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EFECTOS DEL TAMAÑO DEL FRAGMENTO SOBRE LA INTERACCIÓN PLANTA-HERBÍVORO-ENEMIGOS NATURALES, EN LA SELVA DE “LOS TUXTLAS”, VER.

TESIS

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PRESENTA

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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 29 de junio de 2009, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **RUIZ GUERRA BETSABE** con número de cuenta **91002196** con la tesis titulada: **"Efectos del tamaño del fragmento sobre la interacción planta-herbívoro-enemigos naturales, en la selva de Los Tuxtlas, Ver."**, realizada bajo la dirección del **DR. RODOLFO DIRZO MINJAREZ:**

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CONTENIDO

RESUMEN

Aunque la pérdida de interacciones ecológicas debido a la fragmentación del hábitat es una de las principales amenazas para la biodiversidad, la información sobre sus consecuencias es escasa, sobre todo si consideramos las consecuencias sobre procesos ecológicos como las interacciones interespecíficas. Para el caso de la herbivoría en sistemas tropicales, la evidencia se restringe a siete estudios con resultados contrastantes. Estos trabajos, excepto uno, se enfocan en dos niveles tróficos (planta-herbívoro o herbívoro-enemigo natural). Sin embargo, la variación en los patrones de herbivoría está determinada tanto por los controles ascendentes (características defensivas-nutricionales de las plantas), como descendentes (depredadores y/o parasitoides). En este estudio se evaluaron las consecuencias del tamaño del fragmento sobre la interacción planta-herbívoro-enemigos naturales en tres fragmentos de selva y tres sitios de selva conservada en Los Tuxtlas, Veracruz. La predicción fue encontrar mayores niveles de herbivoría fragmentos que en la selva conservada debido a: 1) una mayor disponibilidad y calidad del follaje, y 2) una disminución en la abundancia y diversidad de enemigos naturales en fragmentos. Para poner a prueba estas expectativas se evaluaron : a) los niveles de herbivoría en brinzales (altura > 50 cm < 1.30 m y un DAP < 1cm) en la comunidad de plantas leñosas (97 especies) y en un conjunto de especies compartidas entre fragmentos y selva continua, b) la calidad nutritiva (concentración de nitrógeno, carbono y contenido de agua) y características defensivas del follaje (fenoles totales, taninos condensados y dureza de las hojas) de las especies compartidas, c) la abundancia de insectos fitófagos, d) la diversidad y abundancia de aves insectívoras y tasas de depredación de orugas artificiales, y e) la diversidad y abundancia de parasitoides (Ichneumonidae). Se encontró que los niveles de herbivoría, tanto a nivel de comunidad como de especies compartidas, fueron mayores en la selva continua que en los fragmentos. Esta respuesta fue consistente entre las especies tolerantes a la sombra. Sin embargo, las especies pioneras mostraron tanto un efecto positivo (incremento en los fragmentos) como negativo (disminución en los fragmentos). No se encontraron diferencias significativas en la concentración de metabolitos secundarios ni en la calidad nutritiva entre fragmentos y selva continua. El número de insectos fitófagos particularmente lepidópteros, así como la abundancia y diversidad de parasitoides fueron mayores en la selva continua. La abundancia y riqueza de aves insectívoras no cambio entre fragmentos y selva continua. No obstante, la diversidad fue mayor en la selva continua y las tasas de depredación de orugas artificiales fueron mayores en los fragmentos que en la selva continua. Se concluye que la fragmentación del hábitat trae consigo una reducción en la herbivoría ya que afecta los controles descendentes: las poblaciones de herbívoros, parasitoides y aves. Este estudio aporta evidencia de que los regímenes de herbivoría se ven afectados por la fragmentación a través de un efecto indirecto, poco reconocido hasta ahora: el impacto sobre los enemigos naturales de los herbívoros.

SUMMARY

Even though the loss of ecological interactions due to habitat fragmentation remains as one of the major threats to biodiversity, the information about its consequences on interespecific interactions is still scarce. For the case of herbivory in tropical systems, the evidence is restricted to seven studies with opposite results. These works, except one, focuses on two trophic levels (plant-herbivore or herbivores-natural enemies). However, the variation in herbivory levels may be influenced by bottom-up (plant nutritive and defensive quality) and top-down forces (predators and/or herbivore parasitoids) as well. In this study the consequences of habitat loss on plant-herbivore-natural enemies interaction was evaluated. Higher levels of herbivory are predicted in forest fragments than in continuous forest because of: 1) an increase in food quantity/ quality, and 2) a disrupted top-down regulation of herbivores (diversity and abundance of herbivore's natural enemies). These expectations were evaluated in three forest fragments and three sites in continuous forest at Los Tuxtlas, Veracruz: a) herbivory levels in saplings (height > 50 cm < 1.30m and diameter at breast height < 1cm) in a large sample (97 species) and a subset of shared species between fragments and continuous forest, b) leaf quality (nitrogen, carbon and water content) and leaf defensive compounds content (total phenols, condensed tannins and leaves toughness) from shared species, c) phytophaguos insect abundance, d) insectivorous birds diversity, abundance, and depredation rates of artificial caterpillars) and e) parasitoids diversity and abundance (Ichneumonidae). Herbivory levels at both community and shared species were higher in continuous forest compared to forest fragments were found. This results were consistent in shade-tolerant species, whereas light-demanding species demonstrated positive (increase in herbivory in fragments) and negative (decrease in herbivory in fragments) effects. Neither secondary metabolites concentration nor nutritive quality differs between forest fragments and continuous forest. Lepidoptera and parasitoids abundance as well as diversity were higher in continuous forest compared to forest fragments. Insectivorous birds diversity was higher within continuous forest when compared to forest fragments however the abundance and richness did not differ between treatments. Furthermore, predation rates on artificial caterpillars were significantly higher in forest fragments compared with continuous forest. Overall, these results suggest that habitat fragmentation decrease herbivory levels through the negative effects on top-down forces: herbivores, parasitoids and birds populations. This study supports the negative effects of habitat fragmentation on herbivory levels through an indirect effect of natural enemies on herbivore’s abundance and diversity which have been poorly explored.

INTRODUCCION GENERAL

Deforestación y fragmentación

Aunque el impacto humano sobre los ecosistemas es milenario, y probablemente durante mucho tiempo de relativamente bajo impacto, a partir de la última mitad del siglo XX los patrones del uso de la tierra han ocasionado la rápida deforestación de grandes extensiones de diversos ecosistemas en todo el mundo (Dirzo y Raven, 2003; Henle *et al*., 2004; Orians *et al*., 1996; Achard *et al*., 2002). De acuerdo con la Organización de Naciones Unidas para la Agricultura y la Alimentación (FAO) cada año se pierden 13 millones de hectáreas a causa de la deforestación, lo que ha producido la pérdida de la mitad del total de la masa forestal mundial (http://www.fao.org/forestry/fra2005/en/). Los datos más recientes señalan que las selvas tropicales húmedas del mundo han perdido más de la mitad de su superficie original (Achard *et al*., 2002).

A la par de la deforestación se produce la fragmentación del hábitat, la cual se caracteriza por la pérdida de cobertura vegetal y su reconfiguración espacial en fragmentos de diversos tamaños y formas rodeados por una matriz transformada más simple (Farigh, 2003), aunque generando a veces mayor heterogeniedad a nivel del paisaje por la presencia de de diversos tipos de uso de la tierra. En conjunto, los procesos de cambio de uso y cobertura de la tierra son considerados como la principal amenaza a la biodiversidad en el mundo (Sala *et al*., 2000; Dirzo y Raven, 2003), de hecho el Programa Internacional de la Geosfera y Biosfera (IGBP por sus siglas en Inglés, http://www.igbp.kva.se/), tiene entre sus subprogramas específicos uno sobre uso de la tierra ("Land-Use and Land-Cover Change" o LUCC por sus siglas en Inglés, http://www.igbp.net/page.php?pid=250). Estas modificaciones en el uso del suelo, han marcado profundos cambios sociales, económicos y ambientales a nivel mundial, siendo más agudos en los trópicos (Butler y Laurance, 2008; Souza, 2006).

En México, como en otros países en desarrollo, la presión sobre los recursos naturales es extremadamente fuerte debido a varios factores, entre los cuales podemos mencionar el incremento en la población humana, que tiene como consecuencia un aumento en la demanda de productos básicos, y por el otro, la adopción de un modelo económico de desarrollo que ha promovido la explotación no regulada de los recursos naturales (Challenger y Dirzo, 2009). Esto ha propiciado que el total de la vegetación primaria (*i.e.*, la más conservada y madura) del país disminuyera en un 38% para 1976, y hacia 1993 sólo quedaba un 54% de la cobertura original (Challenger y Dirzo, 2009). La tasa de cambio en la cobertura de vegetación en esos periodos fue de 946,000 hectáreas al año, lo que corresponde a una tasa del 0.8% anual. Para el caso de las selvas tropicales húmedas mexicanas — el ecosistema con mayor riqueza tanto biológica como cultural (Toledo, 1996; Dirzo y Raven, 2003) — se ha estimado que en las ultimas 4 décadas se han reducido en un 83% de su extensión original debido principalmente a actividades agropecuarias (CONABIO, 2006, Challenger y Dirzo, 2009). Este ecosistema originalmente ocupaba un área de aproximadamente 24 millones de hectáreas y para el 2002 se estimó un área de tan sólo 4 millones de hectáreas (CONABIO, 2006).

En el caso particular de las selvas tropicales húmedas de México la expansión ganadera ha sido el principal factor de deforestación (Guevara *et al*., 1997). En la selva de Los Tuxtlas, la cual destaca por encontrarse en el límite boreal de la distribución de la selva tropical en el continente (Dirzo y Miranda, 1991) y por su gran diversidad de flora (3, 356 especies de plantas vasculares) y fauna (32% de los vertebrados conocidos en México) (González-Soriano *et al*., 1997; Guevara *et al*., 2006) se registró una pérdida de casi el 90% de la superficie original entre 1960 y 2002 (Dirzo y García, 1992; Mendoza *et al*., 2005). De este modo, el paisaje que hasta hace pocas décadas estaba dominado por una exuberante selva, hoy en día está caracterizado por un mosaico conformado de potreros**,** campos de cultivo (*e.g.*, cítricos, tabaco, y cacao, entre otros) así como de remanentes de selva y zonas de vegetación secundaria (Guevara *et al*., 2006). La vegetación conservada de selva alta perennifolia de la zona ha sido restringida principalmente a los terrenos de la estación de Biología Tropical Los Tuxtlas de la UNAM (700 hectáreas), que se conecta con el Volcán San Martín y en conjunto constituyen un área de aproximadamente 9, 500 ha (Mendoza *et al*. 2005). La mayoría de los fragmentos remanentes d e selva son menores a 10 ha, con un gran déficit de fragmentos grandes (>10 ha) (Mendoza *et al*., 2005).

En la zona de los Tuxtlas la deforestación y fragmentación del hábitat han provocado la extinción local de flora y fauna. Se ha documentado que al menos tres especies de aves han sido extirpadas de manera local: el zopilote rey (*Sarcoramphus papa*), el águila arpía (*Harpia harpyja*), la guacamaya roja (*Ara macao*), y otras 85 más se encuentran en las categorías de peligro de extinción o amenazadas (Winker, 1997). Diez especies de mamíferos han sido catalogadas en peligro de extinción: mono araña (*Ateles geoffroyi*), jaguar (*Panthera onca*), puma (*Panthera concolor*), tapir (*Tapirus bairdii*), venado de cola blanca (*Odocoileus virginianus*), oso hormiguero (Tamandua mexicana) y el brazo fuerte (*Cyclopes didactylus*), ocelote (*Leopardus pardalis*), pecarí de labios blancos (*Tayassu pecari*) y el temazate (*Mazama americana*) (R. Coates com. pers.)

Dado que los ecosistemas involucran la existencia de redes de interacciones bióticas y abióticas, la pérdida o disminución de las poblaciones de alguna especie o grupo funcional puede tener efectos que pueden simultáneamente afectar a otras especies del mismo o de diferente nivel trófico (Turner, 1996), y así modificar la estructura y dinámica de las comunidades (Pace *et al.*, 1999; Komonen *et al*., 2000; Terborgh *et al*., 2001; Koh *et al*., 2004). Por ejemplo, en Los Tuxtlas, la ausencia de mamíferos herbívoros del sotobosque, ha provocado que algunas especies de árboles generen bancos de plántulas densos y extensos, , lo cual provoca la reducción de la diversidad florística del sotobosque (Dirzo y Miranda, 1990; Dirzo *et al*. 2007).

Si bien el énfasis central en los estudios de fragmentación en los trópicos ha sido el análisis de la extinción de especies, actualmente se ha señalado que el riesgo de extinción de procesos ecológicos es una consecuencia muy importante del impacto antropogénico (Dirzo 2001, Laurance, 2008). A pesar de la gran importancia de las interacciones entre plantas y animales, éstas han sido muy poco estudiadas desde la perspectiva de la fragmentación del hábitat (Farhig, 2003). En Los Tuxtlas, de un total de 46 estudios referentes a las consecuencias de la fragmentación del hábitat, sólo 8 han abordado el tema de las interacciones bióticas desde esta perspectiva: i) polinización (Cuartas, 2006; Meneses, 2002; Aguirre y Dirzo, 2008), ii) herbivoría (Zenteno, 2001; Ruiz 2003), iii) dispersión de semillas (Ortiz-Pulido *et al*., 2000; Zenteno, 2006) y iv) depredación de nidos de aves (Estrada *et al.*, 2002).

Herbivoría y fragmentación

Entre las interacciones planta-animal en las selvas tropicales húmedas destaca la herbivoría, debido a su papel en procesos ecosistémicos tales como la sucesión vegetal, el reciclaje de nutrientes (Showalter, 2000; Edwards y Guillman, 1987) y en el mantenimiento de la diversidad florística tropical (Janzen, 1970; Conell, 1971). Aunado a esto, más de la mitad de la especies descritas hasta ahora (plantas, insectos herbívoros, y enemigos naturales de los herbívoros) están involucradas en esta interacción (Price 1997, Novotny y Basset, 2005), por lo que el estudio de la herbivoría en un sistema fragmentado es un tema que demanda atención en el campo de la ecología y el de la conservación biológica.

En el caso de la herbivoría, los estudios realizados se enfocan típicamente a los niveles tróficos planta-herbívoro. Sin embargo, existe suficiente evidencia en la literatura que muestra que además del control ascendente o “bottom-up” (cantidad y calidad del recurso) la variación en los patrones de herbivoría están determinados por el efecto de los depredadores y parasitoides (control descendente o “top-down”), ya que en muchos casos regulan la dinámica poblacional de los insectos herbívoros y por tanto de los niveles de herbivoría (Hairston *et al*., 1960; Pace *et al*., 1999; Price *et al*., 1980). No obstante, solo un estudio ha explorado el papel del control ascendente y descendente en los niveles de herbivoría sufridos por las plantas en un sistema fragmentado (Fáveri *et al*., 2008).

La falta de información sobre el tema de las interacciones bióticas como la herbivoría en el contexto de la fragmentación, y considerando que Los Tuxtlas actualmente representa uno de los últimos reductos de selva tropical alta en la costa del Golfo de México motivan el presente estudio. Específicamente, el presente trabajo tiene por objetivo entender las consecuencias de la fragmentación del hábitat en la relación planta-herbívoro-enemigos naturales, considerando las consecuencias de la fragmentación sobre los controles ascendentes (la calidad del follaje) y sobre los controles descendentes (los enemigos naturales de los herbívoros, aves y parasitoides). En este estudio, el enfoque utilizado para evaluar el impacto de la fragmentación del hábitat sobre la interacción de herbivoría se basó en comparar tres sitios distribuidos dentro de un área de selva conservada (Reserva de la UNAM) con tres fragmentos de selva de tamaño contrastante pero con características similares (*e.g.*, antigüedad, altitud, composición florística). Bajo este enfoque, asumo que la porción de selva húmeda comprendida dentro de la reserva de la UNAM, con un área aproximada de 700 ha y que forma parte de un corredor de vegetación que desciende del volcán San Martín cubriendo aproximadamente 9 500 ha (Mendoza et al 2005), representa de manera más cercana las características que la interacción en la que me enfoco presentaría en un continuo de selva, sirviendo entonces como punto de comparación para los fragmentos.

Se predice un incremento en los niveles de herbivoría en los fragmentos que en la selva continua. Este escenario se basa en evidencia de las consecuencias de la fragmentación del hábitat sobre las plantas (control ascendente) y de los enemigos naturales de los herbívoros (control descendente) que a continuación se describen. Los cambios en el microclima que ocurren en los bordes de los fragmentos pueden modificar tanto la calidad como la cantidad de follaje disponible para los herbívoros, así como la abundancia y diversidad de sus depredadores y parasitoides. En primer lugar, el incremento en la incidencia lumínica producto del efecto de borde pueden provocar un incremento en la tasas de producción del follaje y una mayor disponibilidad de hojas jóvenes, las cuales son más palatables para los herbívoros debido a su alta calidad nutricional y bajos niveles de defensa (Coley, 1998; Wirth *et al*., 2008). También existe evidencia de que los cambios en el microclima pueden provocar modificaciones en las características químicas y físicas de las plantas, las cuales pueden alterar la calidad del alimento para los herbívoros. Por ejemplo, en Canadá se ha encontrado que las hojas del maple (*Acer saccharum*) son más aceptables en los bordes de los fragmentos que en el interior debido a un incremento en la concentración de nitrógeno y azúcares solubles de las plantas, características relacionadas positivamente con el desempeño de los insectos herbívoros (Fortín y Mauffete, 2001). Por otra parte, en general se ha demostrado que las poblaciones de enemigos naturales de los herbívoros (*i.e*., aves y parasitoides) disminuyen en sitios perturbados, lo cual puede ocasionar un aumento de las poblaciones de insectos fitófagos y por tanto de la herbivoría (Kruess y Tscharntke, 1994; Roland y Taylor, 1997). Por ejemplo, Kruess y Tscharntke (2000) reportaron que las tasas de parasitismo del escarabajo *Oxystoma ochropus* disminuyeron con el área del fragmento y el aislamiento, y Koh y Menge (2006) reportan que las tasas de depredación de orugas artificiales fue mayor en la isla de Barro colorado (1 500 ha) que en Península Gigante (2 600 ha).

