*, **206**, 270–282.

Lande, R. (1987) Extinction Thresholds in Demographic Models of Territorial Populations. *The American Naturalist*, **130**, 624–635.

Laurance, W.F. (1991) Society for Conservation Biology Ecological Correlates of Extinction Proneness in Australian Tropical Rain Forest Mammals. *Conservation Biology*, **5**, 79–89.

Laurance, W., Bierregaard, R. & Moritz, C. (1997) *Tropical Forest Remnants : Ecology, Management, and Conservation of Fragmented Communities*. University Of Chicago Press.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, **16**, 605–618.

Law, B. & Chidel, M. (2002) Tracks and Riparian Zones Facilitate the Use of Australian Regrowth Forest by Insectivorous Bats. *The Journal of Applied Ecology*, **39**, 605–617.

Lebrija-trejos, E., Pérez-garcía, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by : Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly. *Ecology*, **91**, 386–398.

Lemaître, J.-F., Gaillard, J.-M., Pemberton, J.M., Clutton-Brock, T.H. & Nussey, D.H. (2014) Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer. *Proceedings. Biological sciences / The Royal Society*, **281**, 20140792-.

Lenth, R.V. (2014) lsmeans: Least-square means.

Lintott, P.R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R.J., Olley, L. & Park, K.J. (2014) City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal society open science*, **1**, 1–8.

Lloyd, A., Law, B. & Goldingay, R. (2006) Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation*, **129**, 207–220.

Lobo, J.A., Quesada, M. & Stoner, K.E. (2005) Effects of pollination by bats on the mating system of Ceiba pentandra (Bombacaceae) populations in two tropical life zones in Costa Rica. *American Journal of Botany*, **92**, 370–376.

Lundy, M. & Montgomery, I. (2010) Summer habitat associations of bats between riparian landscapes and within riparian areas. *European Journal of Wildlife Research*, **56**, 385–394.

Martínez-Ramos, M. & García-Orth, X. (2007) Sucesión ecológica y restauración de las selvas húmedas. *Bol. Soc. Bot. Méx*, **80**.

Mayaux, P., Holmgren, P., Achard, F., Eva, H.D., Stibig, H.-J.J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **360**, 373–84.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesk, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.

McCracken, G.F. & Wilkinson, G.S. (2000) Bat Mating Systems. *Reproductive Biology of Bats*, pp. 321–362.

Mcgill, J. & Kalko, V. (2015) Climate , habitat , and species interactions at different scales determine the structure of a Neotropical bat community Author (s): Sergio Estrada-Villegas , Brian J . McGill and Elisabeth K . V . Kalko Published by : Ecological Society of America Stabl. , **93**, 1183–1193.

Medellin, R. a. (1994) Mammal Diversity and Conservation in the Selva-Lacandona, Chiapas, Mexico. *Conservation Biology*, **8**, 780–799.

Medellín, R. a, Equihua, M. & Amin, M. a. (2000) Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests\rDiversidad y Abundancia de Murciélagos como Indicadores de Perturbaciones en Selvas Húmedas Neotropicales. *Conservation Biology*, **14**, 1666–1675.

Medellín, R.A., Equihua, M. & Amin, M.A. (2011) *Identificación de Los Murciélagos de México: Clave de Campo*. México, D.F.

Medina, A., Harvey, C. a, Sánchez, D., Vílchez, S. & Hernández, B. (2007) Bat diversity and movement in a Neotropical agricultural landscape. *Biotropica*, **39**, 120–128.

Meli, P., Ruiz, L., Aguilar, R., Rabasa, A., Rey-Benayas, J.M. & Carabias, J. (2017) Bosques ribereños del trópico húmedo de México: Un caso de estudio and aspectos críticos para una restauración exitosa. *Madera Bosques*, **23**, 181–193.

de Mello, M.A.R. & Fernandez, F.A.S. (2000) Reproductive ecology of the bat Carollia perspicillata (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest. *International Journal of Mammalian Biology*, **65**, 340–349.

Meyer, C.F.J., Fr??nd, J., Lizano, W.P. & Kalko, E.K. V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.

Meyer, C.F.J. & Kalko, E.K. V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.

Miller, K., Chang, E. & Johnson, N. (2001) *Defining Common Ground for the Mesoamerican Biological Corridor*.

Montoya Gómez, G., Hernández Ruiz, J.F., Velasco Pérez, A., Reygadas, L. & Ramos Maza, T. (2006) Organización comunitaria para la conservación forestal: estudio de caso en la Selva Lacandona de Chiapas, México. *Papeles de población*, **14**, 11.

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. , 149–158.

Morrison, D.W. (1978) Lunar phobia in a neotropical fruit bat, Artibevs jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852–855.

Mouillot, D., Graham, N.A.J., Vill??ger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Muench, C. & Martínez-Ramos, M. (2016) Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico. *Tropical Conservation Science*, **9**, 178–202.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecological Applications*, **3**, 209–212.

Nardone, V., Cistrone, L., Di Salvo, I., Ariano, A., Migliozzi, A., Allegrini, C., Ancillotto, L., Fulco, A. & Russo, D. (2015) How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat Myotis daubentonii. *PLoS ONE*, **10**, 1–15.

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **316**, 335–427.

Nowak, R. (1991) *Walker's Mammals of the World*. Johns Hopkins Univ Pr.

Nupp, T. & Swihart, R. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512–526.

Ober, H.K. & Hayes, J.P. (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, **256**, 1124–1132.

Ortega, J. & Arita, H.T. (1999) Structure and Social dynamics of harem groups in Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, **80**, 1173–1185.

Ortega, J. & Maldonado, J.E. (2006) Female interactions in harem groups of the Jamaican fruit-eating bat, Artibeus jamaicensis (Chiroptera : Phyllostomidae). *Acta Chiropterologica*, **8**, 485–495.

Ortiz-Ramírez, D., Lorenzo, C., Naranjo, E. & León-Paniagua, L. (2006) Selección de refugios por tres especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en la Selva Lacandona, Chiapas, México. *Revista Mexicana de Biodiversidad*, **77**, 261–270.

Perry, R.W., Carter, S.A. & Thill, R.E. (2010) Temporal Patterns in Capture Rate and Sex Ratio of Forest Bats in Arkansas. *American Midland Naturalist*, **164**, 270–282.

Perry, R.W., Thill, R.E. & Carter, S.A. (2007) Sex-specific roost selection by adult red bats in a diverse forested landscape. *Forest Ecology and Management*, **253**, 48–55.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Pinto, N. & Keitt, T.H. (2008) Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, **117**, 1725–1731.

Presley, S.J., Willig, M.R., Wunderle, J.M. & Saldanha, L.N. (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology*, **45**, 14–25.

Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates Sunderland, Massachusetts.

Racey, P.A. (1998) The importance of the riparian environment as a habitat for British bats. *Symposia of the Zoological Society of London*, pp. 69–91. London: The Society, 1960-1999.

Racey, P.A. & Speakman, J.R. (1987) The energy costs of pregnancy and lactation in heterothermic bats. *Symposia of the zoological society of London*, pp. 107–125.

Ramos Pereira, M.J., Marques, J.T. & Palmeirim, J.M. (2010) Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in amazonian forests. *Biotropica*, **42**, 680–687.

Ramos Pereira, M.J., Marques, J.T., Santana, J., Santos, C.D., Valsecchi, J., De Queiroz, H.L., Beja, P. & Palmeirim, J.M. (2009) Structuring of Amazonian bat assemblages: The roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, **78**, 1163–1171.

Rocha, R., Ferreira, D.F., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B., Palmeirim, J.M. & Meyer, C.F.J. (2017) Does sex matter ? Gender-specific responses to forest fragmentation in Neotropical bats. *Biotropica*, 1–10.

Russo, D., Cistrone, L., Garonna, A.P. & Jones, G. (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodiversity and Conservation*, **19**, 2501–2515.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Jani, A., Katz, G., Soykan, C., Watts, J., Welter, J., Ecology, S., Jan, N. & Heffernan, J.I.M. (2005) Riparian Zones Increase Regional Species Richness by Harboring Different , Not More , Species. *Ecology*, **86**, 56–62.

Safi, K., König, B. & Kerth, G. (2007) Sex differences in population genetics, home range size and habitat use of the parti-colored bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biological Conservation*, **137**, 28–36.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321–1333.

Scott, S.J., McLaren, G., Jones, G. & Harris, S. (2010) The impact of riparian habitat quality on the foraging and activity of pipistrelle bats (Pipistrellus spp.). *Journal of Zoology*, **280**, 371–378.

Seaman, B.S. & Schulze, C.H. (2010) The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. *Biological Conservation*, **143**, 391–

398.

Senior, P., Butlin, R.K. & Altringham, J.D. (2005) Sex and segregation in temperate bats. *Proceedings. Biological sciences / The Royal Society*, **272**, 2467–73.

Sgroi, M.P. & Wilkins, K.T. (2010) Roosting Behavior of the Mexican Free-Tailed Bat (Tadarida Brasiliensis) in a Highway Overpass. *Western North American NaturaHst63*, **63**, 366–373.

Smith, P.G. & Racey, P.A. (2008) Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *Journal of Zoology*, **275**, 314–322.

Sosa, M., De Ascencao, A. & Soriano, P. (1996) Dieta y patrón reproductivo de Rhogessa minutilla (Chiroptera: Vespertilionidae) en una zona árida de Los Andes de Venezuela. *Revista de Biología Tropical*, **44**, 867–875.

Soule, M.E. & Gilpin, M.E. (1991) The teory of wildlife corridor capability. *Nature Conservation 2: The Role of Corridors* (eds D.A. Saunders & R.J. Hobbs), pp. 3–8. Surrey Beatty and Sons, Chipping Norton, Australia, New South Wales, Australia.

StrauB, A., Reeve, E., Randrianiaina, R.-D., Vences, M. & Glos, J. (2010) The world 's richest tadpole communities show functional redundancy and low functional diversity : ecological data on ecological data on Madagascar 's stream-dwelling amphibian larvae. *BMC Ecology*, **10**, 1–10.

Taylor, P.D., Fahrig, L. & Henein. (1993) Connectivity is a Vital Element of Landscape Structure. *Oikos*, **68**, 571–573.

Tilman, D. (2001) Functional Diversity. *Encyclopedia of Biodiversity*, pp. 587–596.

van Toor, M.L., Jaberg, C. & Safi, K. (2011) Integrating sex-specific habitat use for

conservation using habitat suitability models. *Animal Conservation*, **14**, 512–520.

Turner, I.M. (1996) Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Society*, **33**, 200–209.

La Val, R. (2017) Banding Returns and Activity Periods of Some Costa Rican Bats. *The Southwestern Naturalist*, **15**, 1–10.

Vandermeer, J. & Perfecto, I. (2007) The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, **21**, 274–277.

Villéger, Mason & Mouillot. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Ramos Miranda, J., Flores Hernández, D. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological applications*, **20**, 1512–1522.

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

Vleut, I., Levy-Tacher, S.I., Galindo-González, J., de Boer, W.F. & Ramírez-Marcial, N. (2012) Tropical rain-forest matrix quality affects bat assemblage structure in secondary forest patches. *Journal of Mammalogy*, **93**, 1469–1479.

Walsh, A.L. & Harris, S. (1996) Foraging Habitat Preferences of Vespertilionid Bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Warkentin, I.G., Greenberg, R. & Ortiz, J.S. (1995) Songbird use of Gallety Woodlands in Recently Cleared and Older Settled Landscapes of the Selva Lacandona, Chiapas, Mexico. *Conservation Biology*, **9**, 1095–1106.

Wearmouth, V.J. & Sims, D.W. (2008) Sexual Segregation in Marine Fish , Reptiles , Birds and Mammals : Behaviour Patterns , Mechanisms and Conservation Implications., pp. 108–170.

Weller, T.J., Cryan, P.M. & O'Shea, T.J. (2009) Broadening the focus of bat conservation and research in the USA for the 21st century. *Endangered Species Research*, **8**, 129–145.

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245–258.

Williams-Guillén, K. & Perfecto, I. (2010) Effects of agricultural intensification on the bat assemblage in a coffee landscape in Chiapas, Mexico. *Biotropica*, **42**, 605–613.

Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008) Bats limit insects in a neotropical agroforestry system. *Science (New York, N.Y.)*, **320**, 70.

Willig, M., Presley, S.J., Bloch, C.P., Yanoviak, S.P., Díaz, M.M., Arias Chauca, L., Pacheco, V. & Weaver, S.C. (2007) Phyllostomid Bats of Lowland Amazonia: Effects of Habitat Alteration on Abundance. *Biotropica*, **39**, 737–746.

Wordley, C.F.R., Sankaran, M., Mudappa, D. & Altringham, J.D. (2017) Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biological Conservation*, **210**, 48–55.

Zarazúa-Carbajal, M., Avila-Cabadilla, L.D., Alvarez-Añorve, M.Y., Benítez-Malvido, J. & Stoner, K.E. (2017) Importance of riparian habitat for frugivorous bats in a tropical dry forest in western Mexico. *Journal of Tropical Ecology*, **33**, 74–82.

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J. & Martínez-

Ramos, M. (2015) Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, **18**, 443–455.

Table 1. Traits of bat species used for functional diversity analyses in an agricultural landscape of the Lacandona rain forest, Chiapas, Mexico; where: FMAXE = frequency of maximum energy; FM= frequency modulated, QCF = frequency modulated call with a quasi-constant frequency tail; FMmulti = multi-harmonic frequency modulated call, ---- = not classified.

Species	**Conservation status NOM 059,^{A} IUCN^{B}**	**Forearm (mm)**	**Aspect ratio**	**Relative wing loading**	**Greatest length of skull**	**Breadth across upper molars**	**Zygomatic breadth**	**FMAXE (kHz)**	**Call type**	**Diet**	**Space preference**	**Foraging preference**
Artibeus jamaicensis	----, C	62	6.2	42.5	29.8	12.4	18.6	57.0	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Artibeus lituratus	----, LC	70	6.1	39.9	30.7	13.6	18.8	61.4	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Carollia perspicillata	----, LC	43	6	39.4	23.2	7.6	11.4	62.7	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Chiroderma villosum	----, LC	43	6.4	44.5	24.3	11.2	15.8	91.8	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Platyrrhinus helleri	----, LC	40	6.3	45.2	22	9.0	12.3	99.0	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Sturnira lilium	----, LC	39	6.5	46.9	22.4	10.1	13.5	72.4	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Uroderma bilobatum	----, LC	44	6.3	40.7	23.3	9.3	12.9	74.7	FMmulti	Frugivore	narrow	Passive_active_gleaning-foragers
Mimon crenulatum	A, LC	52	7.4	30.0	21.9	8.4	12.3	66.1	FMmulti	Insectivore	narrow	Passive_gleaning-foragers
Trachops cirrhosus	A, LC	59	6.1	39.6	28.6	10.1	14.5	66.8	FMmulti	Insectivore	narrow	Passive_gleaning-foragers
Tonatia saurophila	A, LC	53	5.9	30.4	27.4	8.3	13.6	56.5	FMmulti	Insectivore	narrow	Passive_gleaning-foragers
Eptesicus brasiliensis	---, LC	39	6.3	33.6	16.5	7.3	10.5	37.1	FM.QCF.multi	Insectivore	edge	Aerial_foragers
Eptesicus fuscus	---, LC	38	6.4	36.9	19.4	8.0	13.0	34.8	FM.QCF.multi	Insectivore	edge	Aerial_foragers
Mormoops megalophyla	---, ---	56	7.1	43.0	15	6.9	9.6	52.0	FMmulti	Insectivore	edge	Aerial_foragers
Myotis keaysi	---, LC	40	6.4	33.3	13.6	5.3	7.9	60.9	FM.QCF.multi	Insectivore	edge	Aerial_foragers

Pteronotus parnelli	----, ---	56	7	27.9	22.5	8.7	12.4	63.6	FM.LCF. multi	Insectivore	narrow	Flutter detecting foragers
Pteronotus davyi	----, LC	43	7.3	35.5	16.1	6.6	8.9	66.8	CF.LFM. multi	Insectivore	edge	Trawling foragers
Rhynchonycteris naso	Pr, LC	37	6.7	28.8	11.8	4.4	6.2	95.8	CF.LFM. multi	Insectivore	edge	Trawling foragers
Saccopteryx bilineata	----, LC	44	7.3	28.2	16.3	7.5	10	47.3	FM.QCF. multi	Insectivore	edge	Aerial_foragers
Choeroniscus godmani	----, ----	36	6.2	45.5	20.4	8.2	8.5	97.9	FMmulti	Nectarivore	narrow	Passive_active_gleaning-foragers
Glossophaga soricina	----, ----	36	6.2	43.1	21.4	5.5	9.4	94.5	FMmulti	Nectarivore	narrow-space	Passive_active_gleaning-foragers
Lampronycteris brachyotis	A, LC	41	5.8	41.4	22	7.1	11.1	74.6	FMmulti	Omnivore	narrow-space	Passive_active_gleaning-foragers
Desmodus rotundus	----, LC	61	6.7	43.5	24.4	6.1	12.2	56.9	FMmulti	Sanguivore	narrow-space	Passive_gleaning-foragers

[A] NOM-059-2010 categories: A = Threatened, P = Endangered. Source: SEMARNAT. 2010. Norma Oficial Mexicana NOM-059, Protección ambiental de especies nativas de México de Flora y fauna silvestres- Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio – Lista de especies en riesgo. Diario Oficial de la Federación, Mexico City, Mexico.

[B] IUCN conservation status: LC, least concern. Source: IUCN.2017.IUCN Red List of Threatened Species. www.iucnredlist.org.

Table 2. Bat species included in the analysis of species richness, number of samples, total abundance and abundance per habitat types. Habitat types were the following: riparian mature forest (RF), riparian vegetation in pastures (RP), mature continuous forest (F), and open pastures away from riparian vegetation (P). Bat guilds are as follows: F, Frugivores; N, Nectarivores; C, Carnivores; S, Sanguivores; I, Insectivores.

FAMILY **Subfamily**		Habitat				
Species	Guild	F	P	RF	RP	TOTAL
EMBALLONURIDAE						
Rhynchonycteris naso	I	0	0	0	3	3
Saccopteryx bilineata	I	0	0	0	4	4
PHYLLOSTOMIDAE						
Carolliinae						
Carollia perspicilatta	F	5	1	20	35	61
Desmodontidae						
Desmodus rotundus	S	1	4	1	8	14
Glossophaginae						
Choeroniscus godmani	N	1	0	2	0	3
Glossophaga soricina	N	3	21	6	88	118
Phyllostominae						
Lampronycteris brachyotis	I	0	0	1	0	1
Mimon crenulatum	I	0	0	0	7	7
Trachops cirrhosus	C	1	0	2	0	3
Tonatia saurophila	I	3	0	3	2	8
Stenodermatinae						
Artibeus jamaicensis	F	43	29	72	61	205
Artibeus lituratus	F	29	74	113	195	411
Chiroderma villosum	F	1	0	0	3	4
Platyrrhinus helleri	F	2	9	24	49	84
Sturnira lilium	F	27	120	68	348	563
Uroderma bilobatum	F	1	30	48	98	177
MORMOOPIDAE						
Pteronotus davyii	I	0	0	4	1	5
Pteronotus parnelli	I	2	1	3	8	14
VESPERTILLIONIDAE						

Eptesicus fuscus	I	0	0	0	3	3
Total abundance		119	289	367	913	1688
Samples		17	18	18	18	
Richness		13	9	14	16	
Completeness %		64%	89%	93%	95%	
Species diversity		1.710	1.580	1.880	1.850	
Species evenness		0.667	0.719	0.712	0.667	

Table 3. Functional diversity measurements for bats considering different habitat types, including: mature continuous forest (RF), riparian sites in pastures (RP), mature continuous forest (F), and open pastures away from riparian vegetation (P).

Habitat type	**Functional diversity measure**			
	Functional richness	Functional evenness	Functional divergence	Functional specialization
Continuous forest	0.090	0.549	0.738	0.273
Pasture	0.066	0.365	0.480	0.215
Riparian Forest	0.144	0.363	0.686	0.261
Riparian Pasture	0.128	0.434	0.647	0.223

Table 4. Functional traits of bat species inhabiting different habitat types in the Lacandona rain forest, Mexico.

Trait (units)	Trait type	Categories	Source
Forearm (mm)	Cont.	N/A	Average obtained from this study.
Aspect ratio	Cont.	N/A	Norberg and Rayner, 1987; Marinello and Bernard 2011; García-García *et al*. 2014;
Relative wing loading	Cont.	N/A	
Greatest length of skull (mm)	Cont.	N/A	Averages obtained per species from: Acosta & Aguanta, 2005; Adams, 1989; Alvarez et al. 1991; Anderson, 1972; Anderson, 1997; Carter *et al*. 1966 (C. godmani Breadth across molars based on C.minor measurements) ; Cloutier & Thomas, 1992; Cramer et al. 2001; Eisenberg & Redford, 1992; Ferrel & Wilson, 1991; Gannon et al. 1989; Goodwin et al. 1946; Goodwin et al. 1969; Greenhall et al. 1983; Guzmán et al. 1999; Hernandez-Meza et al. 2005; Hoffman & Genoway, 2008; Husson, 1978; Knox-Jones, 1964; Kurta & Baker, 1990; Miranda et al. 2006; Nuñez-Garduño, 2005; Orihuela, 2011; Ortega & Arellano, 2001; Owen et al. 2014; Plumpton & Jones, 1992; Rehn, 1900; Rezutek and Cameron 1993; Scultori et al. 2009; Simmons & Voss, 1998; Sosa-Escalante et al. 2001; Watkins et al. 1972; Wilson et al. 1985; Yancey et al. 1998.
Breadth across molars (mm)	Cont.	N/A	
Zygomatic breadth (mm)	Cont.	N/A	
FmaxE (kHz)	Cont.	N/A	Zamora-Gutiérrez et al. 2016; Pio et al. 2010
Call type	Cate.	Fmmulti (FM multiharmonics), CF-Long FM- multiharmonics, FM-Long CF- multiharmonics, FM-Quasiconstant frequency-multiharmonics	Based on call descriptions from Pio et al. 2010; Briones-Salas et al. 2013; Rydell et al 2002; Jennings et al 2004 (C. godmani and S. lilium based on *C.minor* and *S. tildae* measurements respectiveley)

Diet	Cate.	Frugivore,Insectivore,Nectarivore, Omnivore,Sanguivore	Kalko et al. 1996; Marinello and Bernard 2011
Space preference	Cate.	Edge-space Narrow-space	Zamora-Gutierrez et al. 2016
Foraging preference	Cate.	Passive-active gleaning Aerial foragers Flutter detecting foragers Trawling foragers	Zamora-Gutierrez et al. 2016

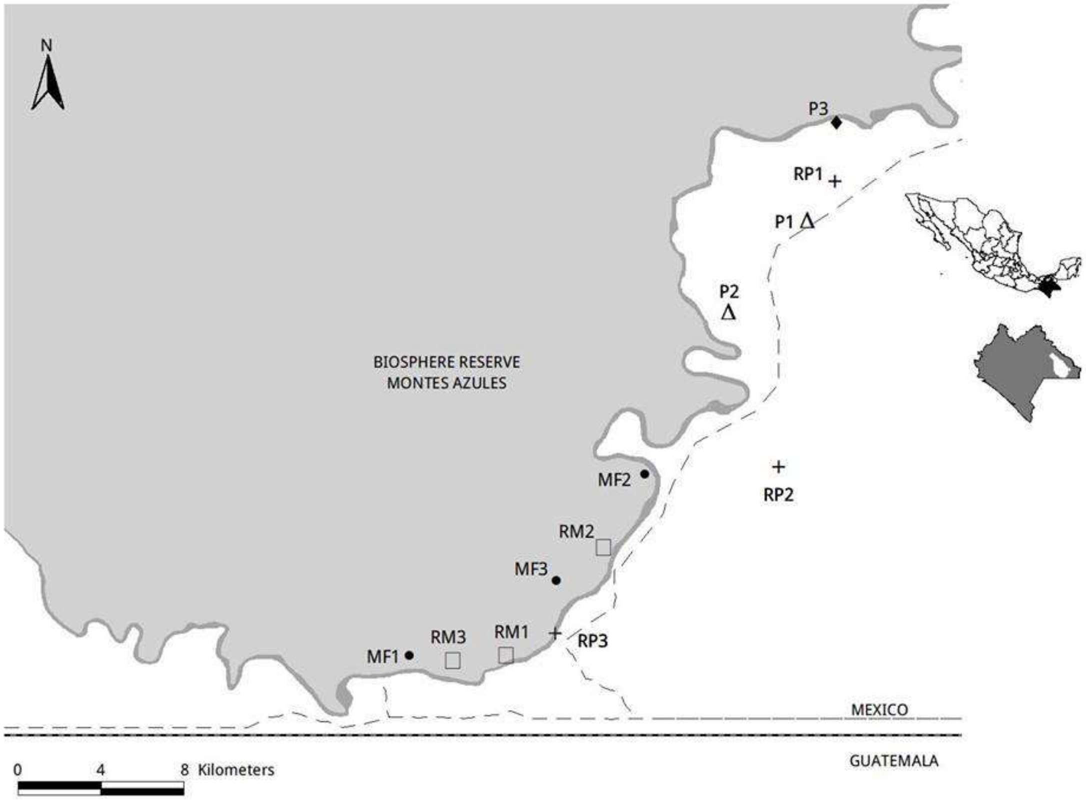


Figure 1. Study area and bat sampling sites at the Lacandona rain forest, Chiapas, Mexico. The map shows the distribution of the habitat types used to sample bat species: riparian vegetation in mature forest (RM), riparian vegetation in pasture (RP), mature forest (MF), Pasture (P).