El contenido de este trabajo ha sido organizado en seis capítulos. En el primer capitulo se presenta una reseña histórica de los estudios de la fragmentación del hábitat sobre la interacción planta-herbívoro con el fin de construir el marco teórico a partir del cual se desarrollaría esta tesis. Recientemente se publicó una revisión sobre las consecuencias del efecto de borde en la interacción planta herbívoro (Wirth *et al.*, 2008). Sin embargo, esta revisión no incluye los efectos de la disminución del área y del aislamiento, a pesar que se ha demostrado que estos dos últimos factores tienen consecuencias tanto positivas como negativas en las poblaciones de plantas y de insectos herbívoros, por lo que resulta importante considerarlos para poder entender las modificaciones en los niveles de herbivoría sufridos por las plantas en sitios fragmentados. La principal contribución de este capitulo es la recopilación y el análisis de la literatura referente al tema. En el segundo capítulo (Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: Evidence from a Mexican Tropical Rain Forest; Ruiz-Guerra *et al.*, en prensa) se analiza el efecto de la fragmentación del hábitat sobre los niveles de herbivoría en: a) la comunidad de brinzales (50 cm> 130 cm de altura y 1 cm de DAP) y b) en un conjunto de siete especies representativas de la selva de los Tuxtlas, considerando la estrategia de regeneración de las plantas (demandantes de luz y tolerantes a la sombra), e identificando los principales agentes de daño (insectos, mamíferos, y patógenos). Este capitulo aporta resultados novedosos, que reportan que los efectos de la fragmentación sobre los niveles de herbivoría covarían con el tipo de estrategia de regeneración. Ningún estudio previo había considerado que las diferencias en los niveles de herbivoría en sistemas fragmentados dependen, de manera compleja, con la estrategia de regeneración de las plantas, la cual es reconocida como un factor que explica la variación interespecífica en la herbivoría (ver Coley *et al*., 1995). En el tercer capítulo (Are plant defensive and nutricional traits affected by forest fragmentation?) se analizan las consecuencias de la pérdida del hábitat sobre la calidad del recurso vegetal para los herbívoros, específicamente las características nutricionales (carbono/nitrógeno, y contenido de agua) y defensivas de las plantas (fenoles totales, taninos condensados y dureza de las hojas) y se presentan los resultados de un experimento de palatabilidad utilizando un herbívoro generalista (*Spodoptera fugiperda*). Estos resultados representan la primera aproximación de las consecuencias de la pérdida del hábitat sobre las características defensivas y nutricionales de brinzales en la selva de Los Tuxtlas. El cuarto capítulo (Consequences of fragmentation of tropical moist forest for avian communities and insect predation) evalúa cómo la fragmentación afecta la riqueza, abundancia, diversidad y similitud de aves insectívoras y se determina el papel de las aves insectívoras como reguladoras de las poblaciones de insectos, mediante un experimento diseñado con orugas artificiales y el conteo de insectos herbívoros (coleópteros, ortópteros y lepidópteros). En el quinto capítulo (Forest fragmentation affects abundance and richness of ichneumonid parasitoids in a Mexican tropical site) se exploran las consecuencias de la fragmentación en las poblaciones de avispas parasitoides (Ichneumonidae) con el fin de determinar la diversidad, abundancia y similitud de ese grupo de especies controladoras de herbívoros, comparando la selva continua y un fragmento en Los Tuxtlas. Se describe la composición de icneumónidos a nivel de subfamilia y en algunos a casos a nivel de especie. Este estudio representa el primer registro de las consecuencias de la fragmentación sobre la fauna de Icneumónidos en Los Tuxtlas. Por último, se presenta una discusión y las conclusiones generales de esta tesis, así como las perspectivas de estudio en este campo de investigación. En conjunto este trabajo hace un aporte a la historia natural y a la ecología de los sistemas fragmentados tomando como base la interacción de plantas, insectos y sus depredadores y parasitoides. La intención era pintar una imagen lo más incluyente posible de las consecuencias de la fragmentación de la selva tropical sobre una interacción predominante en la ecología, y con perspectivas complementarias a lo hasta ahora conocido en la biología de la conservación, a través del lente de la selva de Los Tuxtlas.

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Capítulo 1

Estudios sobre la interacción planta-herbívoro en sistemas fragmentados.

1 Estudios sobre la interacción planta-herbívoro en sistemas fragmentados

RESUMEN

El conocimiento de las consecuencias de la pérdida del hábitat sobre las interacciones ecológicas, es un tema de gran interés en nuestros días debido al papel que estas desempeñan en el mantenimiento y diversidad de los ecosistemas del mundo. Sin embargo, pocos estudios han evaluado el impacto de la fragmentación sobre procesos ecológicos, tales como la herbivoría. En este capitulo reviso y analizo los estudios publicados de las consecuencias de la fragmentación (*i.e* tamaño del fragmento, aislamiento, efecto de borde) sobre la interacción planta-herbívoro. Reviso los trabajos referentes al tema en el periodo comprendido entre los años 1999 - 2008. El tópico más estudiado hasta ahora ha sido el tamaño del fragmento. El primer dato importante que arroja esta revisión es que el estudio de la herbivoría (en su mayoría por insectos) en el contexto de la fragmentación del hábitat es un área poco explorada, que en general, no muestran una respuesta consistente, dado que se reportan efectos positivos, negativos e incluso neutros. La inconsistencia de resultados se puede deber a que los estudios se han realizado en diferentes escalas espaciales y temporales, se han utilizado diferentes metodologías de medición del daño, y se han comparado niveles de herbivoría en especies de plantas con diferentes historias de vida y estadios de desarrollo. Lo que ultima instancia hace poco comparables los resultados obtenidos. Destaca la carencia de estudios que evalúen los mecanismos subyacentes a los niveles de herbivoría encontrados y respuestas a largo plazo. Discuto las tendencias generales y las líneas futuras de investigación.

INTRODUCCION

Deforestación y fragmentación del hábitat

A nivel mundial, la deforestación de los ecosistemas tropicales ha causado la pérdida y fragmentación del hábitat. Dichos hábitats originalmente cubrían una extensión de aproximadamente 14.5 millones de km^2 de los cuales en nuestros días solo se conservan 7.5 millones de km^2 , lo que significa una reducción a la mitad de su extensión original (Achard *et al*., 2002). Para el caso particular de las selvas húmedas mexicanas se ha estimado que en las últimas cuatro décadas se han reducido en un 83% de su extensión original (Challenger y Dirzo 2009). Los patrones de uso de la tierra que impulsan la destrucción de las selvas tropicales se deben básicamente a la conversión a potreros dedicados a la ganadería, la apertura de terrenos agrícolas y en menor escala, la explotación forestal y el desarrollo de infraestructura urbana y de comunicaciones (Guevara et al., 2006).

Una de las principales consecuencias de la deforestación es la creación de paisajes fragmentados caracterizados por remanentes de bosque original, de tamaños y formas variables, que quedan inmersos en una matriz de hábitats modificados (*i.e.* campos de cultivo, pastizales, etc.) dando lugar al fenómeno conocido como fragmentación del hábitat. Las consecuencias directas de la deforestación y de la subsecuente fragmentación del hábitat son: i) disminución del área remanente, ii) incremento en el aislamiento entre los fragmentos y iii) efecto de borde, el cual se ha demostrado que genera cambios en los factores abióticos en las orillas de los fragmentos, así como en fragmentos de tamaño pequeño (Murcia 1995). Por ejemplo, en Los Tuxtlas, tenemos evidencia que la temperatura y la incidencia lumínica aumentan en el borde de los fragmentos, mientras la humedad relativa del aire y del suelo disminuye. Estos cambios en las condiciones abióticas pueden penetrar una distancia de hasta 70 m al interior de los fragmentos (Ruiz-Guerra 2003).

Efectos ecológicos de la fragmentación

La pérdida y fragmentación del hábitat son consideradas como las principales causas por las que se está perdiendo la diversidad biológica, en términos de variabilidad genética, especies, poblaciones, interacciones bióticas e incluso a nivel de ecosistemas (Dirzo y Raven, 2003; Hoekstra *et al.*, 2005).

La fragmentación del hábitat puede provocar a extinción de muchas especies tanto a nivel local como regional. En la mayoría de los casos, al reducirse la cobertura vegetal, se reduce no solo la diversidad de hábitats a nivel regional, sino el área total disponible. Por otro lado, el aislamiento de los fragmentos de selva produce una subdivisión de las poblaciones originales, con lo cual se generan reducciones en los tamaños poblacionales, lo cual incrementa el riesgo de extinción ya sea por factores demográficos o por factores estocásticos (Kattan 2002).

Los efectos de la fragmentación conducentes a la extinción serán mayores para aquellas especies de distribución restringida como es el caso de las especies endémicas y/o raras, así como para las especies con bajas capacidades reproductivas, con requerimientos muy especializados o particulares, con bajas capacidades de movimiento, y aquellas que requieren grandes territorios o que existen en bajas densidades (Didham *et al*., 1996).

La desaparición de una determinada especie puede provocar un aumento en la probabilidad de extinción de las especies con las que interactúa. Por ejemplo, Koh y colaboradores (2004), mostraron que el número promedio de especies de mariposas extintas aumenta exponencialmente con el número total de plantas hospederas extintas, lo que indica que la extinción de plantas ha contribuido significativamente a la extinción de mariposas. Esta evidencia sugiere que la pérdida de especies no solo implica la desaparición de las mismas sino que puede provocar efectos en cascada a través de las redes de interacciones bióticas (Turner, 1996), lo que en última instancia puede ocasionar alteraciones de procesos fundamentales para el funcionamiento, mantenimiento y diversidad de los ecosistemas (Gilbert, 1980; Asquit *et al.*, 1997; Pace *et al.*, 1999; Komonen *et al.*, 2000; Terborgh *et al.*, 2001; Dyer y Letourneau, 2003; Feeley y Terborgh, 2006). Desafortunadamente, la evidencia sobre la ocurrencia de estos procesos en sistemas fragmentados aún es muy limitada debido a que la mayoría de los estudios se han centrado en la pérdida de especies. En contraste, los estudios referentes a procesos ecológicos son muy escasos. No obstante, en los últimos años el estudio de esta línea de investigación ha crecido, a través de investigaciones relacionadas con interacciones planta-animal tales como: polinización (Aizen y Feinsinger, 1994), depredación (Fonseca y Robinson, 1990), parasitismo (Roland y Taylor, 1997), herbivoría (Benitez Malvido *et al.*, 1999; Meiners *et al.*, 2000; Benitez-Malvido, 2001; Rao *et al.*, 2001; Terborgh *et al.*, 2001; Arnold y Asquit, 2002; Tscharntke y Brandl, 2004), e incluso interacciones de tres niveles tróficos entre plantas, herbívoros y sus enemigos naturales (Thies y Tscharntke, 1999; Tscharntke y Hawkins, 2002; Thies *et al.*, 2003; Valladares *et al.*, 2006; Fáveri *et al.*, 2008).

Entre las interacciones planta-animal destaca la herbivoría en la cual más del 50 % de la biota conocida del planeta esta involucrada, ya que del total aproximado de 1.8 millones de especies descritas, el 26% corresponde a los insectos herbívoros, el 22% a las plantas (el recurso central de esos insectos) y el 31% a los enemigos naturales de los herbívoros tales como depredadores y parasitoides (May, 2000). Por tanto, no resulta sorprendente que la herbivoría contribuya en diversos procesos ecosistémicos, entre los que destacan, el reciclaje y conservación de nutrientes (Price, 1987; Singer y Shoenecker, 2003; Feeley y Terborgh, 2005), la sucesión, la regeneración, el reclutamiento de especies (Janzen, 1970), el desempeño de las mismas (Crawley, 1983; Dirzo, 1984) y por tanto en la organización de comunidades (Janzen, 1970; Connell y Slater, 1977; Crawley, 1983; Dirzo y Miranda, 1990).

A pesar de la gran importancia de la interacción planta-herbívoro en las comunidades naturales, ésta ha sido poco estudiada desde la perspectiva de la fragmentación del hábitat. No obstante, es previsible que esta interacción sea afectada, a través de efectos de la fragmentación del hábitat sobre las plantas, los herbívoros o ambos. En principio, la herbivoría puede verse afectada tanto por las características del fragmento (tamaño, forma, aislamiento, edad), como por el efecto de borde y en particular por los cambios en los factores abióticos. Estos afectan el número y abundancia de las especies de las comunidades de plantas (Williams-Linera, 1990), insectos (Didham *et al.*, 1996; Ozzane *et al.*, 1997; Jokimäri *et al.*, 1998), así como de sus depredadores y parasitoides (Kareiva, 1987; Roland, 1993; Kruess y Tscharntke, 1994; Didham *et al.*, 1996). Por otra parte también es posible que las tasas de crecimiento, asignación de recursos (Benedict y Halfield, 1988; Speight *et al.*, 1999; Schowalter, 2000), y la concentración de metabolitos secundarios de las plantas sean alterados debido a cambios microclimáticos asociados a la fragmentación (Benedict y Hatfield, 1988; Landsberg, 1990; Anaya, 2003; Yamasaki y Kikuzawa 2003).

En este capitulo presento una revisión de la evidencia con que se cuenta hasta ahora sobre el efecto de la fragmentación del hábitat en la interacción planta-herbívoro a partir de la búsqueda electrónica en la literatura en los buscadores ISI Web y CSA, de los últimos 10 años. La búsqueda se basó en el uso de las siguientes palabras clave: Fragmentación del hábitat, deforestación, interacciones bióticas, herbivoría, insectos herbívoros, daño por herbívoros, interacciones tróficas e interacciones planta-insecto. Con base en esta búsqueda realicé una base de datos que se presenta en el apéndice 1, a partir de la que analicé los siguientes aspectos: a) curso temporal de los estudios realizados, b) la distribución de estudios por tipo de hábitat, c) la distribución de estudios de acuerdo al tema abordado, d) el enfoque de los estudios, e) nivel de organización, y f) organismos estudiados. Por último, presento una discusión sobre las tendencias generales y algunas perspectivas para el estudio de la interacción planta herbívoro en el marco de la fragmentación del hábitat.

ESTUDIOS REVISADOS

El total acumulado fue de 21 publicaciones de estudios de efectos de la fragmentación sobre la interacción planta-herbívoro, incluyendo dos modelos teóricos y dos revisiones sobre fragmentación del hábitat e insectos. Es importante puntualizar que el efecto de borde no fue considerado en este trabajo debido a que este tema ha sido ampliamente revisado por Wirth y colaboradores (2008). En dicha revisión los autores reportan 32 estudios que han evaluado las consecuencias del efecto de borde sobre la herbivoría. Los estudios abarcan un amplio rango de niveles de organización, que van desde de interacciones de dos especies hasta nivel comunidad en un gradiente de tipos de vegetación, con una predominancia de investigaciones realizadas en bosques templados. La mayoría de los trabajos revisados señalan efectos positivos del borde sobre la herbivoría (*i.e.* un incremento de la herbivoría en los bordes), aunque también reportan respuestas negativas (disminución de la herbivoría en los bordes) y neutras (no se detectó ningún efecto) (Wirth *et al.*, 2008).

a) Curso temporal de los estudios

Los estudios publicados referentes al efecto de la fragmentación sobre la interacción planta-herbívoro comienzan en 1999 y muestran un máximo de cuatro publicaciones en 2001, después del cual el número de publicaciones disminuye y tiene otro pico en el año 2006, con tres publicaciones (Fig. 1). Estos resultados reflejan que: 1.- el estudio de la herbivoría en el contexto de la fragmentación del hábitat es un área de investigación reciente, y 2.- el hecho de que solo se han publicado 21 trabajos en 10 años o 2.1 publicaciones al año indica que este tópico ha sido muy poco estudiado. Cabe señalar, que Roland (1993) reporta que la fragmentación del hábitat y en particular el efecto de borde aumentan la duración de los brotes de la plaga *Malacosoma disstria* en Ontario, Canadá. Sin embargo, en este estudio los autores no midieron los niveles de herbivoría como tal, sino que fue una comparación de a partir de datos históricos de la perdida de cobertura vegetal y la aparición de la plaga, por lo cual no fue considerado en esta revisión.

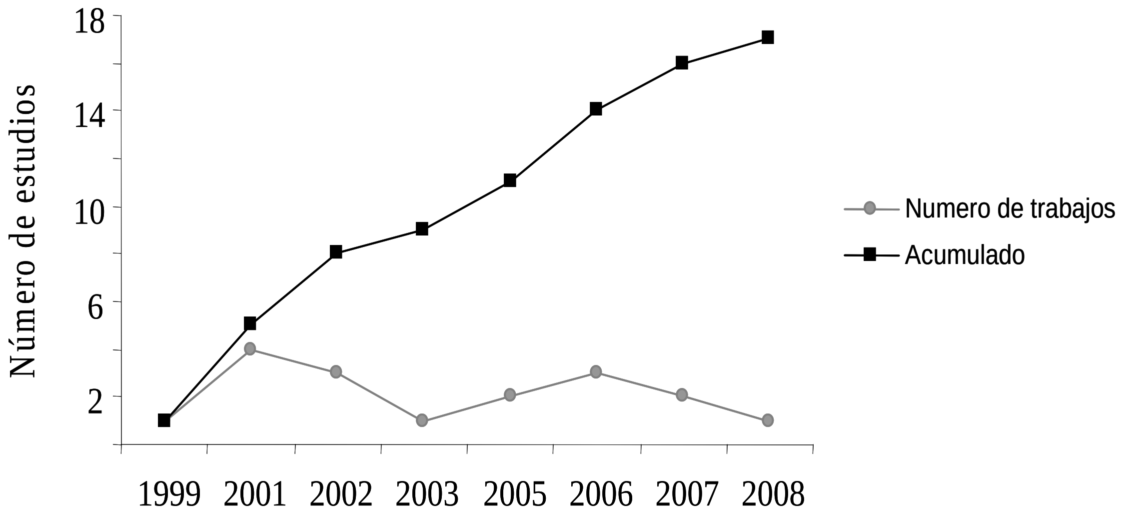

Figura 1. Estudios publicados del efecto de la fragmentación sobre la interacción planta-herbívoro 1999-2009. La línea negra representa el total acumulado. La línea gris representa el número total de estudios por año.

b) Tipos de vegetación

Los tipos de vegetación se clasificaron en cinco categorías generales que incluyen: 1.- Bosque tropical (incluyendo selvas húmedas y secas), 2.- Bosques templados, 3.- Zonas áridas (chaparrales), 4.- Praderas y 5.- humedales (Fig. 2a), distribuidos en 10 países (ver apéndice). Los estudios por tipos de vegetación muestran que los tipos de vegetación predominantes donde se han llevado a cabo estudios son los bosques tropicales y los bosques templados, que contribuyen con el 54.5% y el 36.4% respectivamente. El 23% de los estudios han sido llevados a cabo en Suiza, mientras que países como Estados Unidos, Brasil, Chile y Venezuela han contribuido con un 12% o dos estudios cada uno, y México, Argentina, Australia, Holanda y Panamá con un 6%, o un trabajo publicado en cada país (Fig. 2b).