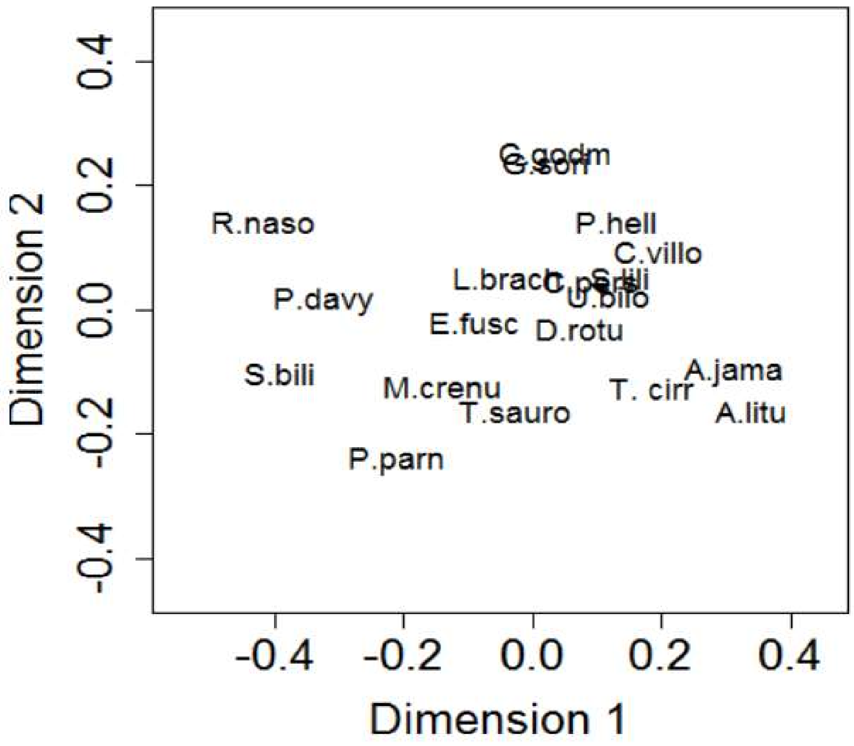


Figure 2. Principal coordinate analysis biplot based on Gower distances between bat species from all families.

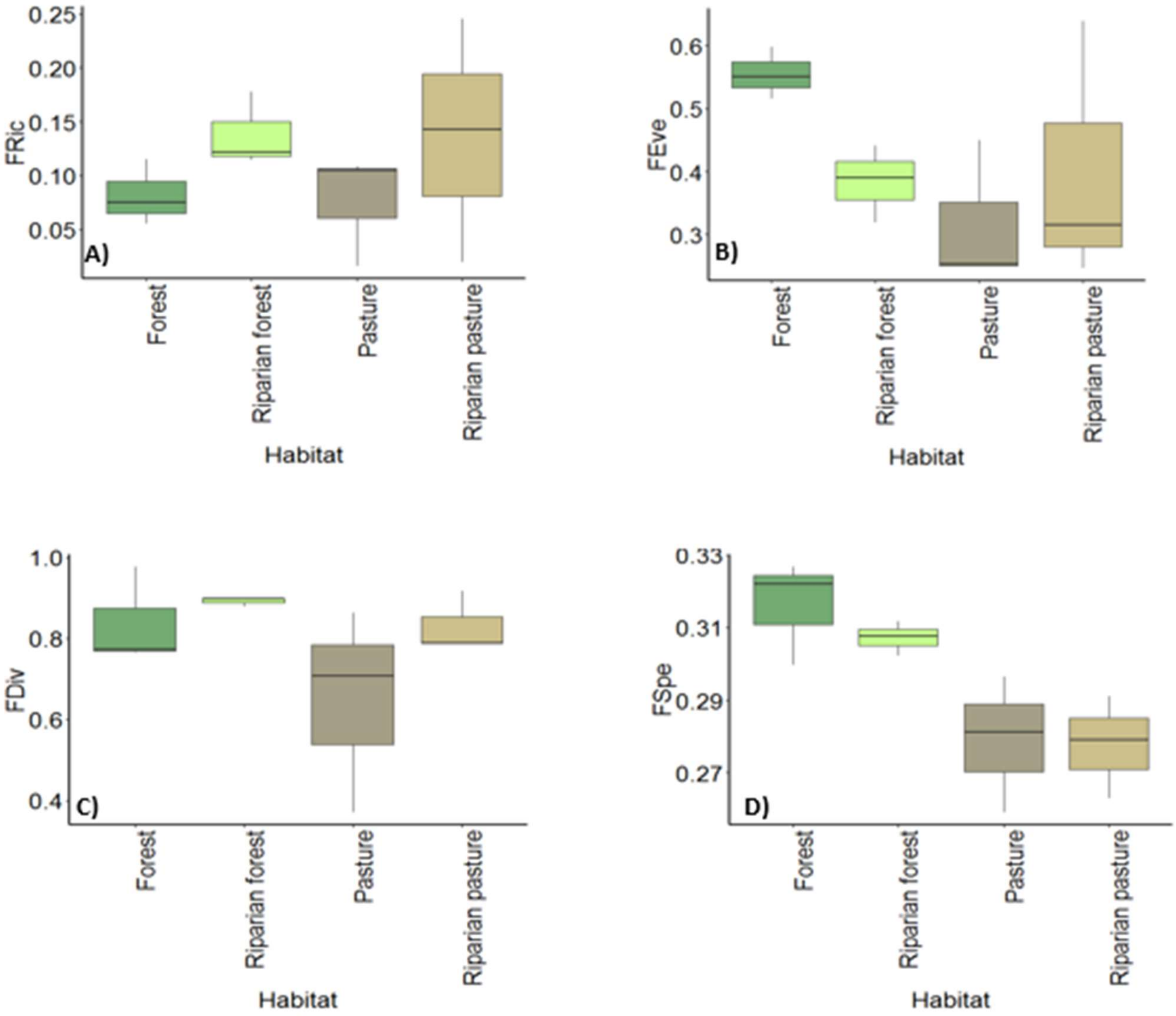
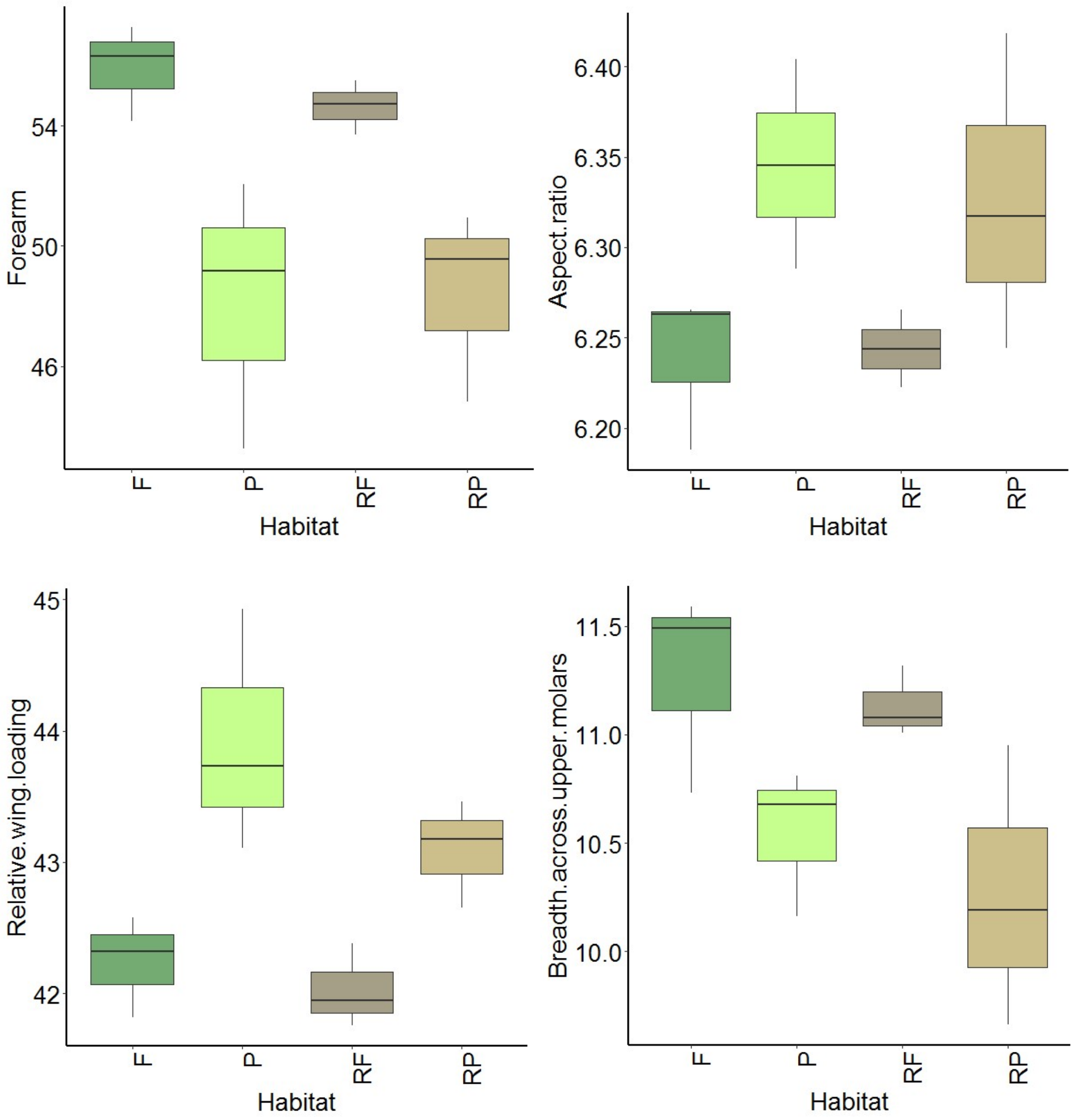


Figure 3. Boxplots showing values of bat species functional diversity in different habitat types: A) Functional richness (FRic), B) Functional evenness (FEve), C) Functional divergence (FDiv), and D) Functional specialization (FSpe). Whiskers extending to 1.5 times the interquartile range of the nearest hinge.