Al agrupar los trabajos en América del sur, incluyendo Brasil, México, Panamá, Venezuela, Argentina y Chile —aunque geográficamente México pertenece a América del norte y Central fue incluido en este grupo por que los trabajos revisados corresponden a sistemas tropicales— encontramos que la mayor parte de los estudios ha sido realizada en esa región (América del Sur), seguida por Europa (Holanda y Suiza), América del Norte (Estados Unidos), y Oceanía (Australia) (Fig. 2c).

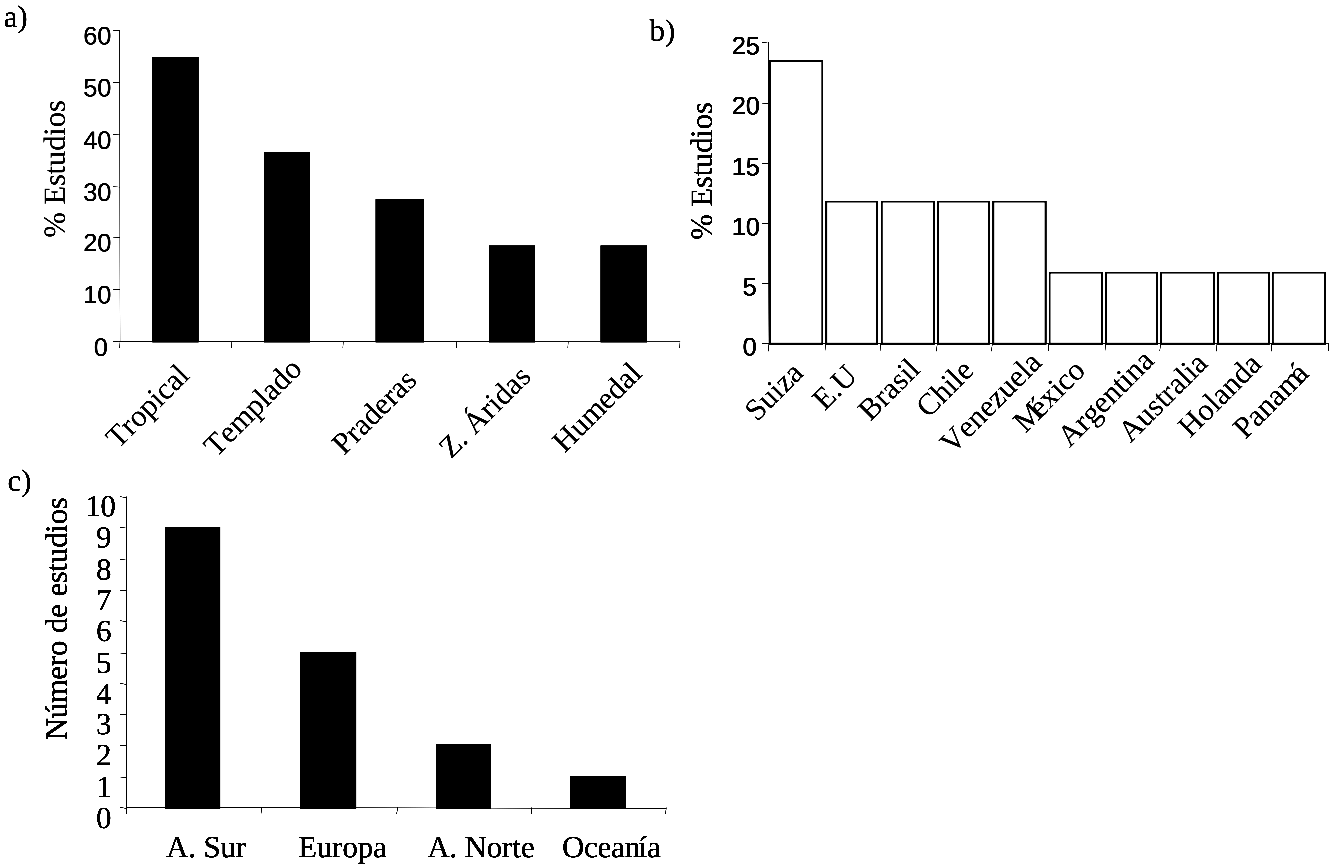

Figura 2.- Estudios del efecto de la fragmentación sobre la interacción planta-herbívoro en: a) diferentes tipos de vegetación, b) países, c) América del Norte, América del Sur, Europa y Oceanía.

c) Variables analizadas

Los estudios revisados analizaron las siguientes variables: a) efecto del tamaño del fragmento, b) el efecto del aislamiento, c) efecto de borde y tamaño del fragmento, y d) tamaño del fragmento y asilamiento (Fig. 3).

El efecto del tamaño del fragmento fue el tópico más estudiado desde la perspectiva de la fragmentación del hábitat y la interacción planta-herbívoro. Los resultados de estos trabajos muestran que no hay un patrón consistente: ocho trabajos mostraron un aumento en los niveles de herbivoría en fragmentos pequeños, siete estudios mostraron el patrón contrario, y uno mostró un efecto nulo (Fig. 4). En general, los primeros sugieren que los resultados obtenidos se pueden explicar debido a una disminución en los depredadores y parasitoides en fragmentos pequeños, lo cual liberaría de la presión de la depredación y parasitismo a las poblaciones de herbívoros (Rao *et al.* 2001; Terborgh *et al.*, 2001; Lienert y Fisher, 2003; Elzinga *et al.*, 2005; Fiona y Hochuli, 2005), un aumento en la calidad nutricional de las plantas (Lienert *et al.*, 2002; Fiona y Hochuli 2005; del-Val *et al.*, 2007) ó un aumento en las tasas de oviposición (Elzinga *et al.*, 2005). En contraste, los segundos (disminución en los niveles de herbivoría en fragmentos), atribuyen los resultados a efectos negativos de la fragmentación sobre la diversidad y abundancia de los herbívoros (Zenteno, 2001; Arnold y Asquit, 2002;Vázquez *et al.*, 2007; Fáveri *et al.*, 2008), a efectos negativos producto del efecto de borde sobre las poblaciones de herbívoros en fragmentos pequeños, tales como un aumento en la desecación (Ledergerber *et al.*, 2001; Zenteno, 2001;Valladares *et al.*, 2006), a una disminución en sus plantas hospederas (Groom, 2001;

Zenteno, 2001; Arnold y Asquit, 2002) o a un aumento de parasitotes debido a una mayor exposición en sitios abiertos como los bordes (Valladares *et al.*, 2006). El caso de carencia de efecto fue atribuido a la variabilidad interanual en la abundancia de insectos herbívoros (Benítez-Malvido *et al.*, 1999).

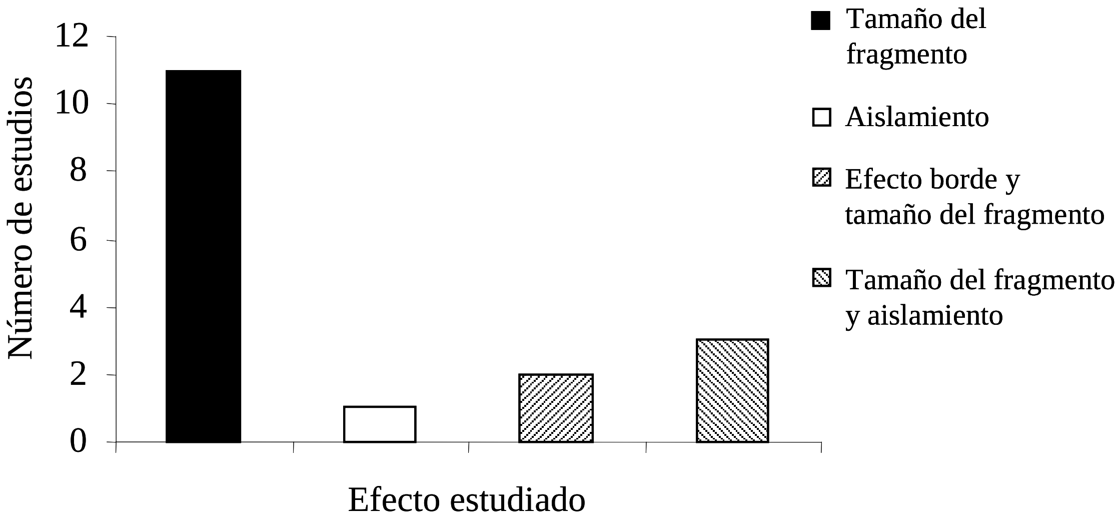

Figura 3. Número de estudios que han evaluado las consecuencias de la fragmentación sobre los niveles de herbivoría, por tipo de variable independiente analizada.

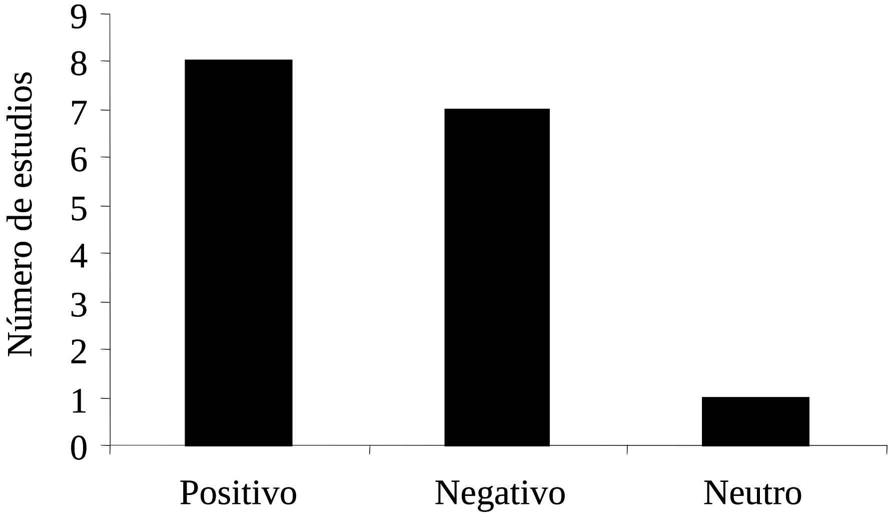

Figura 4. Efecto del tamaño del fragmento en la interacción planta-herbívoro. Positivo: mayor herbivoría en fragmentos pequeños, Negativo: menor herbivoría en fragmentos pequeños, neutro: efecto no detectado.

d) Enfoques de los estudios

Los estudios de la fragmentación del hábitat se han abordado desde diferentes aproximaciones que incluyen observaciones de campo, experimentos y modelos matemáticos. En el caso de los estudios de herbivoría en sistemas fragmentados, el 62% fueron realizados en condiciones naturales, es decir en fragmentos naturales, mientras que el 19% fue realizado en condiciones experimentales, donde los investigadores diseñaron un sistema fragmentado en el que controlaron el tamaño, forma y grado de asilamiento de los fragmentos. El 19% restante corresponde a modelos teóricos y revisión de estudios. Cabe destacar que en los sistemas tropicales, bosques templados, zonas áridas y humedales la mayoría de los estudios fueron realizados en condiciones naturales, mientas que en las praderas la aproximación fue a través de experimentos (Fig. 5). La razón de pocos estudios experimentales es fácil de ver, pues la manipulación de grandes áreas implica un gran esfuerzo y es muy costoso. Sin embargo, los datos generados en dichos experimentos son muy valiosos dado que pueden controlar diversas variables y pone a prueba teorías y metodologías referentes a la dinámica espaciotemporal (Tilman y Kareiva, 1997). En contraste, los estudios en condiciones naturales si bien no tienen control de muchas variables poseen más realismo respecto a las especies utilizadas así como en escala.

Los modelos teóricos proponen que las poblaciones de depredadores y parasitoides son mas afectadas por la fragmentación que las de sus presas y hospederos. Cuando se considera una comunidad en la que cada uno de los integrantes depende de la presencia del nivel trófico inferior, el modelo predice que a niveles extremadamente altos de fragmentación el sistema se puede colapsar. Este escenario es posible cuando los herbívoros son liberados del control descendente y consumen el recurso hasta llevarlo a la extinción. En contraste, a niveles bajos de fragmentación plantas, herbívoros y enemigos naturales pueden coexistir (Kondoh, 2003).

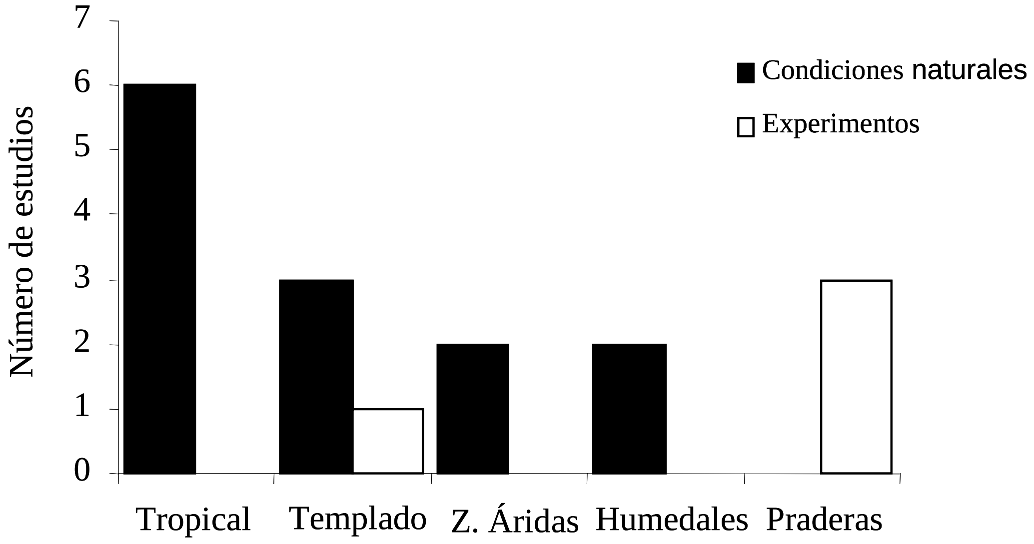

Figura 5. Tipos de vegetación y enfoques utilizados en los estudios planta herbívoro en sistemas fragmentados.

e) Nivel de organización

Los trabajos revisados se realizaron a dos niveles de organización: el 65% a nivel población y el 35% a nivel comunidad. Al analizar cada uno de los casos, encontramos que en los trópicos el 80% de los estudios ha sido realizado a nivel de comunidad, y sólo el 20% a nivel población. En contraste, en sistemas templados, en los humedales y las praderas todos los trabajos fueron realizados a nivel de la población, mientras que de los dos estudios realizados en las zonas áridas uno fue a nivel de comunidad y el otro a nivel de población (Fig. 6).

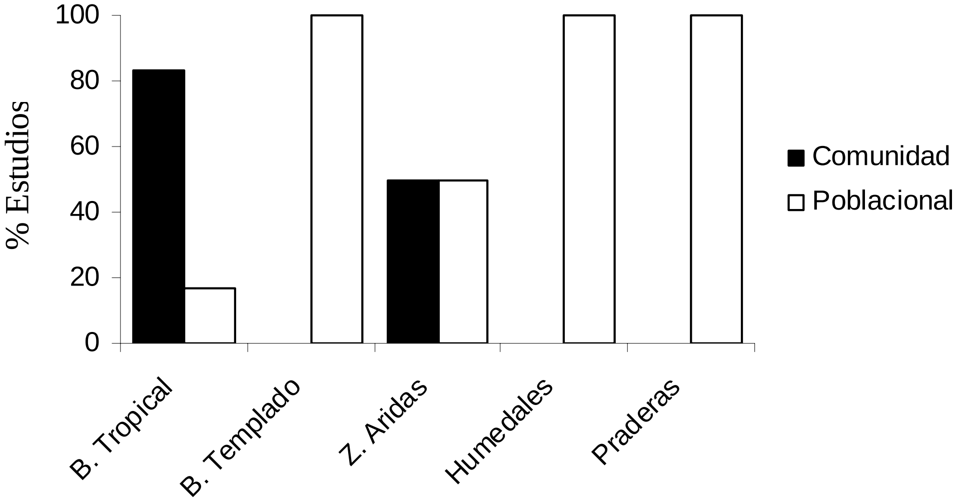

Figura 6. Porcentaje de estudios a nivel comunidad y población en sistemas en diferentes tipos de vegetación.

f) Organismos estudiados

Existe un sesgo de los organismos estudiados, pues del total de estudios revisados el 82% fue con invertebrados, el 5.8% vertebrados y el 12% restante con ambos grupos (Fig. 7). Los primeros incluyen: insectos en general, larvas de lepidópteros, escarabajos, hormigas, ortópteros y caracoles. Y entre los vertebrados, destacan el venado de cola blanca, roedores, liebre americana, monos, iguanas y un marsupial. La predominancia de trabajos con insectos puede estar relacionada con el hecho de que éstos son los principales responsables del daño que experimentan las plantas tanto en el trópico como en la zona templada (Coley y Barone, 1996). Otros argumentos a favor del estudio con insectos son la gran diversidad de especies y el hecho de que son pequeños y presentan tiempos generacionales muy cortos. Por lo tanto, se podría esperar que este grupo de organismos muestre respuestas a la fragmentación en escalas de tiempo relativamente cortas.

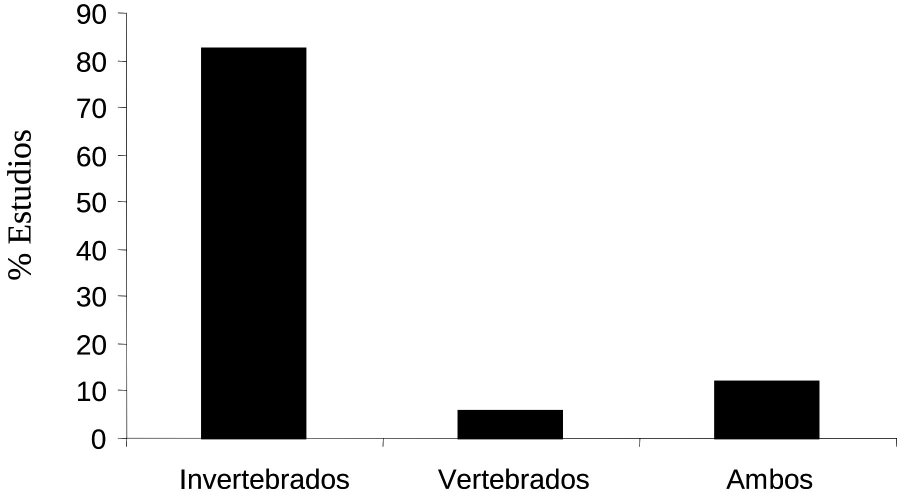

Figura 7. Principales organismos estudiados

DISCUSION

La presente revisión hace evidente que el estudio de la interacción planta-herbívoro desde la perspectiva de la fragmentación es un área relativamente nueva que ha sido poco estudiada, a pesar de su gran importancia en los ecosistemas. La mayor parte de la investigación se ha realizado en sistemas tropicales a nivel de comunidad. En contraste, en los sistemas templados los trabajos han sido realizados a nivel de población. En general, los estudios realizados en los trópicos han trabajado con comunidades de invertebrados, en su mayoría insectos, a excepción de un trabajo, mientras que en los sistemas templados se ha trabajado tanto con poblaciones de vertebrados como de invertebrados. En suma, los trabajos desarrollados en los sistemas templados son especie-específicos y algunos de ellos bajo condiciones muy controladas, mientras que en el trópico el enfoque ha sido más general. El tópico mas estudiado ha sido el efecto de la reducción del área. Al respecto, los trabajos revisados muestran que no existe un patrón de los efectos del tamaño del fragmento sobre la interacción planta-herbívoro. Esta inconsistencia puede deberse a diferentes factores entre los que destacan: a) Diferentes escalas espaciales y temporales, b) Utilización de distintas metodologías en la medición de la herbivoría, y c) Comparación de niveles de herbivoría en especies con diferentes historias de vida y en diferentes estadios de desarrollo.

a) Escalas espaciales y temporales

Los estudios de la herbivoría en sistemas fragmentados se han realizado a diferentes escalas espaciales que varían desde un parche de 100m con 25 plantas (Groom, 2001) hasta un conjunto de fragmentos distribuidos en un área de 15 ha (Valladares *et al.*, 2006) (ver apéndice 2). La comparación de resultados a diferentes escalas espaciales resulta difícil debido a los factores que pueden determinar el resultado de la interacción son diferentes. Por ejemplo, a escala de un parche pequeño los factores determinantes pueden ser el microclima, la diversidad de microhábitats y recursos. En contraste, a grandes escalas espaciales los factores determinantes pueden ser la conectividad entre parches, la calidad del hábitat, o el tipo de matriz circundante que pueden proveer de recursos adicionales y determinar la dinámica de la interacción (Tscharntke y Brandl, 2004). Por ejemplo, Tscharntke y colaboradores (2002) encontraron que 10 ha pueden contener 98% de la diversidad de especies de mariposas cuando el área estaba compuesta de 30 fragmentos, mientras que un área grande solo albergaba entre el 50-60% de todas las especies. Hill *et al.* (1996) mostraron que la distancia de dispersión de la mariposa *Hesperia comma* fue de 1,070 m, pero el 67% del movimiento ocurrió entre parches que se encontraban separados por menos de 50 m.

Por otra parte, uno de los principales problemas con los estudios de fragmentación es la repetición experimental, pues la mayoría de estudios no tienen repeticiones o son “pseudoreplicados” (Hurlbert, 1984). La repetición experimental es muy difícil de conseguir debido a la escala espacial del fenómeno y la limitación de recursos. La falta de control de las variables independientes, además de la dificultad de la repetición experimental puede provocar sesgos en los resultados, lo que hace difícil la comparación de estudios y la identificación de los mecanismos responsables de los resultados obtenidos.

La forma más directa de demostrar que la fragmentación del hábitat provoca la extinción local de especies, es comparando las especies de un área determinada antes y después del proceso de fragmentación. Sin embargo, son pocos los estudios que han abordado este enfoque, debido a la dificultad tanto espacial como temporal que estos trabajos requieren, de manera que una gran proporción de los estudios de fragmentación se han realizado comparando las especies contenidas en parches de diferentes tamaños. De hecho, más del 50% de los trabajos revisados evaluaron las consecuencias del área sobre la interacción planta-herbívoro. Es sobresaliente el hecho de que la mayoría de los estudios en los sistemas tropicales se realizaron en condiciones naturales, a diferencias de los estudios en sistemas templados. Esta aproximación, tiene la ventaja de que ganan en realismo y en escala espacial, a expensas del control de algunas variables (*e.g.* diferencias entre sitios y cambios temporales); en otras palabras ganan generalidad al costo de precisión (Diamond, 1986; Debrinski y Holt, 2000).

Es muy probable que las respuestas a corto plazo no reflejen los impactos a largo plazo. El 41% de los trabajos solo midieron los niveles de herbivoría de manera puntual (ver apéndice 2), es decir, el grado de herbivoría que sufre una planta se cuantifica con base en una única colecta de hojas. Este método subestima la herbivoría en un rango que varia de ente 38 a 60% (Coley, 1982) debido a dos factores: a) aquellas hojas que han sido comidas en su totalidad no pueden ser registradas y b) la edad de la hoja no se toma en cuenta, y esto es importante porque las diferencias en edad de las hojas implican diferentes tiempos de exposición al ataque, lo que puede generar datos que pueden ser poco comparables (hojas más viejas pueden presentar más daño debido a que han estado expuestas por más tiempo que las hojas jóvenes). Así mismo, este método no considera las variaciones estaciónales tales como lluvias y secas o invierno y otoño, durante las cuales puede haber un cambio en la abundancia de ambos interactuantes y por tanto un cambio en los niveles de herbivoría (Arnold y Asquit, 2002; Meiners y Martinkovic, 2002; Bach y Kelly, 2004). Los efectos de la fragmentación también pueden ser diferentes a lo largo del tiempo, debido a cambios en la composición de especies de plantas producto del proceso de sucesión en los fragmentos (Benitez-Malvido y Martinez-Ramos, 2003 ab).

Estos resultados muestran que la dinámica de la interacción planta-herbívoro puede depender de procesos a grandes escalas espaciales y temporales. Por lo tanto, para poder entender los patrones y procesos locales en estudios subsecuentes, se deben considerar el tamaño, el arreglo espacial, la conectividad, la calidad del hábitat y la matriz circundante. También es importante generar estudios que incluyan modelos teóricos apropiados a la dinámica particular de cada sistema (*i.e* que consideren sistemas más complejos que incluyan varios niveles tróficos y factores abióticos), así como estudios a largo plazo.

b) Diferencias en la metodología e historias de vida

Los niveles de herbivoría fueron medidos con diferentes métodos, razón por la cual no todos los resultados obtenidos son comparables (ver apéndice 2). De los trabajos revisados la mayoría fue medido con estimaciones visuales lo cual puede generar un sesgo dependiendo de la persona que mida el daño. Cabe destacar que sólo en dos de los casos la herbivoría fue medida con una mayor precisión a partir del empleo de un medidor de área foliar (Stoll *et al.*, 2006; Fáveri *et al.*, 2008).

Las variaciones en los niveles de herbivoría entre los estudios pueden deberse a que se comparan niveles de daño de especies herbáceas *vs* leñosas, y árboles *vs* brinzales con diferentes historias de vida (ver apéndice 2). A este respecto se ha reportado que la calidad de las plantas puede cambiar durante la ontogenia de las plantas y como consecuencia los niveles de herbivoría que pueden sufrir. Por ejemplo, los niveles de herbivoría que sufre *Casearia nitida* son 66% mayores en brinzales que en adultos (Boege, 2005; Boege y Marquis, 2005). Por otra parte, las especies de árboles pioneros experimentan cuatro veces más herbivoría que las especies tolerantes a la sombra (Barone y Coley, 2002). Las hojas jóvenes y en proceso de expansión sufren una tasa diaria de daño que es de 5 a 25 veces más alta que la que experimenta una hoja madura (Coley y Barone, 1996). Si bien la evidencia que se tiene hasta el momento no permite identificar un patrón generalizable, el profundizar en los distintos aspectos previamente mencionados nos permitirá obtener información que apoye de forma más consistente el efecto de la fragmentación sobre la interacción planta herbívoro.

Líneas futuras de investigación

Son sin duda muchas las preguntas que todavía permanecen sin respuesta, por ejemplo: ¿Cómo las interacciones ínter específicas afectan los procesos ecosistémicos en sistemas fragmentados? ¿Cuál es la respuesta a largo plazo? También es necesario tratar de aislar las características de la fragmentación que influyen en los resultados, es decir, por lo general no se identifica el mecanismo que causa las diferencias entre sitios fragmentados y no fragmentados. ¿Cómo interactúa el parche con la matriz? Y si esta tiene efectos en los niveles de herbivoría debido a la posible introducción de especies exóticas, ¿cómo son los patrones de herbivoría a nivel de paisaje? ¿Cómo es el movimiento de los insectos herbívoros? ¿Existen cambios en la genética o viabilidad de las poblaciones de los herbívoros y/o de las plantas especialistas?

Otra línea que merece atención es el efecto de la fragmentación del hábitat sobre las cadenas tróficas. La variación en los patrones de herbivoría están determinados al menos por dos fuerzas reguladoras:1.- Control ascendente ("Bottom-up") el cual hace referencia a que los patrones de daño se determinan por las características defensivas-nutricionales de las plantas (Power 1992); 2.- Control descendente ("top-down") y se refiere al efecto de los depredadores o parasitoides como los posibles determinantes de la dinámica poblacional de los insectos herbívoros y por tanto de los niveles de herbivoría (Hairston *et al.*, 1960). Sin embrago, existen muy pocos estudios que consideren el tercer nivel trófico como determinante de los patrones de herbivoría en un sistema fragmentado. Los trabajos realizados por el grupo de trabajo de T. Tscharntke han evaluado de manera indirecta los efectos de la estructura del paisaje sobre la interacción planta-herbívoro-parasitoides (Thies *et al.*, 2003). De manera general estos trabajos han mostrado que sitios con una baja complejidad estructural tales como monocultivos promueven la "liberación" ("enemy-free space") de insectos herbívoros debido a una disminución en las poblaciones de parasitoides. Por otra parte, Valladares y colaboradores (2006) apuntan que las tasas de parasitismo en el Chaco Serrano (Argentina), no son las responsables de la disminución de la herbivoría en fragmentos. Esta inconsistencia en los resultados enfatiza la necesidad de más estudios enfocados a entender el papel de los enemigos naturales de los herbívoros en la regulación de la abundancia de insectos fitófagos, y consecuentemente en los niveles de herbivoría en un sistema fragmentado.

Finalmente, esta revisión también hace evidente la necesidad de que la comunidad científica enfoque esfuerzos hacia esta línea de investigación, como respuesta a la degradación ecológica que están sufriendo los ecosistemas naturales del país, debido principalmente a las altas tasas de deforestación. En este sentido, sobresalen los trabajos publicados por Benitez-Malvido, y los estudios en preparación de L. Zenteno y R. Dirzo, G. Williams-Linera, A. Lemus-Albor, G.

García-Guzmán e I. Trejo. Un aspecto sobresaliente de estos trabajos es que no se han centrado en un tipo de ecosistema sino que han sido realizados en diferentes ecosistemas como selva alta, bosque mesófilo de montaña y selva seca. Esto nos puede dar un panorama más amplio de las consecuencias del uso de la tierra sobre las interacciones bióticas en diferentes ambientes, y así poder discernir entre los factores que modulan la interacción planta-herbívoro en sistemas fragmentados. El poder entender cómo la herbivoría influye en el desempeño de las plántulas es muy relevante, ya que el desempeño de éstas determina los patrones de reclutamiento de la población y por consiguiente constituyen un factor determinante de la regeneración de especies (Restrepo y Vargas 1999).

Si bien la evidencia que se tiene hasta el momento no permite identificar un patrón generalizable, el profundizar en los distintos aspectos previamente mencionados nos permitirá obtener información que apoye de forma más consistente el efecto de la fragmentación sobre la interacción planta herbívoro. En este contexto, en la presente tesis intento cubrir algunos de los aspectos previamente descritos que pueden enmascarar los resultados obtenidos. En particular, en este trabajo controlé: a) el estadio de desarrollo (utilicé solo brinzales), b) historias de vida (plantas demandantes de luz y tolerantes a la sombra) y c) los métodos de medición de los niveles de daño (tasas y herbivoría puntual),. Por ultimo, exploré dos de los posibles mecanismos subyacentes a los niveles de herbivoría que una planta puede sufrir: el control ascendente y el control descendente.

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APPENDICE 1

Base de información utilizada, CN = condiciones naturales, E = experimentos, Positivo = aumento en los niveles de herbivoría en los fragmentos, Negativo = disminución de los niveles de herbivoría en fragmentos, Neutro = no hubo efecto, MT = Modelo teórico, RE = revisión de estudios.

Hábitat	**Nivel**	**Tipo de Herbívoro**	**Efecto**	**Enfoque**	**Resultado**	**Referencia**
Bosque Tropical (Brasil)	Comunidad	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Negativo	Fáveri *et al.* 2008
Bosque Tropical (Brasil)	Comunidad	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Neutro	Benitez-Malvido *et al.* 1999
Bosque Tropical (México)	Poblacional	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Negativo	Zenteno 2001
Bosque Tropical (Panamá)	Comunidad	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Negativo	Arnold y Asquith 2002
Bosque Tropical (Venezuela)	Comunidad	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Positivo	Rao*, et al.* 2001
Bosque Tropical (Venezuela)	Comunidad	Vertebrados e invertebrados	Efecto del tamaño del fragmento	CN	Positivo	Terborgh *et al.* 2001
Bosque Templado (EU)	Poblacional	Vertebrados e invertebrados	Efecto del tamaño del fragmento y asilamiento	E	Negativo	Groom, M.J. 2001
Bosque Templado (EU)	Poblacional	Invertebrados (insectos)	Efecto del aislamiento	CN	Positivo	McEuen and Curran 2006
Bosque Templado (Chile)	Poblacional	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Negativo	Vásquez *et al.* 2007
Bosque Templado (Chile)	Poblacional	Vertebrados	Efecto del tamaño del fragmento	CN	Positivo	del-Val *et al.* 2007

CONTINÚA APENDICE 1

Habitat	Nivel	Tipo de Herbívoro	Efecto	Enfoque	Resultado	Referencia
Praderas (Suiza)	Poblacional	Invertebrados (Gastrópodos e insectos)	Efecto del tamaño del fragmento	E	Negativo	Ledergerber *et al.* 2002
Praderas (Suiza)	Poblacional	Invertebrados (Gastrópodos e insectos)	Efecto del tamaño del fragmento	E	Positivo	Stoll *et al. 2006*
Praderas (Holanda)	Poblacional	Invertebrados (insectos)	Efecto del tamaño del fragmento y asilamiento	E	Positivo	Elzinga *et al.* 2005
Wetlands (Suiza)	Poblacional	Invertebrados (Gastrópodos e insectos)	Efecto de borde y tamaño del fragmento	CN	Positivo	Lienert y Fischer 2003
Wetlands (Suiza)	Poblacional	Invertebrados (Gastrópodos e insectos)	Efecto del tamaño del fragmento y aislamiento	CN	Positivo	Lienert *et al.* 2002
Zonas Aridas (Australia)	Poblacional	Invertebrados (insectos)	Efecto del tamaño y efecto de borde	CN	Positivo	Fiona y Hochuli 2005
Zonas Aridas (Argentina)	Comunidad	Invertebrados (insectos)	Efecto del tamaño del fragmento	CN	Negativo	Valladares *et al.* 2006
		insectos		RE		Didham *et al.* 1996
		Interacciones con insectos		RE		Tscharntke y Brandl 2004
				MT		Bascompte y Sole 1998
				MT		Kondoh 2003

APENDICE 2

Variables que pueden explicar la inconsistencia de los resultados encontrados. Puntual = la herbivoría se midió solo una vez, y > 1 vez = la herbivoría fue medida dos o mas veces.