Forearm
54
50
46
F
P
RF
RP
Habitat
Aspect.ratio
6.40
6.35
6.30
6.25
6.20
F
P
RF
RP
Habitat
Relative.wing.loading
45
44
43
42
F
P
RF
RP
Habitat
Breadth.across.upper.molars
11.5
11.0
10.5
10.0
F
P
RF
RP
Habitat

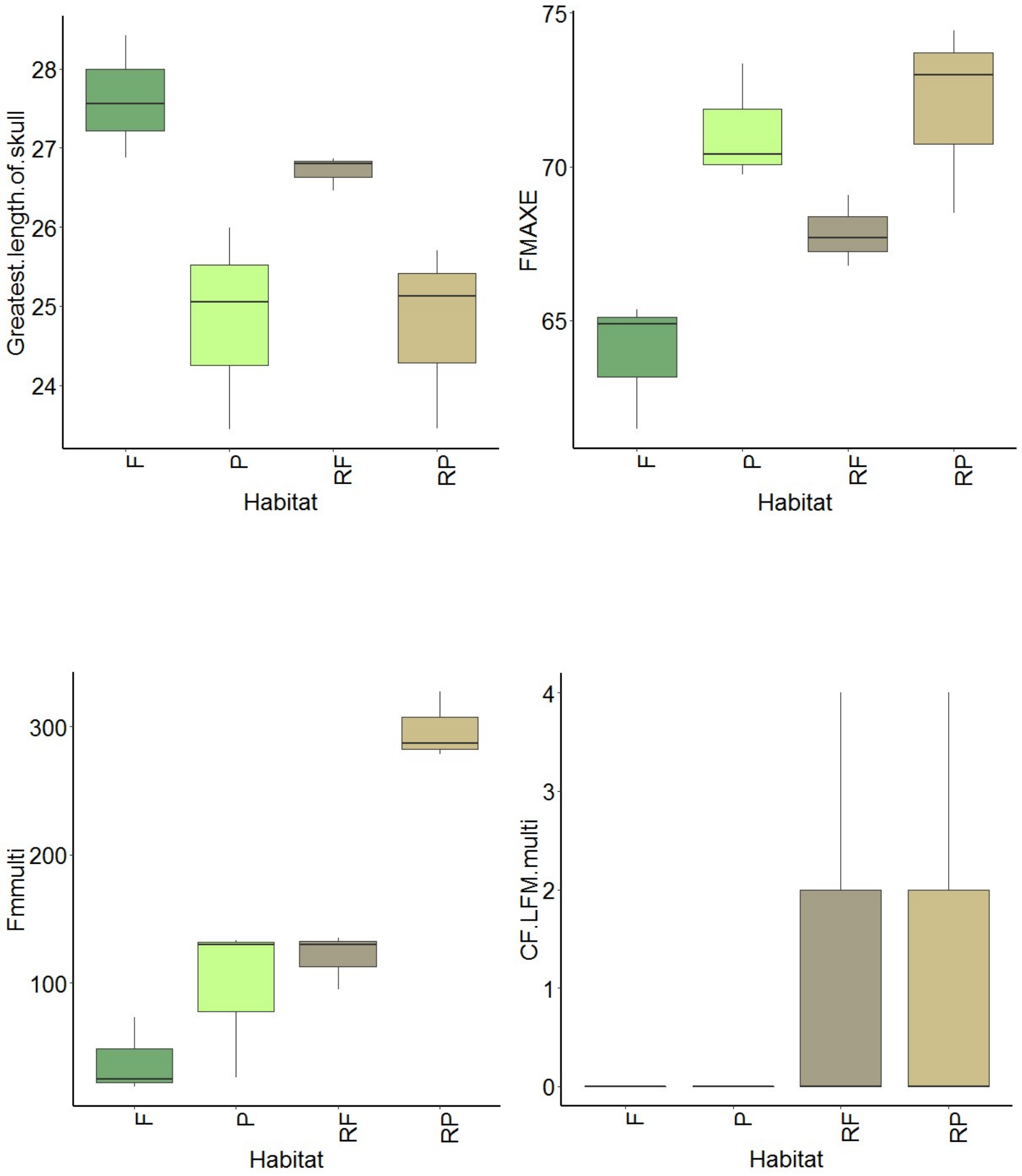
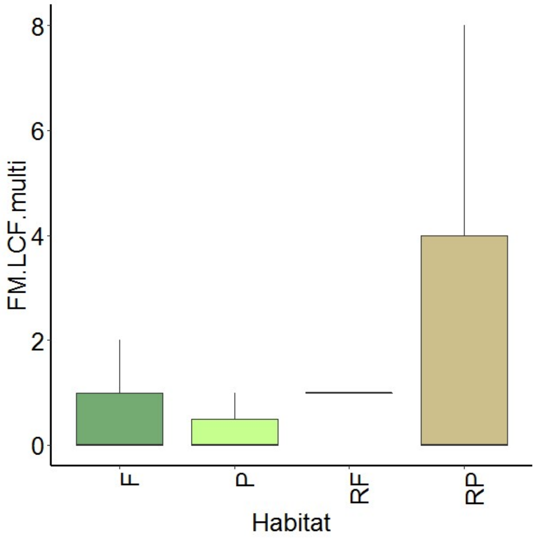
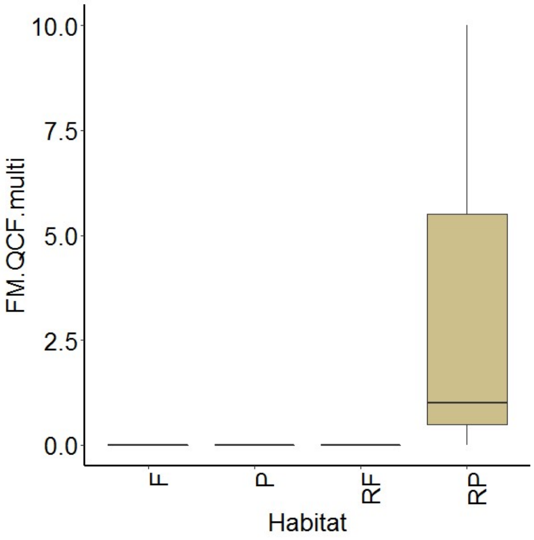


Figure 4. Boxplots showing significant differences among habitats for continuous traits: A) Forearm (FA), B)Aspect ratio (AR), C)Relative wing loading (RWL, D) Greatest length of skull (GLS), E) Breadth across molars (BAM), F) Minimum frequency (FmaxE). Whiskers extending to 1.5 times the interquartile range of the nearest hinge. Asterisks indicate probability of Type I error where * means P= 0.05, ** P≤ 0.01 and *** P ≤0.001.


FM.LCF.multi
0
2
4
6
8
F
P
RF
RP
Habitat


FM.QCF.multi
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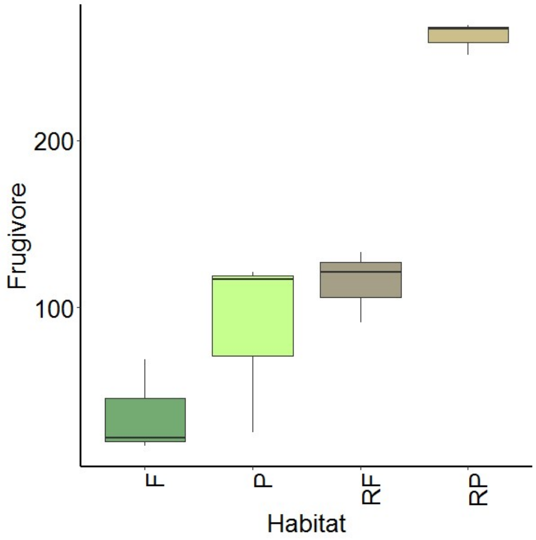
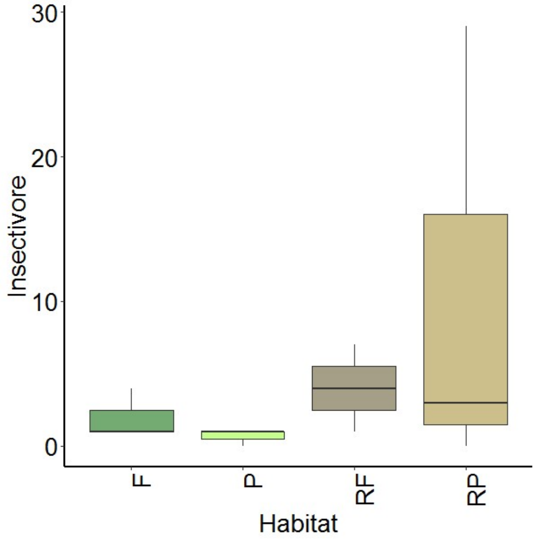
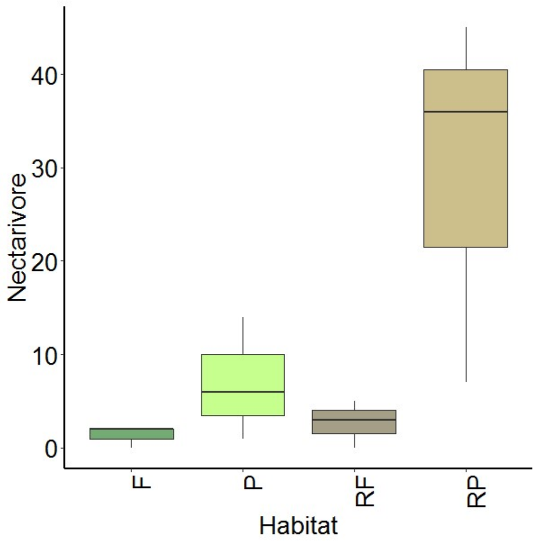
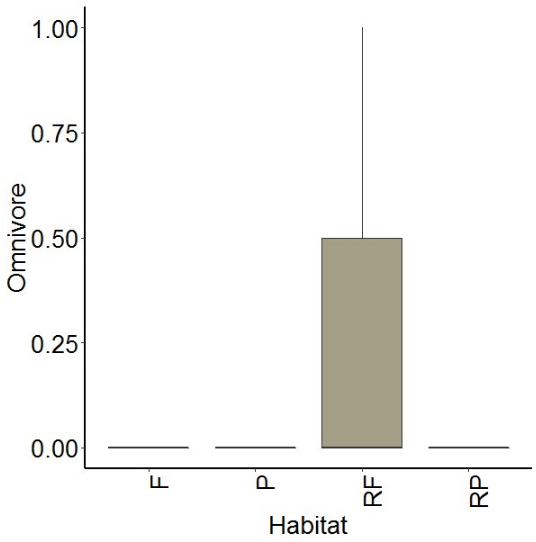
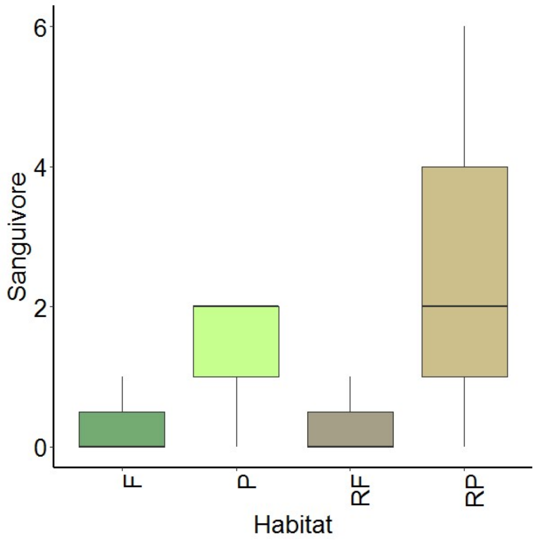
2.5
5.0
7.5
10.0
F
P
RF
RP
Habitat