Referencia	Escala espacial	Escala temporal	N° de frag	Método	Tipo de Medición	Historia de vida
Rao, *et al.* 2001	0.3 a >350 ha	7 semanas	12	Visual (dañado o no dañado)	Puntual	Árboles > 5 cm dap, y juveniles <10 cm dap
Benitez-Malvido *et al.* 1999	1 ha >1000 ha	5 años	PDFFP	Categorías de daño	> 1 vez	Árboles, plántulas
Arnold y Asquith 2002	< 1ha a 1 500 ha	2 años	8	Nº de hojas dañadas /total de hojas	> 1 vez	Árboles
Zenteno 2001	0.3 a 640 ha	2 años	6	Tasas	tasas	Árboles (palma)
Terborgh *et al.* 2001	0.25 a >1 500 ha	2 años	12		> 1 vez	Brinzales árboles
Fáveri *et al.* 2008	1 ha- continuo	60 días	9	% daño (medidor de área foliar)	Puntual	Brinzales árboles
Groom 2001	25 individuos	2 años	8	Presencia ausencia de daño	Puntual	Herbácea
Lienert y Fischer 2003	27 parches	1 mes	27	Visual (% de área perdida)	Puntual	Herbácea
Fiona y Hochuli 2005	<65 a 13 000 km 2	puntual (abril colecta de hojas)	15	Visual (% daño)	Puntual	Árboles grandes

Continúa APENDICE 2

Referencia	Escala espacial	Escala temporal	N° de frag	Método	Tipo de Medición	Historia de vida
Elzinga *et al.* 2005	16 plantas a 256 plantas	3 años	6	Nº de hojas dañadas /total de hojas	> 1 vez	Herbácea
Ledergerber *et al.* 2002	parcelas de 522m2 y eran 12 = 6264 m2	1 año	4	Visual (% de daño)	> 1 vez	Herbácea trébol
Valladares *et al.* 2006	0.13> 15 00ha	1 año	19	Nº de hojas dañadas /total de hojas	Puntual	Todas las especies
Lienert *et al.* 2002	Grandes > 5 ha pequeñas <0,5 ha	1 vez (1998)	18	Visual (% de daño)	Puntual	Herbácea Perene
Mc Euen y Curran 2006	4-15 ha	3 años , 13 censos	4	Visual (categorías de daño)	> 1 vez	Arbusto tolerante
del-Val *et al.* 2007	0.2-22 ha	22 meses	4	Mortalidad de plántulas	> 1 vez	Árbol
Vásquez *et al.* 2007	3- 600 ha	4 meses : medición cada mes	3	Visual (% de daño)	Tasas ó > 1 vez	Árbol
Stoll *et al. 2006*	2 ha	1 año: tres veces	12	% de daño (medidor de área foliar).	> 1 vez	Arbusto tolerante

Capítulo 2

La herbivoría por insectos disminuye en fragmentos y covaría con la estrategia de regeneración de las plantas: Evidencia de una selva tropical Mexicana

Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: Evidence from a Mexican tropical rain forest

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Abstract

The consequences of tropical forest fragmentation on herbivory are poorly understood. The limited evidence suggests that forest fragmentation can have positive, negative or neutral effects on herbivory. Inconsistencies may be partly explained by plant interspecific variation and differential responses related to plant life history. In this study we examined the effects of forest fragmentation and plant regeneration mode (shade-tolerant and light-demanding species) on sapling herbivory using a large sample of the community (97 species, representing 25% of the woody flora of the study site), and a subset of species shared by forest fragments and continuous forest. For the latter, we also analyzed the effects of species identity on variation in herbivory. Also, for the shared species we used two techniques to measure herbivory: standing herbivory (i.e., instantaneous, actual damage) and cumulative herbivory (i.e., damage, accumulated over time, on initially intact leaves). Insect herbivory was the predominant type of damage in the two forest types, and standing herbivory at both the community and the shared species level was significantly higher in continuous forest than in fragments. Considering shared species, both standing and cumulative herbivory were significantly higher in light-demanding than in shade-tolerant species. Cumulative herbivory also showed a significant interaction between forest fragmentation and plant regeneration mode, whereby a significant decline in herbivory in fragments was driven by reduced herbivory in shade-tolerant species, whereas for light-demanding species herbivory did nod change significantly, due to contrasting species-specific responses**.** We conclude that tropical forest fragmentation reduces insect herbivory, but this depends on plant regeneration mode and species identity. These changes could have effects on plant regeneration and diversity in forest fragments via long-term demographic consequences.

Introduction

Although deforestation and habitat fragmentation are recognized as major threats for the maintenance of tropical biodiversity (Dirzo and Raven 2003), we are still far from understanding their ecological consequences, given that most fragmentation studies have focused largely on the loss or changes in abundance of species. It is only recently that studies are beginning to evaluate the consequences of fragmentation on ecological processes, such as species interactions (Terborgh et al. 2001, Tschanstke and Brandl 2004), in part motivated by early calls for attention to be paid to fragmentation effects on plant-insect interactions (Didham et al. 1996). While studies on the consequences of tropical fragmentation for mutualistic interactions are abundant (Ghazoul 2005), there is a dearth of studies on antagonistic interactions such as herbivory (Tschanstke and Brandl 2004). Herbivory influences not only the dynamics and structure of tropical ecosystems, but also individual plant performance and population-level processes (Coley and Barone 1996), thus it has the potential to influence forest regeneration and maintenance of plant diversity (Marquis 2005). Sixteen studies have examined the consequences of habitat fragmentation on plant-herbivore interactions (excluding studies specifically addressed at examining edge effects), but no general conclusion can be drawn from such studies. Half of them show that herbivory increases in small fragments (positive effect) because of: i) a decrease in the abundance of the herbivore’s natural enemies (Rao et al. 2001, Terborgh et al. 2001, Lienert and Fisher 2003, Christe and Hochuli 2005, Elzinga et al. 2005), ii) an increase in phytophagous insect oviposition rates with consequent increases in larvae abundance (Elzinga et al. 2005), iii) an increase in the nutritional quality of plants due to soil fertilization resulting from fertilizer spill over form surrounding agricultural fields (Lienert et al. 2002, Christie and

Hochuli 2005, del- Val et al. 2007), and iv) the predominance of light–demanding plant species (at edges and small fragments), which are more palatable to herbivores than shade-tolerant species (Wirth et al. 2008). In contrast, seven studies show the opposite trend: decreased herbivory in forest fragments as a consequence of: i) a decrease in the abundance of herbivores due to fragment isolation (Vásquez et al. 2007, Fáveri et al. 2008), ii) detrimental edge effects (e.g., increased temperature and decreased relative humidity) on insect herbivore survival and performance (Zenteno 2001, Ledergerber et al. 2002, Valladares et al. 2006), iii) a reduction in the abundance of palatable host plants (Groom 2001, Arnold and Asquith 2002), or iv) negative changes in plant palatability (Simonetti et al. 2007). Finally, one study reports a null effect of forest fragmentation on herbivory (Benitez-Malvido et al. 1999).

The effects of forest fragmentation on herbivory may be masked by multiple sources of variability such as vegetation type (tropical rain forest, grasslands, temperate forest, etc.), levels of biological organization (community, individual species), life forms (trees, herbs, palms), species-specific responses, and different methods used to measure herbivory. We argue that in order to understand the consequences of forest fragmentation on herbivory, those sources of heterogeneity need to be taken into account. In particular, no study has examined the effects of fragmentation on herbivory considering variability across plant regeneration modes (light-demanding and shade-tolerant species), a key life history trait for forest colonization, and known to be a main driver of interspecific variation of herbivory in tropical ecosystems (Coley 1983). Furthermore, while standing levels of herbivory are readily obtained, and used in numerous studies (see Coley and Barone 1996), they tend to underestimate damage levels by 38% - 60% (Lowman 1984, Filip et al. 1995) because entirely eaten leaves and those that abscise after being heavily damaged are overlooked, and there is unaccounted variability in leaf life spans. These limitations are overcome by measurements of cumulative damage (commonly expressed as herbivory rates), in which individually marked leaves are followed over time (see Coley 1982, Lowman 1984 and Filip et al. 1995, for a detailed description of the contrast between both sampling protocols).

In the present study we analyze the effects of forest fragmentation on herbivory and their covariation with plant regeneration mode (light-demanding vs shade-tolerant species) at two different levels: i) a sample of 97 species representative of the community (standing herbivory), and ii) a subset of species shared by fragments and continuous forest (standing herbivory and cumulative herbivory). We restricted our measurements to saplings (> 50 cm height and diameter at breast height (1.3 m) < 1 cm), to control for size/ontogeny-related changes in herbivory (Boege and Marquis 2005), and because saplings are more likely to be affected in their performance by herbivory than large/older plants (Dirzo 1984, Marquis 1984), thus potentially affecting recruitment, regeneration and species composition in fragments.

The aim of this study was to evaluate the possible consequences of forest fragmentation on herbivory, and the specific questions we addressed were: i) does the magnitude of herbivory change with habitat fragmentation? ii) is herbivory on plants of contrasting regeneration mode (shade-tolerant and light-demanding species) equally affected by forest fragmentation? As a preamble to these comparisons, we determined the type of herbivores responsible for leaf damage in continuous forest and forest fragments.

Materials and methods

Study site

This study was conducted at the Los Tuxtlas Research Station, Veracruz, Mexico (18° 30´-18° 40´N, and 95° 03´- 95° 10´W) and adjacent areas (Fig. 1). The area of study is located within the Sierra de Los Tuxtlas. This region represents the northernmost distribution limit for rain forest in the neotropics (Dirzo and Miranda 1992). Mean annual temperature and total mean annual rainfall are 27 °C and 4900 mm, respectively (Soto and Gama 1997). The region originally comprised extensive tracts of tropical rain forest in the lowlands, with cloud forest, elfin forest and some patches of coniferous forest along the altitudinal range. The flora of the lowland rain forest is composed of plants of neotropical origin, but higher elevation sites include combinations of neotropical and nearctic taxa (Dirzo 1987, 1992).

Conversion of previously extensive tracts of rain forest to agricultural land in the region has produced an agroscape (*sensu* Janzen 1986) in which forest fragments of different size and degree of isolation are imbedded within a human-dominated matrix (Dirzo and García 1992, Mendoza et al. 2005). In the Northern part of Sierra de Los Tuxtlas, the only remaining area of continuous lowland rain forest corresponds to the Los Tuxtlas Research Station (150 to 650 m a.s.l.), and this is connected, through an elevation gradient, with the San Martin Volcano (1, 600 m a.s.l.), encompassing a total area of ca. 9,500 ha (see Fig. 1).

Selection of fragments and continuous forest sites

Our approach was to compare two habitat types: small forest fragments and continuous forest (hereafter referred to as forest types). Based on direct exploration of the study area, and using aerial photographs as described by Aguirre and Dirzo (2008), we selected three small fragments (<19 ha, the predominant fragment size in the region – see Mendoza et al. 2005, Fig. 1) of similar age of separation from the continuous forest (~20 yrs.), and three sites within the continuous lowland forest located within the 640-ha Los Tuxtlas Research Station (Fig. 1). All six sites were of similar ecological conditions, located within a restricted altitudinal range (15 - 150 m a.s.l.), and with similar vegetation composition. All sites were considered to be independent as they were located on three separate hilltops at distances > 1 km.

Herbivory: damage types

We describe the damage types to determine which herbivores are responsible for the measured damage. Damage types were assessed considering the three major categories present in this and other rain forests: insect, vertebrate (mammal) or pathogen (Dirzo 1987), which were defined by inspection of leaf scars (see de la Cruz and Dirzo 1987 for details) from a bulk sample of 450 leaves for fragments and continuous forest sites, collected in March 2009. The bulk samples were obtained from the first six plants (saplings, as defined above) encountered on each of five randomly-positioned transects (50m x 2m) in each of three fragments and three continuous forest sites (N = 90 plants from fragments, and 90 from continuous forest). From each sapling we collected the five oldest (most basal) leaves to determine the frequency of damage types.

Herbivory: fragmentation-related changes

We considered three levels of analysis: a) standing herbivory at the community level, represented by all sampled saplings in each forest type (82 species in continuous forest and 64 species in fragments, for a total of 97 species), b) standing levels of herbivory in a subset of species shared between forest types (see Table 1), and c) cumulative herbivory for the subset of shared species (see Table 1). Plant species shared between forest types were selected on the basis of their importance value (IV), which was calculated as: IVi = RFii, where: RFi, the relative frequency of the ith species, is the proportion of sites, out of six, where the ith species was present, divided by the sum all species' frequency, multiplied by 100; and RAi, the relative abundance of the ith species, is the number of individuals of the ith species divided by the total number of individuals from all species in all six sites, multiplied by 100 (Skeen 1973). The range of variation of IV was 0.33 to 8.5, and we selected the shared species that: i) were among the twenty species with highest IV, ii) belong to different families (to increase phylogenetic variation), iii) are representative of the two regeneration modes, and iv) were present in all six sampling sites. In total nine species met these criteria (Table 1).

Sampling design and estimation of leaf damage per plant

To evaluate herbivory, we established 0.1-ha permanent observation plots in the center of each fragment, and therefore as far from edges as fragment size would permit. In continuous forest the observation plots were located more than 500 m from forest edges. Each permanent observation plot consisted of ten 50 m x 2 m randomly selected transects. For the community-wide survey, in July 2002, we sampled herbivore damage on leaves of saplings from all woody plants rooted in each transect. We identified each individual plant to the species level, and randomly collected 10 leaves (or the maximum number possible if the plant had less than 10). Leaves were collected by assigning a number to all leaves on the plant, and a random sample of 10 of them was selected using a random numbers table. In total, we sampled 1054 individuals from 97 species, excluding singletons. In August 2002, we collected ten randomly selected leaves (as described before) from ten individuals of each of seven shared species in the permanent observation plots (see Table 1) to measure standing levels of herbivory. We classified plants by regeneration mode as either shade-tolerant or light-demanding species, based on our own knowledge, information provided by the station's resident botanist (Alvaro Campos), and from published literature on plant regeneration modes in the study site (Martínez-Ramos 1994).

From all collected leaves we quantified standing herbivory damage as the percent leaf area eaten by herbivores. We considered leaf damage when parts of the lamina were missing, including holes, scraped-off areas, or incomplete leaf margins. Most of this damage corresponds to chewing insects (alone or combined with pathogen). Upon collection, leaves were flattened out and oven-dried. We then obtained a digital image of each leaf using a lamp-box attached to a photographic camera. These images were imported to WinDias software (Delta-T Devices Ltd, Ver. 2), which measures the actual leaf area (ALA), and we estimated the potential leaf area (PLA) by drawing out the contours and filling in the spaces of damaged area. When damage was very extensive we estimated PLA by matching the remaining area of leaves with a comparable, intact leaf of the same species. When a leaf only had part of its central vein left, we considered it to have 100% damage. Leaf herbivory (LH), defined as the percentage of leaf area damaged, was calculated as: LH = ((PLA-ALA)/PLA)*100. We estimated herbivory per plant using the average herbivory of all leaves sampled from the plant. From an additional sample of plants, we also determined cumulative herbivory on marked leaves from shared species in forest fragments and in continuous forest (Table 1), following the same criteria of location of sampled plants away from edges, as described above. In April 2007, we selected two undamaged leaves (position 1 and 2 of the phyllotaxis) from 10 individuals of eight species in each site. All selected plants were located in the permanent observation plots referred to above, thus N = 240 plants per forest type, or 480 in total. The selected leaves were marked with plastic rings placed at the base of the petioles, and were harvested after six months. We then measured the leaf damage accumulated over 180 days using the same method as for standing herbivory. Only those leaves which still maintained the plastic ring were considered in the analysis, and we excluded marked leaves that died from unknown causes.

Statistical analyses

We compared the frequency of damage types between forest fragments and continuous forest using a chi-square test; we did not include damage by mammals in the analysis since their values were zero. To evaluate the effect of forest type (fragments vs. continuous forest) and plant regeneration mode (light-demanding vs. shade-tolerant) on herbivory levels, we used mixed-effects models based on restricted maximum likelihood estimation of parameters. Forest type (FT), plant regeneration mode (PRM), and their interaction were defined as fixed factors, whereas the random component of the model was defined as the overall mean of herbivory given the identity of the species nested within sites. Further, we modeled the variance in the hierarchical nesting structure with the varPower command of R. We also applied a mixed effect model to test the effect of species identity on herbivory. In this model, forest type, species identity, and their interaction were defined as fixed factors while the random component was defined as the overall mean of herbivory given the plant regeneration mode. Contrasts in cumulative herbivory for each species in the two forest types were performed with a t-test based on the estimated standard error of the differences. In the case of standing damage analyses, average percent leaf herbivory per plant was angular-transformed to meet model assumptions for the distribution of residuals. In the case of cumulative herbivory we used the rank-transformation (see Conover and Iman 1981), which is robust for additive factorial designs (cf. Seaman et al. 1994). In addition, a simulation analysis showed that Type-I error of the models described above, fitted to rank-transformed data, was unbiased compared to untransformed data (results not shown). In all cases we report mean and standard error values for untransformed data. All statistical analyses were carried out using R 2.5.1 GUI 1.2 (R Development Core Team 2007). We fitted linear mixed-effects models using the lme function in R (Pinheiro et al. 2007).

Results

Herbivory: damage types

Overall distributions of damage types on leaves were similar in both forest types (Table 2). The most evident feature is the prevalence of insect herbivory. Damage by pathogens alone was present in a proportion of only 2.9% of the leaves in continuous forest and 1.3% in forest fragments, but it occurred at higher frequencies when combined with insect damage. Considering the incidence of insect damage, alone and combined with pathogens, the overall predominance of insect herbivory becomes even more marked in both forest types. Nonetheless, the frequency distribution of damage types was significantly different between forest types ($\chi2 = 10.59$, DF = 3, $p = 0.01$). Leaves with insect damage, pathogen damage, and the combination thereof, were more frequent in continuous than in fragmented forests, while intact leaves were less frequent in continuous than in fragmented forests. In most of the insect-damaged leaves we further identified the general type of insect damage. Damage by lepidopteran caterpillars, beetles and orthopterans, was predominant in both forest types. No evidence of damage by vertebrates was evident in either forest types.

Herbivory: fragmentation-related changes

Considering all levels of analysis, we measured herbivory on 13,163 leaves collected from 1,839 saplings of 97 plant species. This represents 25.5% of the total richness of woody plant species reported for Los Tuxtlas, and includes the most common as well as several rare species (Ibarra-Manríquez and Sinaca-Colín 1997). Overall, 93% of the sampled plants showed signs of damage, with an average standing herbivory of 10.7% ± 0.6% per plant.

a) Plant community: standing herbivory

At the community level, standing herbivory was significantly different between forest fragments and continuous forest (Table 3). Herbivory was 1.3-times greater in continuous forests (11.7 ± 0.53%) than in forest fragments (9.04 ± 0.28%, Fig. 2a). In addition, we found that light-demanding species had on average 1.2 times more herbivory (11.6% ± 0.58%) than shade-tolerant species (9.5% ± 0.30%), although this was not significantly different. The interaction term of forest fragmentation and regeneration mode was not significant either.

b) Shared species: standing damage

Standing levels of herbivory for seven shared species also differed significantly between fragmented and continuous forest (Table 3). Shared plant species had 1.9-times more herbivory in continuous forests (16.5% ± 0.84%) than in forest fragments (8.9% ± 0.64%, Fig. 2b). There was a significant effect of plant regeneration mode on standing herbivory (Table 3), with herbivory levels 1.7-times greater in light-demanding species (15% ± 0.75%) than in shade-tolerant species (8.9% ± 0.71%, Fig. 2c). We did not detect a significant interaction between forest type and plant regeneration mode (Table 3).

c) Shared species: cumulative herbivory

Cumulative herbivory over 180 days varied significantly between plant regeneration modes (Table 3). Cumulative herbivory was 2.7-times greater in light-demanding species (12.5% ± 1.19%) than shade-tolerant species (4.6% ± 0.79%). The interaction term forest type x plant regeneration mode was statistically significant (Table 3), as cumulative herbivory among shade-tolerant species was 4-fold greater in continuous forest (6.6% ± 1.28%) than in forest fragments (1.7% ± 0.49%, $t = 3.5$, $DF = 4$, $p < 0.024$), while light-demanding species did not differ in cumulative herbivory between fragmented and continuous forest ($t = 0.5$, $DF = 4$, $p = 0.696$). When considering the identity of the shared species as a factor, we found that differences in herbivory between forest fragments and continuous forest were consistent among shade-tolerant species, showing significantly higher damage in continuous forest ($t > 2.1$, $p \leq 0.03$ in all cases), while light-demanding plant species varied in their herbivory response between forest types (Table 3, Fig. 3): *Hampea nutricia* and *Myriocarpa longipes* were less damaged in forest fragments than in continuous forest ($t = 2.3$, $DF = 357$, $p = 0.023$; and $t = 2.5$, $DF = 357$, $p = 0.013$, respectively), while *Acalypha diversifolia* and *Siparuna andina* experienced higher herbivory in forest fragments than in continuous forest ($t = 2.2$, $DF = 357$, $p = 0.025$ and $t = 1.97$, $DF = 357$, $p < 0.049$, respectively).

Discussion

No other study seems to have addressed the consequences of forest fragmentation on sapling herbivory, considering such a large and representative sample of the plant community in a tropical rain forest. Another similar study in Amazonia (Fáveri et al. 2008) considered a very large sample also, but it focused on juvenile plants. Our results, based on a survey of 97 woody species (1,822 reliably identified saplings) show that fragmentation significantly affects herbivory, and underscore the fact that changes in herbivory due to habitat fragmentation are dependent on plant regeneration mode, species identity, and the technique used to estimate herbivory. A salient finding of this study is that herbivory declined in forest fragments, as compared to continuous forest. This finding was consistent when we considered herbivory for the entire community and the shared species (measured both as standing damage or cumulative herbivory). Furthermore, when we measured leaf damage as cumulative herbivory our study uncovered that this effect covaries with plant regeneration mode and species identity: while fragmentation effects are strong and consistent in shade-tolerant species, light-demanding species showed a species-specific response, yielding the overall result that the species of this regeneration mode did not show fragmentation-related effects. Given that shade-tolerant species represent the most abundant regeneration mode in tropical rain forests in general, and in this study site in particular (cf. Dirzo and Boege 2008), we posit that studies attempting to assess the effects of habitat fragmentation on herbivory need to take into account plant regeneration mode, particularly the response of shade-tolerant species.

Herbivory: damage types

Our data showed a predominance of insect damage in the continuous forest, as has been shown by previous studies in this and other tropical forests (Dirzo 1987, Coley and Barone 1996). The incidence of pathogen damage mostly co-occurred with insect damage in continuous forests, confirming previous patterns detected by Dirzo (1987) and García-Guzmán and Dirzo (2001) in the same study site. In addition, we detected a total absence of mammalian damage, consistent with a previous finding by Dirzo and Miranda (1991). In this study we found that the same trends occur in forest fragments: a predominance of insect damage (alone and combined with pathogen damage), low incidence of pathogen damage alone, and absence of mammalian herbivory. Therefore, it was appropriate to focus this study on insect herbivory. Nevertheless, we detected an overall contrast in the frequency of damage across forest types: damage of all types was more frequent in continuous forest than in forest fragments, while the frequency of undamaged leaves showed the opposite trend. This suggests that insect herbivory is lower in fragments than in continuous forest, a result that was confirmed by the analysis of leaf area damaged across forest types.

Herbivory: fragmentation-related changes

We found consistently lower levels of herbivory in forest fragments than in continuous forest at the level of the plant community and when comparing the shared species. This finding is concordant with other studies demonstrating similar effects of fragmentation (Gromm 2001, Zenteno 2001, Arnold and Asquith 2002, Ledergerber et al. 2002, Valladares et al. 2006, Vásquez et al. 2007, Fáveri et al. 2008). However, other studies have reported results in the opposite direction: herbivory increases in fragments (Rao et al. 2001, Terborgh et al. 2001, Lienert et al. 2002, Christie and Hochuli 2005, Elzinga et al. 2005, Stoll et al. 2006, del Val et al. 2007). This discrepancy among studies could be related to site-specific differences and a host of other sources of potential variation in herbivory, including plant regeneration mode, plant life form, species identity, and even measurement technique.

In general terms, changes in herbivory resulting from fragmentation can be driven by changes in top-down or bottom-up controls. For instance, there is evidence that top-down controls of herbivores, such as parasitism and predation, are negatively affected by habitat fragmentation (Didham et al. 1996, Kruess 2003), and this would increase herbivory in fragments, a situation contrary to our findings. On the other hand, several studies have shown that fragmentation increases predation (González-Gómez et al. 2006, Koh and Menge 2006, Fáveri et al. 2008) or parasitoid (Roland and Taylor 1997, Doak 2000) attack rates, potentially or actually leading to a reduction in herbivory in fragmented sites, consistent with our findings. In summary, these studies show that forest fragmentation can either increase or decrease top-down controls of herbivores, and this may be responsible, at least in part, for the inconsistency of results of studies addressing forest fragmentation effects on herbivory.

Independent of alterations in biotic top-down controls of herbivores due to fragmentation, changes in the abundance of phytophagous insects in forest fragments leading to reduced herbivory could be explained by habitat isolation, patch size and quality, and microclimate changes due to edge effects. For example, it has been speculated that warmer microclimatic conditions and exposure to strong winds at fragment edges could negatively affect herbivore survival or performance (Barone and Coley 2002), potentially leading to results similar to ours. Alternatively, foliage quality, a bottom-up control, may be altered by the prevailing conditions at the edge of forest fragments and in small fragments (Coley 1998, Fortín and Mauffette 2001, Yamasaki and Kikuzawa 2003, Wirth et al. 2008). For example, it has been suggested that high solar radiation can induce an increase of secondary metabolites such as tannins, terpenes and phenolic compounds (Coley and Barone 1996, Waterman and Mole 1994). Such changes would produce results similar to the ones we uncovered. However, we have evidence that a variety of leaf defensive traits (including secondary metabolites, water and nutrient content and, in general, plant palatability) remain unchanged in a set of species shared in fragments and continuous forest at Los Tuxtlas (Ruíz-Guerra 2009), suggesting that such plant trait-related changes in bottom-up controls may not be responsible for the observed decline in herbivory with fragmentation at Los Tuxtlas. This, and other related bottom-up controls, such as changes in plant community composition, is an aspect that warrants further work in this and other sites.

The decline in herbivory with fragmentation, considering all species, included both light-demanding and shade-tolerant species. Likewise, the comparison using a set of shared species, which included species of both types of plant regeneration mode, also showed a decline in herbivory in forest fragments. These results showed a consistency of response in both groups of plants. However, we also observed fragmentation-related differences in herbivory between shade-tolerant and light-demanding species in 2007 (using cumulative damage). While herbivory in all shade tolerant species consistently declined with fragmentation, herbivory in light-demanding species, as a group, did not, due to the fact that species responses were idiosyncratic: herbivory in some species declined while in others it increased with fragmentation, an aspect that merits subsequent examination with a larger pool of species. Still, we emphasize that this group of species represents only a lower proportion of the woody flora of this and other tropical sites, compared to the mature-forest, shade-tolerant species (Dirzo and Boege 2008).

It is puzzling that we detected a significant interaction between plant regeneration mode and forest type in 2007, using cumulative herbivory measurements, and not in 2002, when we measured standing damage of shared species. Standing damage underestimates herbivory (Lowmanm 1984, Filip et al. 1995), particularly when damage is high and entirely eaten or heavily damaged leaves are abscised and, therefore, overlooked in the standing damage estimates (Bundell and Peart 2000). Since herbivory was greater in light-demanding species and leaf turnover is faster in these species (Coley and Barone 1996), standing measurements might have underestimated herbivory to a larger extent in these species, compared to shade-tolerant species. This suggests that the contrast between light-demanding and shade-tolerant species using standing measurements (a

1.7-fold difference) might have been even greater. Indeed, our cumulative measurements showed that to be the case (a 2.7-fold difference). Nonetheless, absolute levels of damage were, in general, greater when we used standing measurements compared to cumulative damage (12.4% vs. 8.1%, respectively). However a comparison of the results using the two methods is not warranted, given that measurements were conducted in different years and temporal variation in a host of variables (see discussion of drivers above) can lead to temporal variations in herbivory (see Benitez-Malvido et al. 1999).

As indicated above, insect herbivory was the predominant type of damage. The frequency of pathogen damage alone was low, but was much greater when it occurred in combination with insect damage. A detailed analysis of pathogen damage in continuous forest at Los Tuxtlas (García-Guzmán and Dirzo 2001) showed that the amount of leaf area infected by pathogens alone was very low, compared to insect damage, and that the incidence of infection depends on insect herbivory. Therefore we expect that pathogen infection in relation to fragmentation will follow a similar trend as that of insect herbivory. Interestingly, an ongoing study on leaf pathogen infection in fragments and continuous forest shows that to be the case (R. Dirzo, unpub. data) but, again, this an aspect that warrants further work.

This study underscored the complexity of the consequences of fragmentation on herbivory. At the same time, it exposed numerous important aspects that need to be addressed to advance in this field, not only to inform patterns of change in the face of fragmentation, but also to elucidate underlying mechanisms responsible for such patterns. In addition, this study addresses a lacuna in the study of fragmentation effects on saplings, the phenostage in which herbivory can have stronger detrimental effects on plant fitness (Dirzo 1984, Marquis 1984). Since saplings represent the potential future composition of the tropical plant community and this study revealed that sapling herbivory changes with fragmentation and covaries with plant regeneration mode and species identity, further research is needed to understand the long-term consequences of the changes in herbivory regimes driven by habitat fragmentation.

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Table 1. Species shared between forest fragments and continuous forest. Shared species were defined on the basis of their importance value (IV, see materials and methods). S = standing levels of herbivory and C = cumulative herbivory.

Species	Family	Plant regeneration mode	IV (%)	Herbivory measurement
Acalypha diversifolia	Euphorbiaceae	Light-demanding	3.11	S and R
Hampea nutricia	Malvaceae	Light-demanding	2.54	S and R
Myriocarpa longipes	Urticaceae	Light-demanding	3.10	S and R
Siparuna andina	Monimiaceae	Light-demanding	2.94	S and R
Nectandra ambigens	Lauraceae	Shade-tolerant	2.60	S
Pseudolmedia oxhyphyllaria	Moraceae	Shade-tolerant	5.39	S and R
Rheedia edulis	Guttiferaceae	Shade-tolerant	2.38	S and R
Cymbopetalum baillonii	Annonaceae	Shade-tolerant	2.31	R
Faramea occidentalis	Rubiaceae	Shade-tolerant	2.05	R

Table 2. Types of damage present in a sample of leaves from forest fragments and continuous forest (N= 90 plants and 450 leaves in each forest type). Numbers correspond to the number (and percentage) of leaves. Types of damage were defined from the scars left by herbivores on the leaves (see text for details).

Type of damage	Forest types	
	Continuous forest	Forest fragments
Insects	99 (22%)	80 (17.8%)
Pathogenic agents	13 (2.9%)	6 (1.3%)
Insects and Pathogens	213 (47.3%)	199 (44.2%)
Mammals	0	0
Intact	125 (27.8%)	165 (36.7%)

Table 3. Summary of mixed-effects models comparing the fixed factors of forest type (fragments or continuous forest), plant regeneration mode (light-demanding or shade-tolerant), and their interaction term on: a) standing levels of herbivory in the plant community (N = 1054 individuals), b) standing herbivory levels for shared species (N = 411 individuals), c) cumulative herbivory for shared species (N = 374 surviving individuals, out of the initial 480), and d) cumulative herbivory for shared species considering species identity as fixed factor.

Effect	DF	F	P
a) Community level			
Forest type	1,4	7.6	0.051
Plant regeneration mode	1,181	3.1	0.079
Forest type* plant regeneration mode	1,181	1.8	0.185
b) Shared species (standing herbivory)			
Forest type	1,4	7.7	0.050
Plant regeneration mode	1,34	8.23	0.007
Forest type* plant regeneration mode	1,34	0.5	0.474
c) Shared species (cumulative herbivory)			
Forest type	1,4	0.17	0.700
Plant regeneration mode	1,40	32.0	<0.001
Forest type* plant regeneration mode	1,40	10.2	0.003
d) Shared species (cumulative herbivory)			
Forest type	1,357	5.02	0.026
Species identity	7,357	2.89	0.006
Forest type * species identity	7,357	4.97	<0.001

Figure legends, Ruiz-Guerra et al.

Figure 1. Location of the study site in the State of Veracruz, Mexico, including the specific location of the three forest fragments (FF) and the three sites of continuous forest (CF) located in the Los Tuxtlas Research Station (LTRS). Gray areas correspond to forest; clear areas correspond to cattle grasslands. Modified from Mendoza et al. (2005).

Figure 2. Percent herbivory (mean ± se) of plants in two types of forest (continuous forest and forest fragments), in the tropical rain forest of Los Tuxtlas. a) Standing herbivory in a representative sample of the community of saplings of woody species (97 species), b) Standing herbivory in a subset of seven species shared between continuous forest and forest fragments, c) Standing herbivory in a subset of seven shared species by regeneration modes: light-demanding and shade-tolerant, d) Cumulative herbivory over 180 days in a subset of eight shared species, by forest type and regeneration mode.

Figure 3. Cumulative percent herbivory over 180 days (mean ± se per plant) in four light-demanding and four shade-tolerant species shared between continuous forest and forest fragments. Light demanding species: *Acalypha diversifolia* (Acdi), *Hampea nutricia* (Hanu), *Myriocarpa longipes* (Mylo), and *Siparuna andina* (Sian); shade-tolerant species: *Cymbopetalum baillonii* (Cyba), *Faramea occidentalis* (Faoc), *Rheedia edulis* (Rheed) and *Pseudolmedia oxyphyllaria* (Psox). All comparisons were statistically significant when tested with rank-transformed data (see text for details).

Figure 1.

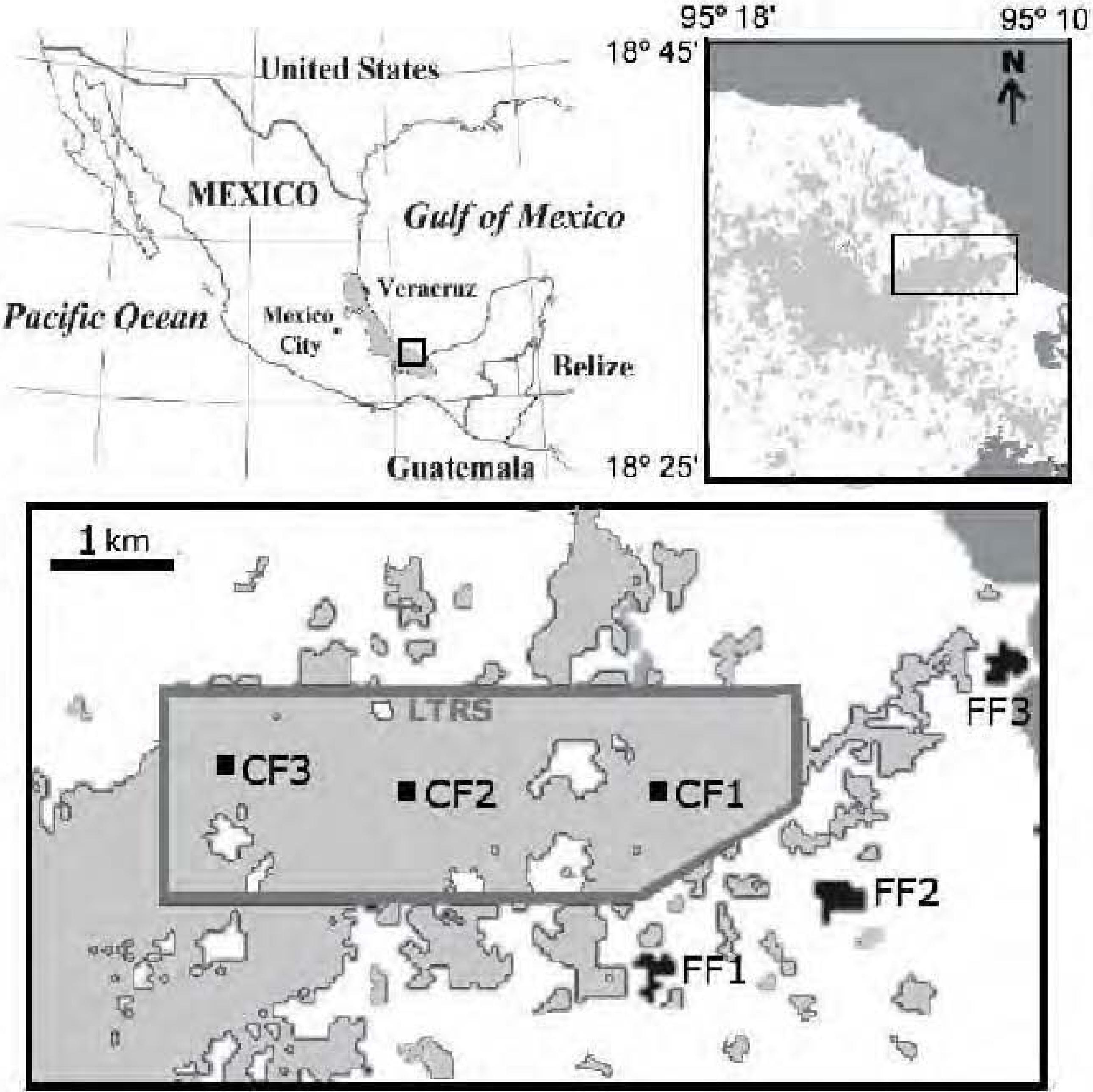

United States
MEXICO
Gulf of Mexico
Pacific Ocean
Veracruz
Mexico City
Belize
Guatemala
95° 18'
95° 10
18° 45'
18° 25'
N
1 km
LTRS
CF3
CF2
CF1
FF3
FF2
FF1

Figure 2.