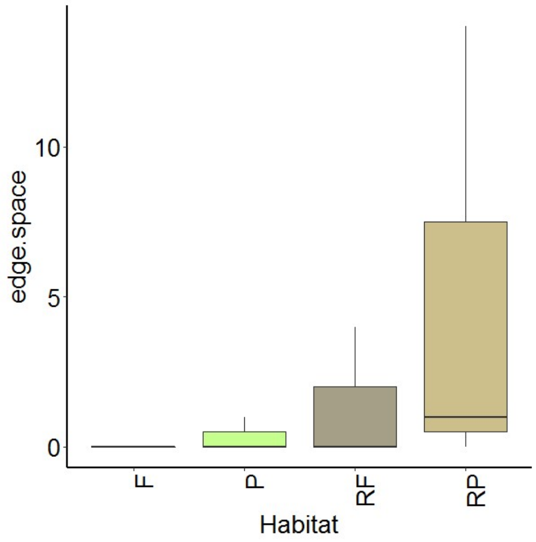

Frugivore
100
200
F
P
RF
RP
Habitat

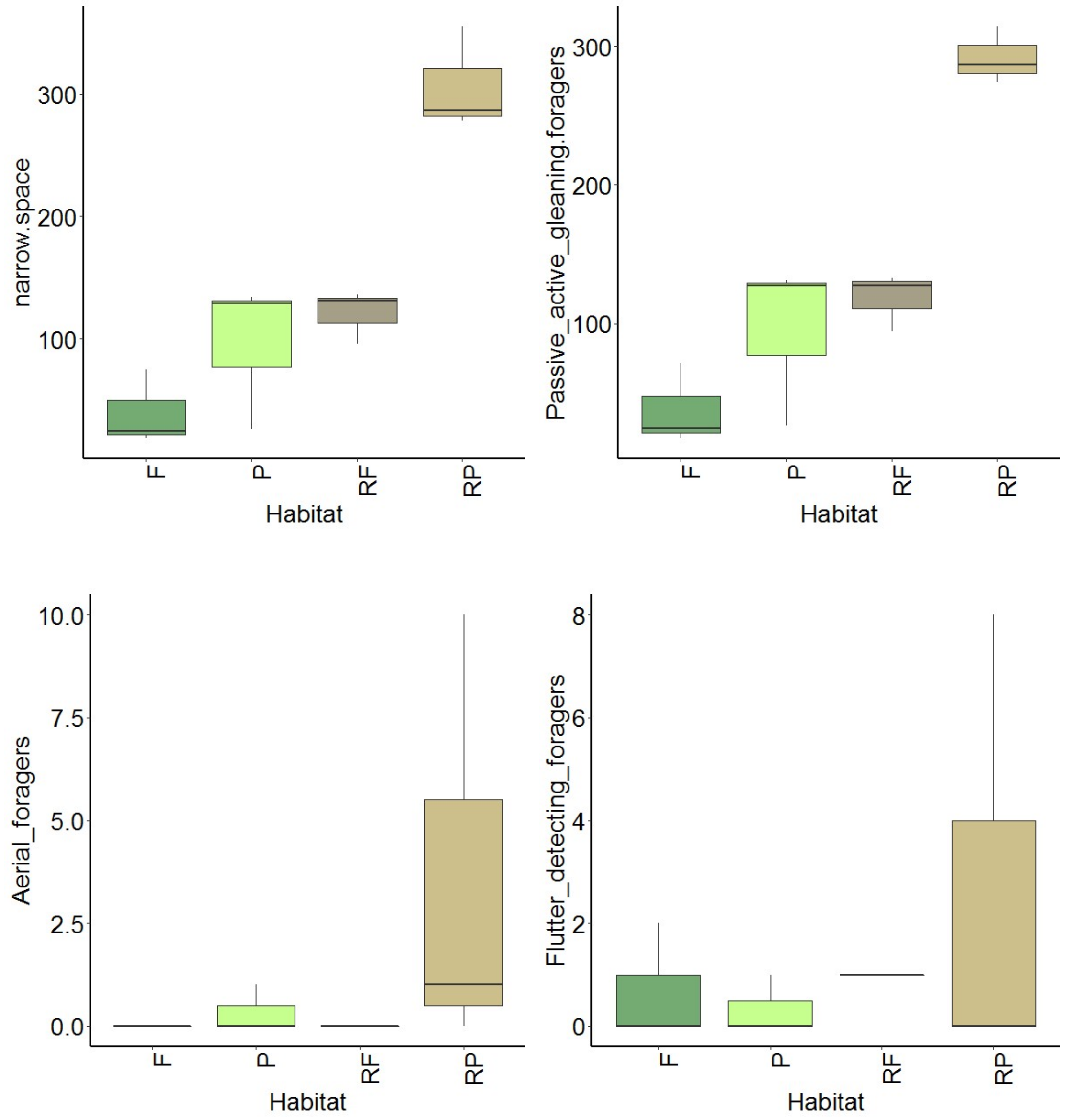

Insectivore
0
10
20
30
F
P
RF
RP
Habitat


Nectarivore
0
10
20
30
40
F
P
RF
RP
Habitat


Omnivore
0.00
0.25
0.50
0.75
1.00
F
P
RF
RP
Habitat


Sanguivore
0
2
4
6
F
P
RF
RP
Habitat


edge.space
0
5
10
F
P
RF
RP
Habitat


narrow.space
300
200
100
F
P
RF
RP
Habitat
Passive_active_gleaning.foragers
300
200
100
F
P
RF
RP
Habitat
Aerial_foragers
10.0
7.5
5.0
2.5
0.0
F
P
RF
RP
Habitat
Flutter_detecting_foragers
8
6
4
2
0
F
P
RF
RP
Habitat

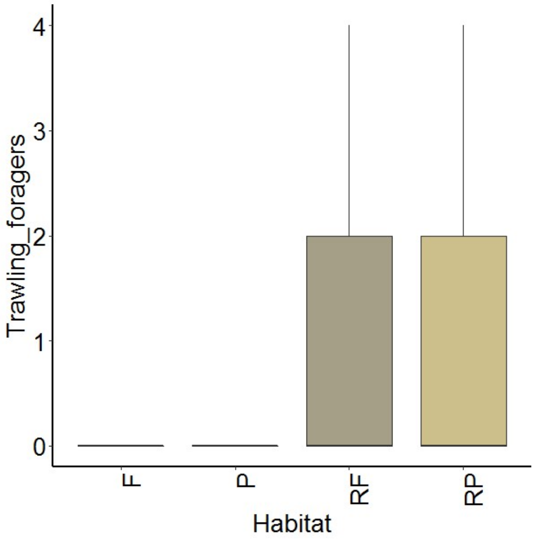
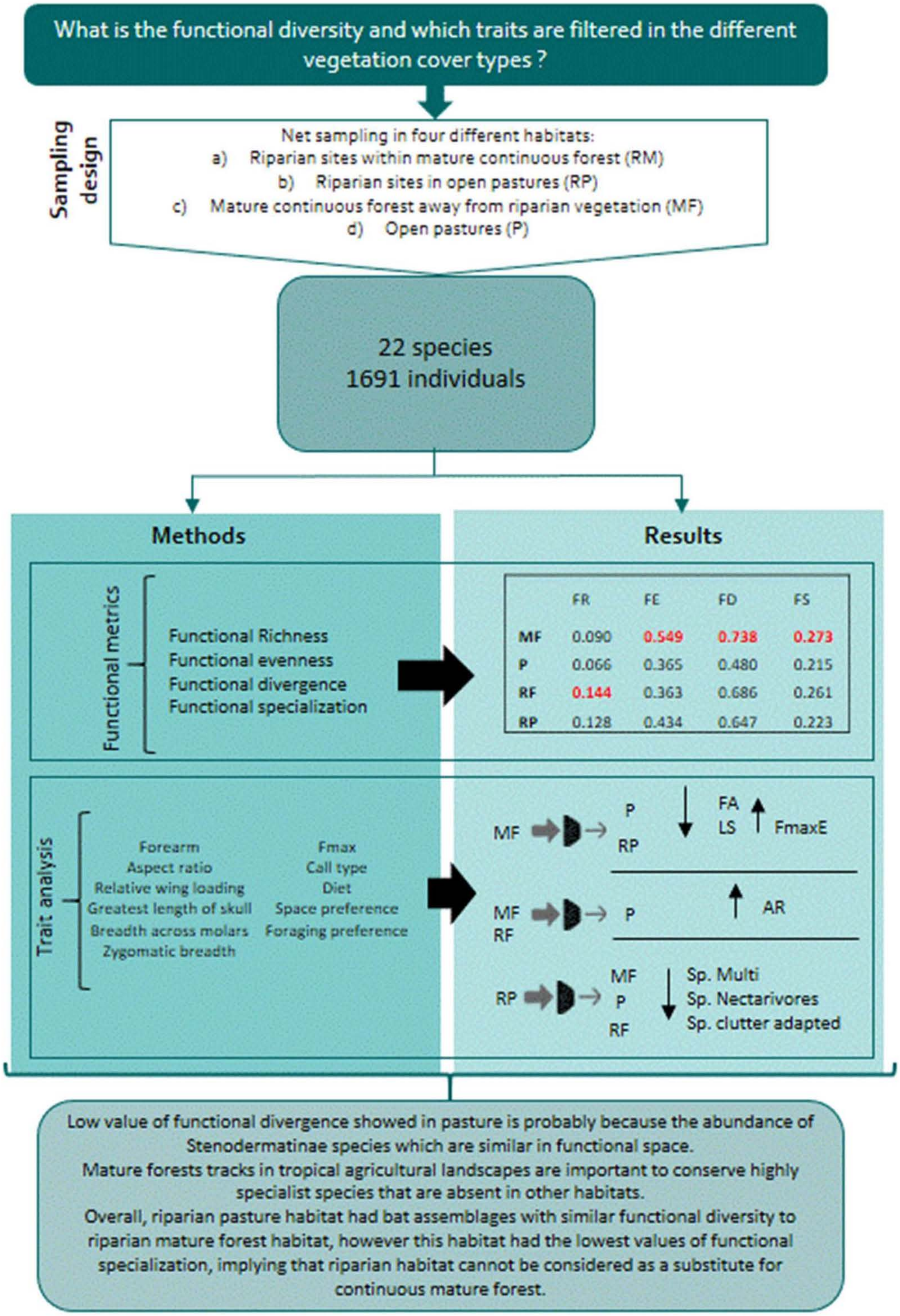


Figure 5. Boxplots showing significant differences among habitats for categorical traits: A) FM multiharmonics (Fmmulti), B) CF-Long FM- multiharmonics (CF.LFM.multi), C) FM-Long CF- multiharmonics (FM.LCF.multi), D) FM-Quasiconstant frequency-multiharmonics (FM.QC.multi), E) Frugivore, F)

Insectivore, G) Nectarivore H) Omnivore, I) Sanguivore, J) Edge-Space, K) Narrow-space, L) Passive-active gleaning, M) Aerial foragers, N) Flutter detecting foragers, O) Trawling foragers. Whiskers extending to 1.5 times the interquartile range of the nearest hinge. Asterisks indicate probability of Type I error where * means P= 0.05, ** P≤ 0.01 and *** P ≤0.001.



What is the functional diversity and which traits are filtered in the different vegetation cover types ?

Net sampling in four different habitats:
a) Riparian sites within mature continuous forest (RM)
b) Riparian sites in open pastures (RP)
c) Mature continuous forest away from riparian vegetation (MF)
d) Open pastures (P)

22 species
1691 individuals

	FR	FE	FD	FS
MF	0.090	0.549	0.738	0.273
P	0.066	0.365	0.480	0.215
RF	0.144	0.363	0.686	0.261
RP	0.128	0.434	0.647	0.223

Low value of functional divergence showed in pasture is probably because the abundance of Stenodermatinae species which are similar in functional space.
Mature forests tracks in tropical agricultural landscapes are important to conserve highly specialist species that are absent in other habitats.
Overall, riparian pasture habitat had bat assemblages with similar functional diversity to riparian mature forest habitat, however this habitat had the lowest values of functional specialization, implying that riparian habitat cannot be considered as a substitute for continuous mature forest.

Figure 6. Diagram of chapter II summary

DISCUSIÓN GENERAL

En la actualidad, la amenaza más grave a la biodiversidad y la causa principal de la crisis de extinción es la fragmentación y pérdida de hábitat (Laurance *et al.* 1997). En el Neotrópico los cambios de uso de suelo derivado de actividades humanas han modificado el paisaje a través de la fragmentación, degradación y destrucción del hábitat natural, dichas actividades son generalmente disturbios de gran extensión y larga duración (Martínez-Ramos & García-Orth 2007; Zermeño-Hernández *et al.* 2014) propiciando la creación de nuevos ambientes antropogénicos. Recientemente, se ha reconocido la importancia de la conservación fuera de las reservas ecológicas, ya que debido a la tendencia al incremento de la frontera agrícola, resulta cada vez menos probable el mantenimiento de grandes extensiones de bosque primario intacto. Uno de los principales retos es conservar la biodiversidad dentro de paisajes fragmentados y se ha señalado ya, que algunas especies nativas pueden continuar viviendo en ambientes que, aun estando sujetos a actividades productivas, mantienen la estructura y funciones básicas del ecosistema original (Laurance *et al.* 1997).

Estudios previos han demostrado que a lo largo del tiempo el paisaje de Marqués de Comillas es capaz de mantener niveles altos de biodiversidad y conservar especies nativas de flora y fauna de gran interés para los planes de conservación (Muench & Martínez-Ramos 2016; de la Torre, Núñez & Medellín 2017). La mayoría de los estudios con comunidades de murciélagos en paisajes fragmentados se basan en descripciones dicotómicas y cualitativas de hábitat, por ejemplo, perturbado *vs*. no perturbado (Estrada & Coates-Estrada 2002), fragmentado *vs.* bosque continuo o en índices sencillos de la composición del paisaje como el tamaño de los fragmentos (Cosson *et al.* 1999). Sin embargo, los efectos de la fragmentación operan a múltiples escalas espaciales, probablemente en función del comportamiento específico de cada especie o las características de su historia de vida (Klingbeil & Willig 2009). Por lo tanto, en la presente tesis se buscó entender la importancia de la vegetación riparia para la dinámica de la comunidad de murciélagos dentro de un paisaje agropecuario. Para responder esta pregunta se siguieron tres enfoques:

La metodología expuesta en el **Capítulo I** permite conocer el papel de la vegetación riparia como reservorio de especies de murciélagos en ambientes altamente perturbados debido a actividades humanas. Para esto, se registró la riqueza y abundancia de murciélagos filostómidos presentes en los diferentes tipos de cobertura vegetal. Los resultados revelaron que existe una clara asociación entre el hábitat de vegetación riparia y la diversidad de especies así como con la abundancia de individuos, encontrando que el hábitat de vegetación riparia dentro de pastizales ganaderos fue superado únicamente por el hábitat de vegetación riparia dentro del bosque maduro en cuanto al número de especies registradas. Se encontró también una asociación positiva entre la composición de especies de murciélagos con árboles de mayor área basal; estos árboles generalmente se encuentran en la vegetación riparia y suelen ser utilizados preferentemente por algunas especies como sitios de percha y/o refugio. Finalmente, encontramos que las especies de murciélagos generalistas y abundantes pueden ser mejores indicadores ecológicos, ya que son capaces de volar sobre diferentes tipos de vegetación cubriendo distancias mayores, en comparación con especies altamente especializadas que disminuyen sus poblaciones rápidamente bajo condiciones de cambio de uso de suelo. Con estos resultados pudimos corroborar la importancia que tienen los corredores de vegetación riparia, ya que permiten la persistencia de especies sensibles a la perturbación del hábitat, demostrando la importancia de mantener diferentes tipos de vegetación y así permitir la conservación de la diversidad de murciélagos en paisajes con uso de suelo agrícola (Medina *et al.* 2007; Williams-Guillén & Perfecto 2010).

Por otra parte, **el Capítulo II** aborda la dinámica social de la comunidad de murciélagos, analizando la importancia del tipo de hábitat para la distribución de la proporción de sexos y patrones de segregación sexual en seis de las especies de filostómidos más comunes. La segregación sexual es un fenómeno ampliamente documentado con murciélagos (Senior *et al.* 2005; Sgroi & Wilkins 2010), sin embargo la mayoría de estos estudios consideran únicamente colonias de murciélagos cavernícolas (Ortega & Arita 1999; Ortega & Maldonado 2006). El presente trabajo es uno de los primeros en explorar la asociación ente la proporción de hembras y el hábitat de vegetación riparia en el Neotrópico. Los resultados obtenidos mostraron que más de la mitad de los individuos capturados fueron hembras. Para la especie de mayor tamaño (*Artibeus lituratus*) la proporción de hembras mostró una fuerte asociación con el tipo de hábitat los cuáles suelen ser el hábitat con mayor disponibilidad de recursos. Otra consideración interesante es que junto con *Sturnira lilium* (especie considerada generalista) mostraron fuerte asociación con la estacionalidad, la cual influye sobre la fenología y producción de frutos de las plantas afectando directamente la disponibilidad de recursos.

Por otra parte las hembras de la especie nectarívora *Glossophaga soricina* están estrechamente relacionadas con atributos muy específicos de la vegetación como árboles de gran altura y mayor área basal los cuáles pueden proporcionarles mayores oportunidades de forrajeo y refugio (Evelyn & Stiles 2003; Ortiz-Ramírez *et al.* 2006). Estos resultados muestran que las respuestas de la comunidad de murciélagos asociadas al hábitat de vegetación riparia en paisajes dominados por actividades humanas son específicas para cada sexo y especie, y el entendimiento de estos cambios puede disminuir las consecuencias generalizadas de la fragmentación además del deterioro y pérdida de hábitat.

El estudio de las respuestas específicas de las especies a los diferentes tipos de vegetación ha cobrado gran relevancia ecológica. Con la finalidad de comprender los efectos específicos que el tipo de hábitat puede tener sobre los atributos funcionales de las especies de murciélagos, el **Capítulo III** tuvo como finalidad cuantificar la diversidad funcional de la comunidad de murciélagos e identificar cuáles atributos están siendo filtrados por el hábitat de vegetación riparia y no riparia. Los resultados revelaron que la divergencia funcional (medida de la proporción de abundancia de las especies y su discrepancia del espacio funcional) registró los valores más altos en el hábitat de ripario maduro y ripario pastizal. Esto puede explicarse debido a que las especies registradas presentan poca especialización y los atributos son redundantes entre ellas. Por otra parte, especies frugívoras de tamaño pequeño y con carga alar alta son más comunes en ambientes perturbados, dichos atributos les permiten ser voladores rápidos y eficientes para viajes de larga distancia en espacios abiertos. Por otra parte las especies con tamaño de cráneo más grande fueron registradas en el bosque maduro y ripario maduro sugiriendo que la especialización trófica suele ser más sensible a las actividades agropecuarias. Los resultados de este capítulo demuestran la importancia de conservar áreas de bosques maduros en los paisajes agropecuarios para asegurar la conservación de especies de murciélagos altamente especializadas.

Implicaciones de manejo para la conservación de murciélagos en paisajes transformados

En el Neotrópico, la vegetación riparia se encuentra bajo gran presión debido principalmente a actividades de origen agropecuario y la extracción de productos maderables, sin embargo, la conservación y manejo de las zonas de vegetación riparia parece ser el método más eficaz y menos costoso para el mantenimiento de la diversidad biológica en general (Jobin *et al.* 2004). Se ha documentado que para grupos faunísticos de invertebrados (Garcia-Martínez *et al.* 2015), aves (Seaman & Schulze 2010) y murciélagos (de la Peña-Cuéllar *et al.* 2015b; Zarazúa-Carbajal *et al.* 2017) la composición de especies y densidad de individuos difiere considerablemente entre franjas de vegetación riparia y la matriz agropecuaria adyacente.

La biodiversidad y las actividades productivas dentro de los bosques están íntimamente relacionadas. Particularmente se ha enfatizado que la conservación de bosques riparios y el establecimiento de cercas vivas son herramienta cruciales para el mantenimiento de la biodiversidad y los servicios ecosistémicos en paisajes seriamente fragmentados (Estrada & Coates-Estrada 2001). Sin embargo, al igual que en la mayoría de los países de América Latina, en México los bosques riparios no suelen ser considerados dentro de los programas gubernamentales ni en las políticas públicas relacionadas con el manejo de recursos (Meli *et al.* 2017).

En un esfuerzo reciente por sistematizar acciones de conservación de la biodiversidad que puedan ejecutarse de manera voluntaria por los propietarios de las tierras, la CONAFOR y el Programa de las Naciones Unidas para el Desarrollo (PNUD) desarrollaron el “Manual de mejores prácticas de manejo forestal para la conservación de la biodiversidad en ecosistemas tropicales de la región sureste de México”(CONAFOR 2016), desafortunadamente en este documento tampoco se consideran prácticas dirigidas hacia los bosques riparios bajo condiciones de manejo agropecuario. No obstante en la tabla 1 se enlistan algunas acciones puntuales que pueden promover y conservar la diversidad de murciélagos en la región.

Tabla 1. Recomendaciones relacionadas con la conservación y manejo de las zonas riparias en el bosque tropical lluvioso del sureste mexicano, modificado de CONAFOR 2016.

Recomendaciones	Beneficio a la diversidad de murciélagos
Identificar los árboles utilizados como refugio o fuente de alimento, con la finalidad de proteger dichos árboles durante las actividades	- Mantener la distribución y abundancia de las poblaciones- Conservación de la diversidad genética de las poblaciones de flora y fauna
Mantener vegetación arbórea que cubra los cauces de los arroyos hasta una distancia de 50 m perpendicular a la dirección de la corriente	Podría garantizar la cobertura vegetal a lo largo del arroyo y favorecer la conectividad del paisaje actuando como corredores de vuelo fomentando la formación de redes de dispersión (Estrada & Coates-Estrada 2001)
En la medida de lo posible evitar el uso de agroquímicos y labores que	Mantener o mejorar la calidad del agua que atraviesa las zonas de pastizales, favoreciendo la

impliquen riesgos de contaminación del agua	abundancia y biomasa de insectos, los cuales sirven de alimento para muchas especies de murciélagos (Ober & Hayes 2008)

Consideraciones finales

El comportamiento de la comunidad de murciélagos en el paisaje transformado del bosque tropical lluvioso del sureste mexicano, depende de las características de los diferentes elementos del paisaje, como el tipo de hábitat y aspectos específicos de la estructura vegetal como altura y área basal de los árboles, además de la estacionalidad y disponibilidad de sitios de refugio y percha. Esto indica que las estrategias de conservación para este grupo y por lo tanto de los servicios ecosistémicos que brindan requieren de la atención tanto de la vegetación de bosque maduro como de la parte sujeta a actividades de agricultura y ganadería. La vegetación riparia es de vital interés ya que resulta fundamental para la conservación un gran número de especies de fauna que habitan el bosque tropical lluvioso.

Con base en los resultados obtenidos y los vacíos de información detectados durante el transcurso del estudio, sugerimos que en estudios futuros se consideren aspectos como: 1) la dinámica que existe entre la estructura de la vegetación y la actividad y biomasa de invertebrados y la relación con la actividad de los murciélagos, en esta parte se pueden también incorporar mediciones de calidad del agua; 2) determinar patrones de uso de hábitat por género y especie de murciélagos, con lo cual se puede también determinar el grado de conectividad del paisaje, y 3) documentar las prácticas de manejo agrícolas y ganaderas para establecer si existe relación de ellas con la dinámica de la comunidad de murciélagos.

La identificación de los patrones ecológicos y poblacionales en la respuesta de la comunidad de murciélagos a la trasformación del hábitat derivados de diferentes regiones y características de disturbio puede garantizar la persistencia a largo plazo de las poblaciones de murciélagos en paisajes modificados, asegurando servicios ecológicos como polinización y dispersión de semillas los cuales tienen influencia indirecta en la provisión de la diversidad de alimentos y mantenimiento de la diversidad de plantas y así como control de plagas asociado con el mantenimiento de la salud pública, los cuales tienen impacto directo al bienestar humano.

LITERATURA CITADA

Abbott, I.M., Sleeman, D.P. & Harrison, S. (2009) Bat activity affected by sewage effluent in Irish rivers. *Biological Conservation*, **142**, 2904–2914.

Adams, R.A. & Hayes, M.A. (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, **77**, 1115–1121.

Aguiar, L.M.S., Bernard, E. & Machado, R.B. (2014) Habitat use and movements of Glossophaga soricina and Lonchophylla dekeyseri (Chiroptera : Phyllostomidae) in a Neotropical savannah. *Zoologia*, **31**, 223–229.

Altringham, J.D. (2011) *Bats: From Evolution to Conservation*, 2nd ed. Oxford University Press, Oxford.