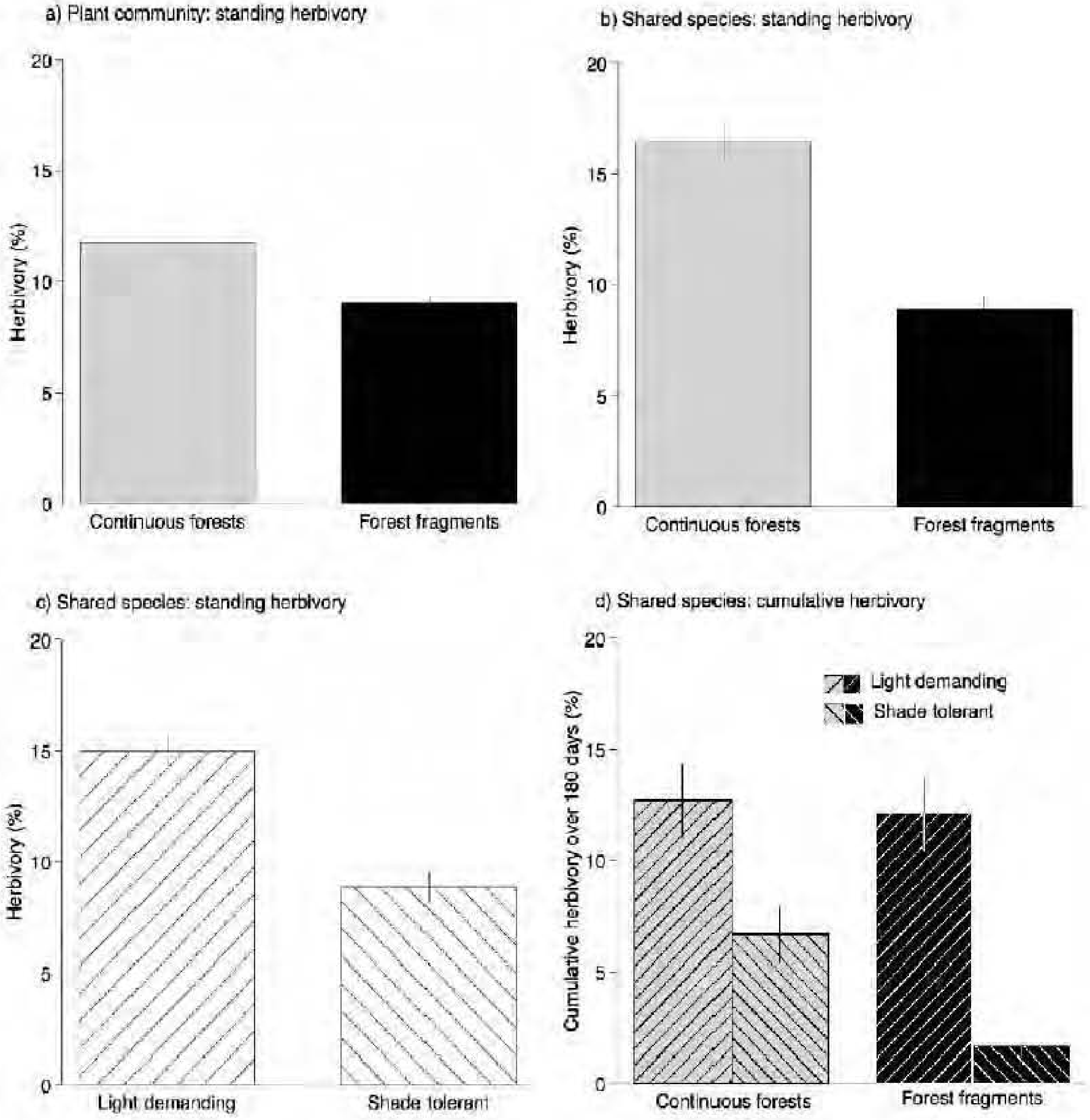
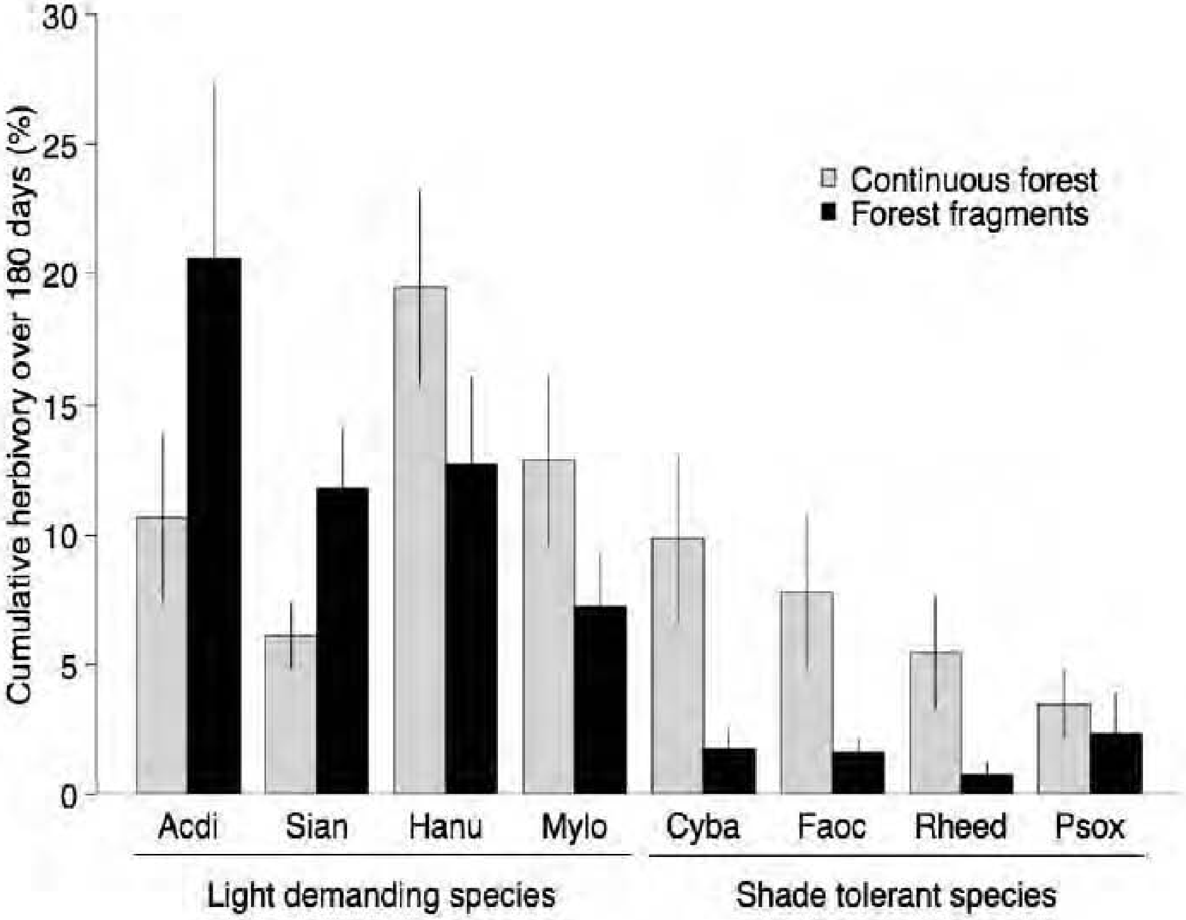

a) Plant community: standing herbivory
Herbivory (%)
0
5
10
15
20
Continuous forests
Forest fragments
b) Shared species: standing herbivory
Herbivory (%)
0
5
10
15
20
Continuous forests
Forest fragments
c) Shared species: standing herbivory
Herbivory (%)
0
5
10
15
20
Light demanding
Shade tolerant
d) Shared species: cumulative herbivory
Cumulative herbivory over 180 days (%)
0
5
10
15
20
Light demanding
Shade tolerant
Continuous forests
Forest fragments

Figure 3.


30
25
20
15
10
5
0
Cumulative herbivory over 180 days (%)
□ Continuous forest
■ Forest fragments
Acdi
Sian
Hanu
Mylo
Cyba
Faoc
Rheed
Psox
Light demanding species
Shade tolerant species

Capítulo 3

¿La fragmentación del hábitat afecta las características nutritivas y defensivas de las plantas?

Are plant anti-herbivore and nutritional traits affected by tropical forest fragmentation?

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ABSTRACT

Plant traits such as defensive compounds and nutritional quality (e.g. water and carbon/nitrogen content) are recognized as a one of the main determinants of herbivory by insects in tropical plants. However, to date most of the studies about forest fragmentation and herbivory damage have not considered changes in these attributes due to forest fragmentation and as a possible explanation to the observed changes in herbivory under fragmentation. In this study we evaluate plant defensive characteristics (total phenolics, condensed tannins and leaf toughness), nutritional traits (water content and percentage of carbon/nitrogen) and palatability of a set of species from the Los Tuxtlas rainforest plant community, as possible drivers of the fragmentation-related reduction in herbivory observed in this site**.** We separated the data for shade-tolerant and light-demanding species, present in fragments and continuous forest. Most of the studied species did not show differences in the defensive characteristics between forest fragments and continuous forest. However, *P. oxyphilaria* showed higher values of defensive traits in continuous forest than in forest fragments. On the other hand, shade-tolerant species were more defended and less consumed by a generalist herbivore than light demanding species. Nutritional traits did not vary between forest fragments and continuous forest. However, light-demanding species had more water content and nitrogen than shade-tolerant species, while carbon by dry mass and the C/N ratio were higher in shade-tolerant than in light-demanding species. We conclude that interespecific variation in plant quality and palatability is consistent with plant life history and that forest fragmentation affects defensive/nutritional characteristics in a species-specific manner, but, overall, the decrease in herbivory levels in forest fragments found in a previous study is not explained by fragmentation-related bottom-up changes in plant traits.

keywords: forest fragmentation, Los Tuxtlas, tropical forests, phenols, condensed tannins, toughness, C/N ratio, water content.

INTRODUCCTION

Over 50% of the global terrestrial biodiversity is engaged in herbivory (Price 2002), and organisms involved in this interaction are largely concentrated in tropical forests (Novotny and Basset 2004). However, extended land use changes across the tropics have put at risk not only individual components of biodiversity (Dirzo and Raven 2003) but entire coevolutionary assemblages are threatened (Tylianakis et al.2008). Recent evidence has shown negative effects of habitat loss and forest fragmentation on plant-herbivore interactions, particularly due to the decrease of area of habitat (Benitez-Malvido et al. 1999, Arnold and Asquit 2001, Rao et al. 2001, Zenteno 2001, Fáveri et al. 2008, Ruiz-Guerra et al., *in press*) and edge effects (Wirth et al. 2008). Until now, the underlying mechanisms that govern changes in plant-herbivore interactions following extensive land use change are poorly explored, and usually through indirect evidence and deductive reasoning (but see Fortin and Mauffete 2001, Fáveri et al. 2008, Urbas 2007). Most studies attempting to uncover the mechanisms ruling changes in plant-herbivore interactions following land use change, have invoked disruptions of top-down controls (Kareiva 1987, Kruess and Tscharntke 1994, Terborgh et al 2001, Valladares et al. 2006). However, few studies have evaluated the possibility of changes in bottom-up controls with fragmentation, through differences in plant defensive attributes (e.g. secondary metabolites and toughness), and nutritional traits (e.g. water, carbon and nitrogen content), and their consequences on plant herbivory (Meyer et al. 2006, Repetto-Giavelli et al. 2007).

Stressful abiotic conditions on plants can be found at forest edges of fragments, where an increase in light, temperature and winds and a decrease in relative humidity have been found (Murcia 1995, Laurance et al. 1998). These changes in the microclimate may in turn enhance foliage nutritional value and hence the palatability of plants to herbivores, as has been postulated by the plant vigour hypothesis (Price 1991) and the plant stress hypothesis (White 1984). These hypotheses address plant-herbivore interactions in complementary ways, yet both predict positive correlations between plant vigour/stress with some metrics of herbivory (consumed tissue, survival and growth rates and abundance of herbivores) although focused on different guilds of herbivores, Price`s hypothesis pointed out that any animal that feeds on new growth (flush-feeders) while White hypothesis is focused in senescent-feeders (White 2009, also see Koricheva and Larson 1998).

Fortin and Mauffete (2001) reported that the performance of forest tent caterpillars (*Malacostroma disstria)* feeding at trees at edges of sugar maple (*Acer saccharum*) stands was better than those feeding from trees in the interior. Trees on the edge of stands produced foliage with higher concentrations on nitrogen and soluble sugars, and both nutrients are positively correlated with insect performance (Coley 1983). However, *Aristotelia chilensis,* an evergreen tree, showed a greater amount of foliar nitrogen in the continuous forest than in forest fragments, whereas the carbon content did not differ between forest fragments and continuous forest (Repetto-Giavelli et al. 2007). On the other hand, drought stress that modified the water content and the concentration of osmolites in the leaves of *Piper marginatum* has been shown to affect plant selection by the leaf-cutting ant *Atta colombica,* whereby stressed plants were more attractive to ants (Meyer et al. 2006).

In addition, changes in the physical environment can lead to changes in the accumulation of secondary metabolites that may serve as defensive compounds. For instance total phenolic compounds tend to be higher in plants grown in sunny conditions relative to those grown in shady environments, as a mechanism to minimize photodestructions of exposed tissues (Waterman and Mole 1994, Yamasaki and Kikuzawa 2003, Brenes-Arguedas and Coley 2005). Given this evidence and the fact that a previous study (Ruiz-Guerra et al. in press) showed that herbivory decreases in small fragments at Los Tuxtlas, here we examine the effects of forest fragmentation on defensive/nutritional traits of six woody plant species including plants of two plant regeneration modes, light-demanding and shade tolerant species. The specific questions we addressed were: i) are defensive/nutritional traits correlated with plant regeneration mode (i.e. shade-tolerant and light demanding species) and forest types (continuous forest and forest fragments), or are those traits species dependent? ii) Do differences in defensive/nutritive traits correlate with the acceptability of leaf tissue by a generalist herbivore (*Spodopera fugiperda*)? Our expectations were that: i) if bottom-up regulation of herbivory is affected by fragmentation, plants form fragments should exhibit less quality and palatability that those of continuous forest, and ii) since both groups of plants are present in continuous forest and fragments, and shade tolerant species are expected to be more defended than light demanding species and the latter are expected to have higher nutritional value than shade tolerant species (Coley 1980).

MATERIALS AND METHODS

Study site

This study was carried out at the Los Tuxtlas Research Station in Veracruz, Mexico and adjacent areas. The station is run by the National University of Mexico (UNAM) and is located between 18° 30´N - 18° 40´N, and 95° 03´W - 95° 10´W. Elevations range is from 0 to 1600 m above the see level, the average annual rainfall is ca. 4700 mm, and mean annual temperature is 25 ºC (Soto and Gama 1997). The predominant vegetation is tropical rain forest in the lowlands with variations along the elevation range, including cloud forest, elfin forest and some patches of coniferous forest (Dirzo et al. 1997). Currently the spatial configuration of the landscape at the study site consists of a large number of small to very small fragments (< 1.0 ha) around the extensive area of forest of the Research Station and its extension towards the San Martin Volcano, ca. 9 500 ha (Mendoza et al. 2005). However, tropical rain forest is restricted to the 700 ha of the Los Tuxtlas Research Station.

Selection of fragments and continuous forest sites

We compared two habitat types: small fragments and continuous forest (hereafter refereed to as forest types). We selected three small fragments (< 19 ha) of similar age of separation from the continuous forest (ca. 20 years), and three sites within the Research station. All sites are located within a restricted altitudinal range, 15-150 m., and have the same vegetation type, tropical rain forest (Aguirre and Dirzo 2008). All sites (forest fragments and sites in the continuous forest) were considered to be independent as they were located on independent hilltops and at distances > 1 km (see map in Ruiz-Guerra et al., *in press*).

Species selection

In the center of each site we established 0.1 ha permanent observation plots. In continuous forest the observation plots were located more than 500 m from forest edges. Each permanent observation plot consisted of ten 50 m x 2 m randomly selected transects. In each site we selected seven species from the top 15 species sorted by their importance values, and using the following criteria: 1) present in all six sites, 2) grouped in different families, and 3) representative of the two regeneration modes (light demanding and shade tolerant species). Details on the calculation of the importance value are presented in Ruiz-Guerra et al (in press). The species that met those criteria were: *Acalypha diversifolia* (Euphorbiaceae), *Hampea nutricia* (Malvaceae), *Myriocarpa longipes* (Urticaceae), *Siparuna andina* (Monimiaceae), *Pseudolmedia oxyphyllaria* (Moraceae) and *Rheedia edulis* (Guttiferae). The first four species are light-demanding while the other three are shade-tolerant. We restricted our measurements to saplings (> 50 cm height and diameter at breast height (1.3 m) < 1cm, given that we know the herbivory responses to habitat fragmentation in saplings of the same species (Ruiz-Guerra et al., in press).

Sampling design

To assess the effects of forest fragmentation on chemical defensive traits, we analyzed three variables of the leaves known to determine herbivory: total phenolic concentration, tannin absorbance and leaf toughness (see Coley and Barone 1996, Harbone 1997). In July 2004 we collected 10 randomly leaves from each of three to five saplings for the six species in each site (N = 167 individuals). To randomize leaves we counted all leaves on a given individual and called ten numbers from a random numbers table. In addition we collected two fully-expanded leaves (position three on the phyllotaxis) of six saplings corresponding to the six study species in each study site to estimate leaf toughness (N = 216 individuals). To estimate foliar nutritional traits, in January 2009 we collected one fully-expanded undamaged leaf (position one or two of phyllotaxis) from each of two individuals/species/site (N = 72 individuals).