Alvarez, T. & Sánchez-Casas, N. (1999) Diferenciación alimentaria entre los sexos de Glossophaga soricina (Chiroptera: Phyllostomidae) en México. *Revista de Biologia Tropical*, **47**, 1129–1136.

Arita, H.T. & Fenton, M.B. (1997) Flight and echolocation in the ecology and evolution of bats. *Trends in Ecology and Evolution*, **12**, 53–58.

Arita, H.T. & Santos-del-Prado, K. (1999) Conservation Biology of Nectar-Feeding Bats in Mexico. *Journal of Mammalogy*, **80**, 31–41.

Arnone, I.S., Trajano, E., Pulchério-Leite, A. & Passos, F.C. (2016) Long-distance movement by a great fruit-eating bat, Artibeus lituratus (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota*

Neotropica, **16**, 1–6.

Barclay, R.M.R. (1989) The effect of reproductive condition on the foraging behavior of female hoary bats, Lasirurus cinereus. *Behavioral Ecology and Sociobiology*, **24**, 31–37.

Barlow, K.E. (1997) The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology*, **243**, 597–609.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2014) Fitting linear mixed-effects models using lme4 Douglas. *Journal of Statistical Software*, 1–51.

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2016) Sexual segregation when foraging in an extremely social killer whale population. *Behavioral Ecology and Sociobiology*, **70**, 189–198.

Bender, D. J., Contreras, T. A., Fahrig, L. (1998) Habitat Loss and Population Decline : a Meta-Analysis of the Patch Size Effect. *Ecology*, **79**, 517–533.

Bernard, E. & Fenton, M.B. (2002) Species diversity of bats (Mammalia : Chiroptera) in forest fragments , primar ...

Bhagwat, S.A., Willis, K.J., Birks, H.J.B. & Whittaker, R.J. (2008) Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution*, **23**, 261–267.

Bianconi, G. V, Mikich, S.B. & Pedro, W.A. (2006) Movements of bats (Mammalia , Chiroptera) in Movements Chiropteroptera) Atlantic For est remnants in southern Brazil Forest remnants southern Brazil. *Revista Brasileira de Zoologia*, **23**, 1199–1206.

van Breugel, M., Martínez-Ramos, M., Bongers, F., Martinez-Ramos, M. & Bongers, F. (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, **22**, 663–674.

Broders, H.G., Forbes, G.J., Woodley, S. & Thompson, I.D. (2006) Range extent and stand selection for roosting and foraging in forest-dwelling Northern Long-eared Bats and Little Brown Bats in the Greater Fundy ecosystem, New Brunswick. *Journal of Wildlife Management*, **70**, 1174–1184.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Castro-Luna, A.A., Sosa, V.J. & Castillo-Campos, G. (2007) Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, **10**, 219–228.

Chacón, M. & Harvey, C.A. (2006) Live fences and landscape connectivity in a neotropical agricultural landscape. *Agroforestry Systems*, **68**, 15–26.

Charles-Dominique, P. (1991) Feeding strategy and activity budget of the frugivorous bat Carollia perspicillata (Chiroptera: Phyllostomidae) in French Guiana. *Journal of Tropical Ecology*, **7**, 243.

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, **21**, 523–533.

Comisión Federal de Electricidad. (2006) *División Hidrométrica Sureste.* Estación Lacantún, Marqués de Comillas, Chiapas, México.

CONAFOR. (2016) *Manual de Mejores Prácticas de Manejo Forestal Para La Conservación de La Biodiversidad En Ecosistemas Tropicales de La Región Sureste de México*. Ciudad de México.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A Trait-Based Test for Habitat Filtering : Convex Hull Volume. , **87**, 1465–1471.

Cosson, J.F., Pons, J.M. & Masson, D. (1999) Effects of Forest Fragmentation on Frugivorous and Nectarivorous Bats in French Guiana. , 515–534.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Denzinger, A. & Schnitzler, H.U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, **4 JUL**, 1–15.

Diamond, G.F. & Diamond, J.M. (2014) Bats and Mines: Evaluating Townsend's Big-Eared Bat (Corynorhinus townsendii) Maternity Colony Behavioral Response to Gating. *Western North American Naturalist VO - 74*, **74**, 416.

Dietz, M., Kalko, E.K. V & Encarnação, J.A. (2006) Small scale distribution patterns of female and male Daubenton's bats (Myotis daubentonii). *Acta Chiropterologica*, **8**, 403–415.

Dirzo, R. & Raven, P.H. (2003) Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, **28**, 137–167.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, **23**, 849–860.

Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S. & Hamer, K.C. (2014) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation*, **17**, 163–173.

Encarnação, J.A. (2012) Spatiotemporal pattern of local sexual segregation in a tree-dwelling temperate bat Myotis daubentonii. *Journal of Ethology*, **30**, 271–278.

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

Estrada, A. & Coates-Estrada, R. (2002) Bats in continous forest, forest fragments and in an agricultural mosiac habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, **103**, 237–245.

Evelyn, M.J. & Stiles, D. a. (2003) Roosting requirements of two frugivorous bats (Sturnira lilium and Arbiteus intermedius) in fragmented Neotropical forest. *Biotropica*, **35**, 405–418.

Fagan, M.E., DeFries, R.S., Sesnie, S.E., Arroyo, J.P., Walker, W., Soto, C., Chazdon, R.L. & Sanchun, A. (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, **8**, 034017.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, **52**, 1381–1391.

Fenton, A.M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K., Syme, D.M. & Adkins, B. (1992) Phyllostomid Bats (Chiroptera : Phyllostomidae) as Indicators of Habitat Disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Frank, H.K., Mendenhall, C.D., Judson, S.D., Daily, G.C. & Hadly, E.A. (2016) Anthropogenic impacts on Costa Rican bat parasitism are sex specific. *Ecology and Evolution*, **6**, 4898–4909.

Freudmann, A., Mollik, P., Tschapka, M. & Schulze, C.H. (2015) Impacts of oil palm agriculture on phyllostomid bat assemblages. *Biodiversity and Conservation*, **24**, 3583–3599.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, **75**, 1252–1258.

Galindo-González, J. (1998) Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. *Acta Zoologica Mexicana*, 57–74.

Galindo-González, J. & Sosa, V.J. (2003) Frugivorous Bats in Isolated Trees and Riparian Vegetation Associated With Human-Made Pastures in a Fragmented Tropical Landscape. *The Southwestern Naturalist*, **48**, 579–589.

Garcia-Martínez, M.A., Escobar-Sarria, F., Pez-Barrera, F.L., Castano-Meneses, G. & Lez, J.E.V.G. (2015) Value of Riparian Vegetation Remnants for Leaf-Litter Ants (Hymenoptera: Formicidae) in a Human-Dominated Landscape in Central Veracruz, Mexico. *Environmental Entomology*, **44**, 1488–1497.

García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez, A.E. & Ávila-Gómez, E.S. (2016) Deforestation Impacts on Bat Functional Diversity in Tropical Landscapes. *Plos One*, **11**, e0166765.

Gorresen, P.M. & Willig, M.R. (2004) Landscape Responses of Bats To Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*, **85**, 688–697.

Grau, H.R. & Aide, M. (2008) Globalization and land-use transitions in Latin America. *Ecology and Society*, **13**.

Griscom, H.P., Kalko, E.K. V & Ashton, M.S. (2007) Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica*, **39**, 278–282.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed : evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii ? , 540–548.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: A case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842–850.

Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñóz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., Navas, A., Saenz, J., Sánchez, D., Medina, A., Vilchez, S., Hernández, B., Perez, A., Ruiz, F., López, F., Lang, I. & Sinclair, F.L. (2005)

Contribution of live fences to the ecological integrity of agricultural landscapes. *Agriculture, Ecosystems and Environment*, **111**, 200–230.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation\t. *Biodiversity and Conservation*, **13**, 207–251.

Henry, M. & Kalko, E.K. V. (2007) Froraging Strategy and Breeding Constraints of Rhynophyla Pumilio (PHYLLOSTOMIDAE) in the Amazon Lowlands. *Journal of Mammalogy*, **88**, 81–93.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) *Global Status Survey and Conservation Action Plan: Microchiropteran Bats*.

INE. (2000) *Programa de Manejo Reserva de La Biósfera Montes Azulez, México.* México.

Instituto Nacional de Ecología. (2000) *Programa de Manejo de La Reserva de La Biosfera Montes Azules*, 1a. Enkidu Editores, S.A. de C.V., México, D.F.

Istvanko, D.R., Risch, T.S. & Rolland, V. (2016) Sex-specific foraging habits and roost characteristics of Nycticeius humeralis in north-central Arkansas. *Journal of Mammalogy*, **97**, 1–9.

Jennings, N.V., Parson, S., Barlow, K.E. & Gannon, M.R. (2004) Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterologica*, **6**, 75–90.

Jennings, N. & Pocock, M.J.O. (2009) Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conservation Biology*, **23**, 1195–1203.

Jobin, B., Bélanger, L., Boutin, C. & Maisonneuve, C. (2004) Conservation value of agricultural riparian strips in the Boyer River watershed, Québec (Canada). *Agriculture,* *Ecosystems and Environment*, **103**, 413–423.

De Jong, B.H.J., Ochoa-Goana, S., Castillo-Santiago, M.A., Ramirez-Marcial, N. & Cairns, M.A. (2000) Carbon flux and patterns of land-use/land-cover change in het Selva Lacandona, Mexico. *A Journal of the Human Environment*, **29**, 504–511.

Jong, D. & Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13_ _**, 275–280.

Jung, K., Kalko, E.K. V & Von Helversen, O. (2007) Echolocation calls in Central American emballonurid bats: Signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.

Kalka, M. & Kalko, E.K. V. (2005) Gleaning bats as underestimated predators of herbivorous insects: diet of Micronycteris microtis (Phyllostomidae) in Panama. *Journal of Tropical Ecology*, **22**, 1.

Kalko, E.K. V & Handley, C.O. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.

Keen, R. & Hitchcock, H.H.B. (1980) Survival and longevity of the little brown bat (Myotis lucifugus) in southeastern Ontario. *Journal of Mammalogy*, **61**, 1–7.

Kelm, D.H., Wiesner, K.R. & Helversen, O. Von. (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conservation Biology*, **22**, 733–741.

Klingbeil, B.T. & Willig, M.R. (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest Brian. *Journal of Applied Ecology*, **46**, 203–213.

Klingbeil, B.T. & Willig, M.R. (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, **119**, 1654–1664.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kurta, A. & Matson, J.O.. (1980) Disproportionate Sex Ratio in the Big Brown Bat (Eptesicus fuscus). , **104**, 367–369.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015a) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**.

de la Peña-Cuéllar, E., Benítez-Malvido, J., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2015b) Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. *Ecology and Evolution*, **5**, 903–913.

de la Peña-Cuéllar, E., Stoner, K.E., Avila-Cabadilla, L.D., Martínez-Ramos, M. & Estrada, A. (2012) Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. *Biodiversity and Conservation*, **21**, 1381–1397.

de la Torre, J.A., Núñez, J.M. & Medellín, R.A. (2017) Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. *Biological Conservation*, **206**, 270–282.

Lande, R. (1987) Extinction Thresholds in Demographic Models of Territorial Populations. *The American Naturalist*, **130**, 624–635.

Laurance, W.F. (1991) Society for Conservation Biology Ecological Correlates of Extinction

Proneness in Australian Tropical Rain Forest Mammals. *Conservation Biology*, **5**, 79–89.

Laurance, W., Bierregaard, R. & Moritz, C. (1997) *Tropical Forest Remnants : Ecology, Management, and Conservation of Fragmented Communities*. University Of Chicago Press.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, **16**, 605–618.

Law, B. & Chidel, M. (2002) Tracks and Riparian Zones Facilitate the Use of Australian Regrowth Forest by Insectivorous Bats. *The Journal of Applied Ecology*, **39**, 605–617.

Lebrija-trejos, E., Pérez-garcía, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by : Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly. *Ecology*, **91**, 386–398.

Lemaître, J.-F., Gaillard, J.-M., Pemberton, J.M., Clutton-Brock, T.H. & Nussey, D.H. (2014) Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer. *Proceedings. Biological sciences / The Royal Society*, **281**, 20140792-.

Lenth, R.V. (2014) lsmeans: Least-square means.

Lintott, P.R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R.J., Olley, L. & Park, K.J. (2014) City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal society open science*, **1**, 1–8.

Lloyd, A., Law, B. & Goldingay, R. (2006) Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation*, **129**, 207–220.

Lobo, J.A., Quesada, M. & Stoner, K.E. (2005) Effects of pollination by bats on the mating system of Ceiba pentandra (Bombacaceae) populations in two tropical life zones in Costa Rica. *American Journal of Botany*, **92**, 370–376.

Lundy, M. & Montgomery, I. (2010) Summer habitat associations of bats between riparian landscapes and within riparian areas. *European Journal of Wildlife Research*, **56**, 385–394.

Martínez-Ramos, M. & García-Orth, X. (2007) Sucesión ecológica y restauración de las selvas húmedas. *Bol. Soc. Bot. Méx*, **80**.

Mayaux, P., Holmgren, P., Achard, F., Eva, H.D., Stibig, H.-J.J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **360**, 373–84.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesk, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.

McCracken, G.F. & Wilkinson, G.S. (2000) Bat Mating Systems. *Reproductive Biology of Bats*, pp. 321–362.

Mcgill, J. & Kalko, V. (2015) Climate , habitat , and species interactions at different scales determine the structure of a Neotropical bat community Author (s): Sergio Estrada-Villegas , Brian J . McGill and Elisabeth K . V . Kalko Published by : Ecological Society of America Stabl. , **93**, 1183–1193.

Medellin, R. a. (1994) Mammal Diversity and Conservation in the Selva-Lacandona, Chiapas, Mexico. *Conservation Biology*, **8**, 780–799.

Medellín, R. a, Equihua, M. & Amin, M. a. (2000) Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests\rDiversidad y Abundancia de Murciélagos como Indicadores de Perturbaciones en Selvas Húmedas Neotropicales. *Conservation Biology*, **14**, 1666–1675.

Medellín, R.A., Equihua, M. & Amin, M.A. (2011) *Identificación de Los Murciélagos de México: Clave de Campo*. México, D.F.

Medina, A., Harvey, C. a, Sánchez, D., Vílchez, S. & Hernández, B. (2007) Bat diversity and movement in a Neotropical agricultural landscape. *Biotropica*, **39**, 120–128.

Meli, P., Ruiz, L., Aguilar, R., Rabasa, A., Rey-Benayas, J.M. & Carabias, J. (2017) Bosques ribereños del trópico húmedo de México: Un caso de estudio and aspectos críticos para una restauración exitosa. *Madera Bosques*, **23**, 181–193.

de Mello, M.A.R. & Fernandez, F.A.S. (2000) Reproductive ecology of the bat Carollia perspicillata (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest. *International Journal of Mammalian Biology*, **65**, 340–349.

Meyer, C.F.J., Fr??nd, J., Lizano, W.P. & Kalko, E.K. V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–

391.

Meyer, C.F.J. & Kalko, E.K. V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.

Miller, K., Chang, E. & Johnson, N. (2001) *Defining Common Ground for the Mesoamerican Biological Corridor*.

Montoya Gómez, G., Hernández Ruiz, J.F., Velasco Pérez, A., Reygadas, L. & Ramos Maza, T. (2006) Organización comunitaria para la conservación forestal: estudio de caso en la Selva Lacandona de Chiapas, México. *Papeles de población*, **14**, 11.

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. , 149–158.

Morrison, D.W. (1978) Lunar phobia in a neotropical fruit bat, Artibevs jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852–855.

Mouillot, D., Graham, N.A.J., Vill??ger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Muench, C. & Martínez-Ramos, M. (2016) Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico. *Tropical Conservation Science*, **9**, 178–202.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecological Applications*, **3**, 209–212.

Nardone, V., Cistrone, L., Di Salvo, I., Ariano, A., Migliozzi, A., Allegrini, C., Ancillotto, L., Fulco, A. & Russo, D. (2015) How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat Myotis daubentonii. *PLoS ONE*, **10**, 1–15.

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **316**, 335–427.

Nowak, R. (1991) *Walker's Mammals of the World*. Johns Hopkins Univ Pr.

Nupp, T. & Swihart, R. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512–526.

Ober, H.K. & Hayes, J.P. (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, **256**, 1124–1132.

Ortega, J. & Arita, H.T. (1999) Structure and Social dynamics of harem groups in Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, **80**, 1173–1185.

Ortega, J. & Maldonado, J.E. (2006) Female interactions in harem groups of the Jamaican fruit-eating bat, Artibeus jamaicensis (Chiroptera : Phyllostomidae). *Acta Chiropterologica*, **8**, 485–495.

Ortiz-Ramírez, D., Lorenzo, C., Naranjo, E. & León-Paniagua, L. (2006) Selección de refugios por tres especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en la Selva Lacandona, Chiapas, México. *Revista Mexicana de Biodiversidad*, **77**, 261–270.

Perry, R.W., Carter, S.A. & Thill, R.E. (2010) Temporal Patterns in Capture Rate and Sex Ratio of Forest Bats in Arkansas. *American Midland Naturalist*, **164**, 270–282.

Perry, R.W., Thill, R.E. & Carter, S.A. (2007) Sex-specific roost selection by adult red bats in a diverse forested landscape. *Forest Ecology and Management*, **253**, 48–55.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Pinto, N. & Keitt, T.H. (2008) Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, **117**, 1725–1731.

Presley, S.J., Willig, M.R., Wunderle, J.M. & Saldanha, L.N. (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology*, **45**, 14–25.

Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates Sunderland, Massachusetts.

Racey, P.A. (1998) The importance of the riparian environment as a habitat for British bats. *Symposia of the Zoological Society of London*, pp. 69–91. London: The Society, 1960-1999.

Racey, P.A. & Speakman, J.R. (1987) The energy costs of pregnancy and lactation in heterothermic bats. *Symposia of the zoological society of London*, pp. 107–125.

Ramos Pereira, M.J., Marques, J.T. & Palmeirim, J.M. (2010) Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in amazonian forests. *Biotropica*, **42**, 680–687.

Ramos Pereira, M.J., Marques, J.T., Santana, J., Santos, C.D., Valsecchi, J., De Queiroz, H.L., Beja, P. & Palmeirim, J.M. (2009) Structuring of Amazonian bat assemblages: The roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, **78**, 1163–1171.

Rocha, R., Ferreira, D.F., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B., Palmeirim, J.M. & Meyer, C.F.J. (2017) Does sex matter ? Gender-specific responses to forest fragmentation in Neotropical bats. *Biotropica*, 1–10.

Russo, D., Cistrone, L., Garonna, A.P. & Jones, G. (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodiversity and Conservation*, **19**, 2501–2515.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Jani, A., Katz, G., Soykan, C., Watts, J., Welter, J., Ecology, S., Jan, N. & Heffernan, J.I.M. (2005) Riparian Zones Increase Regional Species Richness by Harboring Different , Not More , Species. *Ecology*, **86**, 56–62.

Safi, K., König, B. & Kerth, G. (2007) Sex differences in population genetics, home range size and habitat use of the parti-colored bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biological Conservation*, **137**, 28–36.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321–1333.

Scott, S.J., McLaren, G., Jones, G. & Harris, S. (2010) The impact of riparian habitat quality on the foraging and activity of pipistrelle bats (Pipistrellus spp.). *Journal of Zoology*, **280**, 371–378.

Seaman, B.S. & Schulze, C.H. (2010) The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. *Biological Conservation*, **143**, 391–398.

Senior, P., Butlin, R.K. & Altringham, J.D. (2005) Sex and segregation in temperate bats. *Proceedings. Biological sciences / The Royal Society*, **272**, 2467–73.

Sgroi, M.P. & Wilkins, K.T. (2010) Roosting Behavior of the Mexican Free-Tailed Bat (Tadarida Brasiliensis) in a Highway Overpass. *Western North American NaturaHst63*, **63**, 366–373.

Smith, P.G. & Racey, P.A. (2008) Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *Journal of Zoology*, **275**, 314–322.

Sosa, M., De Ascencao, A. & Soriano, P. (1996) Dieta y patrón reproductivo de Rhogessa minutilla (Chiroptera: Vespertilionidae) en una zona árida de Los Andes de Venezuela. *Revista de Biología Tropical*, **44**, 867–875.

Soule, M.E. & Gilpin, M.E. (1991) The teory of wildlife corridor capability. *Nature Conservation 2: The Role of Corridors* (eds D.A. Saunders & R.J. Hobbs), pp. 3–8. Surrey Beatty and Sons, Chipping Norton, Australia, New South Wales, Australia.

StrauB, A., Reeve, E., Randrianiaina, R.-D., Vences, M. & Glos, J. (2010) The world 's richest tadpole communities show functional redundancy and low functional diversity : ecological data on ecological data on Madagascar 's stream-dwelling amphibian larvae. *BMC Ecology*, **10**, 1–10.

Taylor, P.D., Fahrig, L. & Henein. (1993) Connectivity is a Vital Element of Landscape Structure. *Oikos*, **68**, 571–573.

Tilman, D. (2001) Functional Diversity. *Encyclopedia of Biodiversity*, pp. 587–596.

van Toor, M.L., Jaberg, C. & Safi, K. (2011) Integrating sex-specific habitat use for conservation using habitat suitability models. *Animal Conservation*, **14**, 512–520.

Turner, I.M. (1996) Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Society*, **33**, 200–209.

La Val, R. (2017) Banding Returns and Activity Periods of Some Costa Rican Bats. *The Southwestern Naturalist*, **15**, 1–10.

Vandermeer, J. & Perfecto, I. (2007) The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, **21**, 274–277.

Villéger, Mason & Mouillot. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Ramos Miranda, J., Flores Hernández, D. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological applications*, **20**, 1512–1522.

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

Vleut, I., Levy-Tacher, S.I., Galindo-González, J., de Boer, W.F. & Ramírez-Marcial, N. (2012) Tropical rain-forest matrix quality affects bat assemblage structure in secondary forest patches. *Journal of Mammalogy*, **93**, 1469–1479.

Walsh, A.L. & Harris, S. (1996) Foraging Habitat Preferences of Vespertilionid Bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Warkentin, I.G., Greenberg, R. & Ortiz, J.S. (1995) Songbird use of Gallety Woodlands in Recently Cleared and Older Settled Landscapes of the Selva Lacandona, Chiapas, Mexico. *Conservation Biology*, **9**, 1095–1106.

Wearmouth, V.J. & Sims, D.W. (2008) Sexual Segregation in Marine Fish , Reptiles , Birds and Mammals : Behaviour Patterns , Mechanisms and Conservation Implications., pp. 108–170.

Weller, T.J., Cryan, P.M. & O'Shea, T.J. (2009) Broadening the focus of bat conservation and research in the USA for the 21st century. *Endangered Species Research*, **8**, 129–145.

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245–258.

Williams-Guillén, K. & Perfecto, I. (2010) Effects of agricultural intensification on the bat assemblage in a coffee landscape in Chiapas, Mexico. *Biotropica*, **42**, 605–613.

Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008) Bats limit insects in a neotropical agroforestry system. *Science (New York, N.Y.)*, **320**, 70.

Willig, M., Presley, S.J., Bloch, C.P., Yanoviak, S.P., Díaz, M.M., Arias Chauca, L., Pacheco, V. & Weaver, S.C. (2007) Phyllostomid Bats of Lowland Amazonia: Effects of Habitat Alteration on Abundance. *Biotropica*, **39**, 737–746.

Wordley, C.F.R., Sankaran, M., Mudappa, D. & Altringham, J.D. (2017) Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biological Conservation*, **210**, 48–55.

Zarazúa-Carbajal, M., Avila-Cabadilla, L.D., Alvarez-Añorve, M.Y., Benítez-Malvido, J. & Stoner, K.E. (2017) Importance of riparian habitat for frugivorous bats in a tropical dry forest in western Mexico. *Journal of Tropical Ecology*, **33**, 74–82.

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J. & Martínez-Ramos, M. (2015) Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, **18**, 443–455.