Analytical procedures

To assess tannins and phenols, leaves were collected in liquid nitrogen, lyophilized, and ground to a fine powder. Concentrations of total phenolics and condensed tannins were estimated using the modified Prusian blue, and proanthocyanidin (N-Butanol) assays respectively (Waterman and Mole 1994). Total phenolic compounds were expressed as the percentage of dry mass per leaf. Condensed tannins were expressed as absorbance (in nanometers) on a per leaf basis, since we did not have a reliable standard curve needed for the transformation to mg/g. Leaf toughness was estimated as the force (g/mm^2) needed to break the leaf lamina using a penetrometer (Chantillon, Model 516, New York, USA). Five readings of leaf toughness were done for each leaf and then we averaged the values per leaf and individual.

To estimate water content we calculated the difference between fresh weight and dry weight (oven-dried at 60ºC for one week) relative to fresh weight of each individual leaf. For leaf carbon and nitrogen determination, the leaves were dried and ground to a fine powder. Percentage dry mass of nitrogen and carbon was estimated by combustion using a C/N analyzer (TruSpec CN, Leco Corporation 2002).

Acceptability assay

To assess the effects of forest type on plant tissue acceptability to herbivores we conducted an experiment whit the generalist army worm *Spodoptera fugiperda* and two plant species, *Acalypha diversifolia* and *Rheedia edulis,* with each as representative of light demanding and shade tolerant species respectively. In August 2004 we offered 4 cm^2 pieces of leaf lamina to single caged third instar *S. frugiperda* starved for 24 hours prior to the onset of the experiment. Leaves were collected either from plants grown in continuous forest and forest fragments and were offered in a paired design (one 4 cm^2 square of tissue from fragment and one from continuous forest, simultaneously) to the generalist herbivore. After 24 hours we estimated the leaf area eaten for each leaf type by each individual herbivore (N = 48, 12 replicates in each combination of forest type and species).

Statistical analyses

To analyze the effect of forest type (fragments vs. continuous forest), plant regeneration mode (light-demanding vs. shade-tolerant) and species identity on plant defensive and nutritional traits, we used mixed effects models. Fixed factors were defined as Forest type *x* Plant regeneration or Forest type *x* Species identity, whereas the random component was defined as the overall mean of the response variable (PC1) weighed by forest site. In addition, we modelled the variance across the factorial design to account for of the lack of homocedasticity. Prior the application of these analytical procedures we condensed the information for defensive and nutritional traits with principal component (PC) analyses based on the correlation matrix, and used the scores on PC-1 as response variable in the analytical models described above. Post hoc tests were t-test for differences between pairs of means based on model parameters, and we used a sequential Bonferroni approach to avoid type-I error effects. Data of the acceptability assay were analyzed with a generalised linear model with gamma error distribution and link function log to account for differences in variability across treatments. All statistical analysis were done in R 2.5.1 (R Development Core Team 2007) with the *lme* function (in the *nlme* library) to fit linear effects models (Pinheiro et al. 2007), and contrasts were done with the *estimable* function (in the *gmodels* library, Warnes 2007). Descriptive statistics are presented with mean ± standard error.

RESULTS

Plant defensive traits

Defensive traits of the six species analyzed were condensed by a principal component (PC) analysis (Fig. 1A). Scores on PC-1 accounted for 59% of the variability, and correlated strongly with the content of tannins ($r = 0.71$), and leaf-toughness ($r = 0.70$). Visual exploration of the scatter plot based on PC-1 and PC-2 revealed that the two shade tolerant species (*Pseudolmedia oxyphilaria* and *Rheedia edulis*) formed discrete clusters along PC-1 whereas light demanding species intermingled with the exception of *Acalypha diversifolia* which spread along PC-2. No effect of forest type on plant defensive characteristics was even insinuated by the multivariate analysis. Concordantly, the mixed effects model on scores of PC-1 showed no significant effects of forest type as main factor ($F = 0.05$; d.f. = 1, 4; $P = 0.843$) nor in interaction with plant regeneration mode ($F = 0.01$; d.f. = 1, 159; $P = 0.919$). However, plant regeneration mode was statistically significant ($F = 120.0$; d.f. = 1, 159; $P < 0.001$). Values of defensive traits correlated with PC-1 were higher in leaves of shade-tolerant species than in those of light demanding species (Fig. 1B): 3.7- and 2.7-fold of condensed tannins and leaf toughness, respectively (Table 1). In contrast light demanding species had 1.6 times more phenols than shade-tolerant species.

On the other hand, defensive traits varied significantly in terms of the interaction between species identity and forest type ($F = 2.83$; d.f. = 5, 151; $P = 0.018$; Fig. 1C); *P. oxyphilaria* was the only species in which forest type affected the estimates of defensive traits ($t = 2.24$; d.f. = 174; $P = 0.026$). Also, there were significant differences among species ($F = 252.68$; d.f. = 5, 151; $P < 0.001$) but not between forest types ($F < 0.01$; d.f. = 1, 4; $P = 0.973$). *Rheedia edulis* was statistically different from all other six species

(25.6 ≥ t ≤ 31.9; d.f. = 184; and P < 0.001 in all five comparison) and *P. oxyphilaria* was statistically different from all four light demanding species (2.99 ≥ t ≤ 5.97; d.f. = 184; and P < 0.001 in all four comparison). *Rheedia edulis* y *P. oxyphilaria* had higher values for defensive traits correlated with PC-1 than the other species (Table 1).

Foliar nutritional traits

PC-1 based on foliar nutritional traits accounted for 69% of the variability. Water (-0.56) and nitrogen (-0.45) contents were negatively correlated with the score in PC-1 whereas carbon content (0.40) and the ratio carbon/nitrogen (0.58) were positively correlated with PC-1. *Rheedia edulis*, *P. oxyphylaria*, *M. longipes* and *A. diversifolia* grouped into discrete clusters on PC-1 and PC-2, whereas *S. andina* and *H. nutricia* intermingled in the scatter plot (Fig. 2A). The analysis showed that scores on PC-1 were significantly different between light-demanding and shade-tolerant species (F = 247; d.f. = 1, 64; P < 0.001; Fig. 2B). Neither the interaction between forest type and plant regeneration mode (F = 1.32; d.f. = 1, 64; P = 0.255), nor forest type as main factor (F = 0.56, d.f. = 1, 4; P = 0.499) had significant effects on foliar nutritional traits (Fig. 2A). Light demanding species had on average 1.4 and 1.3 times more nitrogen and water content respectively than shade tolerant species whereas the latter group of plants had 1.3 and 1.8 times higher content of carbon and carbon/nitrogen ratio respectively than light demanding species (Table 1).

Species identity also showed significant effects (F = 129.48; d.f. = 5, 56, P < 0.001) but there was no effect of the interaction between species identity and forest site (F = 1.56; d.f. = 5, 56; P = 0.188) nor of forest site as main factor (F = 4.75; d.f. = 1, 4; P = 0.095) on foliar nutritional traits (Fig. 2C). Three groups of species were distinguished mainly on their carbon/nitrogen ratios: tolerant species (*R. edulis* and *P. oxyphyllaris*) with high carbon/nitrogen ratios, and two groups of light demanding species, *H. nutricia*, *S. andina* with the lowest carbon/nitrogen ratios, and *M. longipes, A. diversifolia* with lower carbon/nitrogen ratios compared with shade tolerant species but larger than those of *H. nutricia*, and *S. andina* (Table 1).

Acceptability assay

Overall, in the choice experiment, *Spodoptera fugiperda* consumed 6.3-times more leaf area of *Acalypha diversifolia* than of *Rheedia edulis* (F = 22.71; d.f. = 1, 47; P < 0.001; Fig. 3). Neither forest type (continuous forest/forest fragments, F = 0.05; d.f. = 1, 47; P = 0.821) nor the interaction the interaction forest type by species identity (F = 0.11; d.f. = 1, 47; P = 0.742) affected the amount of leaf area eaten by the generalist herbivore.

DISCUSSION

In general, we found that forest type does not affects plant defensive (i.e. phenolic compounds, condensed tannins and toughness) or nutritional (water content, carbon and nitrogen concentration) traits of most of the species we studied. However, *P. oxyphyllaria* had significantly higher values of anti-herbivore traits (leaf toughness and tannins) from continuous forest compared with plants from forest fragments. Altogether our results suggest that for most species defensive/nutritional traits are not altered by forest fragmentation, but rather these traits seem to be idiosyncratic to species. The most salient result was the consistent differences among plant regeneration modes. Shade-tolerant species were more defended than light demanding species. *Rheedia edulis* was the most defended species in this study. In contrast, *Acalypha diversifolia,* a light-demanding species, showed the lowest levels of defensive traits. In addition, light-demanding species had higher nitrogen and water content, whereas the shade-tolerant species had higher carbon content and carbon/nitrogen ratio. Concordantly, *Spodoptera fugiperda* consumed more tissue of the light demanding species *Acalypha diversifolia* than tissue of *Rheedia edulis,* the shade tolerant species, and there was no effect of the origin of the plant tissues in relation to forest type (continuous forest/forest fragments). In a previous study Ruiz-Guerra et al. (*in press*) found significant effects of forest type on the amount of leaf tissues consumed by herbivores in the same plant species and study site analyzed here. Our results suggest that changes in plant defensive traits (i.e., total phenolics, condensed tannins and toughness) and plant nutritional traits are unlikely an explanation for the observed changes in herbivory due to forest fragmentation observed by Ruiz-Guerra et al (2009). Despite the observed increase in plant defensive traits in continuous forest in *P. oxhypillaria* this does not seem to be related to the changes in herbivory detected in a previous study, in which herbivory levels were higher in the continuous forest than in forest fragments for this species.

Our findings are in agreement with other studies in tropical forests were no effects of fragmentation on plant defensive/nutritional traits has be found. For instance, Fáveri et al. (2008) found no difference in nitrogen, water, and total phenols content of leaves of *Henriettella caudata* from continuous forest and forest fragments. Likewise, Zenteno (2001) found that leaf toughness and acceptability by *Calyptocephala marginipennis* of the palm *Chamaedorea alternans* did not vary for plants from forest fragments and continuous forests in Los Tuxtlas. In contrast, Repetto-Giavelli et al. (2007) reported greater nitrogen concentration in the leaves of *Aristotelia chilensis* from continuous forest compared with plants from forest fragments.

All plants used in this study grew at the center of the study sites, therefore edge effects may be of little importance as to affect plant defensive/nutritional traits. Previous studies at Los Tuxtlas showed that micro-climatic variations due to edge effects are restricted to the first 50 meters (Ruiz-Guerra 2003). Further studies need to address this issue by considering plants growing under the influence of edge effects as well as plants from the center of forest fragments. Variation of secondary compounds within and among species has been reported in several studies (Agrell et al. 2000, Tharall et al. 2001, Brenes-Arguedas and Coley 2005) and has been attributed to a combination of environmental, developmental and genetic sources of variation (Lambers et al. 1998). We found evidence that the light-demanding species as a group were less defended than shade-tolerant species. *Rheedia edulis,* a shade tolerant species, presented the toughest leaves and the highest content of tannins, whereas *P. oxhypillaria,* another shade tolerant species had leaves as tough as some light demanding species but the content of tannins was higher. In addition, the two shade tolerant species presented the highest carbon/nitrogen ration of all six species; in other words, shade tolerant species were of low nutritional quality. This findings are consonant with the findings of Ruiz-Guerra et al. (*in press*) who found higher cumulative herbivory in light demanding species compared with shade tolerant species. In contrast, phenolic compunds concentration did covary consistently with plant regeneration mode. Light demanding species such as *A. diversifolia* and *H. nutricia* had higher or similar concentration, respectively, than *R. edulis*. Many functions have been attributed to phenolic compounds, including defense against microbes, viruses or competing plants, and also as signal compounds to attract pollinators or seed dispersing animals, and as UV filters (Rozema et al. 1997). Considering the widely range of functions of phenols, it is possible to argue that phenolic compunds are produced by the light-demanding species probably not for the primary purpose of herbivore deterrence, but they may play a major role in other functions (Kraus et al. 2003).

Finally, resistance and tolerance (i.e. the ability of plants to maintain fitness through growth and reproduction after sustaining herbivore damage) are two mechanisms that plants have evolved to reduce the negative impacts of herbivores (Rosenthal and Kotanen 1994). This study was limited to defensive characteristics (resistance), and we are aware of no study address the effects of forest fragmentation on plant-herbivore interactions from the perspective of plant tolerance, an aspect that urge investigation.

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Figure 1. Plant anti-herbivore traits of six woody species from Los Tuxtlas tropical rain forest. A) Principal components (PC) of plant defensive traits. B) Effects of plant regeneration mode on plant defensive traits (scores on PC-1). C) Interaction effects between forest type and species identity on plant defensive traits (scores on PC-1). Significant differences among species are indicated by different letters. Bar heights are mean values and error bars are standard errors.

Figure 2. Plant foliar nutritional traits of six woody species from Los Tuxtlas tropical rain forest. A) Principal components (PC) of plant nutritional traits. B) Effects of plant regeneration mode on foliar nutritional traits (scores on PC-1). C) Species identity effects on foliar nutritional traits (scores on PC-1). Significant differences among species are indicated by different letters. Bar heights are mean values and error bars are standard errors.

Figure 3. Acceptability assay. Leaf area eaten by the generalist herbivory *Spodoptera fugiperda* of the light demanding species *Acalypha diversifolia* and the shade tolerant species *Rheedia edulis* grown in two forest types, continuous forest and forest fragments.

Table 1. Mean (±standard error) of antiherbivore and foliar nutritional traits from seven species of the tropical rain forest at Los Tuxtlas, Ver. *Acalypha diversifolia* (Acdi), *Hampea nutricia* (Hanu), *Myriocarpa longipes* (Mylo), *Siparuna andina* (Sian), *Psedolmedia oxyphylaris* (Psox), and *Rheedia edulis* (Rheed).

	Light demanding species				Shade tolerant species	
Trait	Acdi	Hanu	Mylo	Sian	Psox	Rheed
Leaf toughness (g)	54.3 (± 5.2)	71.6 (± 6.2)	127.6 (± 6.7)	138.0 (± 6.2)	134.3 (± 9.5)	443.0 (± 6.5)
Condensed tannins (absorbance)	0.0545 (± 0.0044)	0.1887 (± 0.0105)	0.0663 (± 0.0048)	0.0573 (± 0.0041)	0.2969 (± 0.0261)	0.6928 (± 0.0276)
Phenols (mg/g)	0.0041 (± 0.0005)	0.0020 (± 0.0002)	0.0007 (± 0.0001)	0.0010 (± 0.0001)	0.0009 (± 0.0001)	0.0025 (± 0.0001)
Water content (%)	70.8 (± 1.8)	80.3 (± 2.5)	82.3 (± 1.6)	87.0 (± 0.3)	61.3 (± 0.9)	61.5 (± 0.5)
Carbon (%)	45.167 (± 1.050)	44.942 (± 0.313)	38.833 (± 0.170)	43.358 (± 0.104)	64.858 (± 0.255)	47.442 (± 0.067)
Nitrogen (%)	2.703 (± 0.064)	3.186 (± 0.089)	2.261 (± 0.044)	3.124 (± 0.088)	2.531 (± 0.053)	1.579 (± 0.023)
C/N	16.818 (± 0.578)	14.213 (± 0.345)	17.250 (± 0.339)	13.992 (± 0.356)	25.763 (± 0.523)	30.082 (± 0.421)

Figure 1

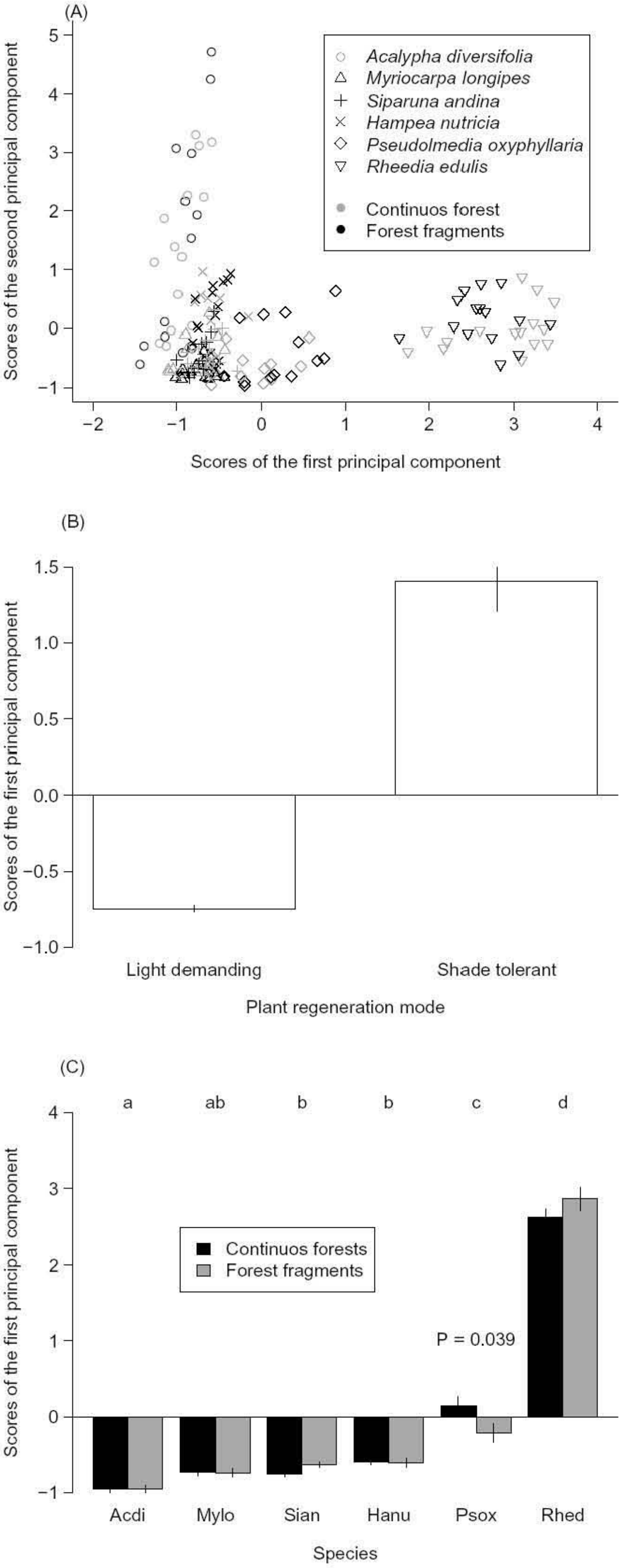


Figure 2

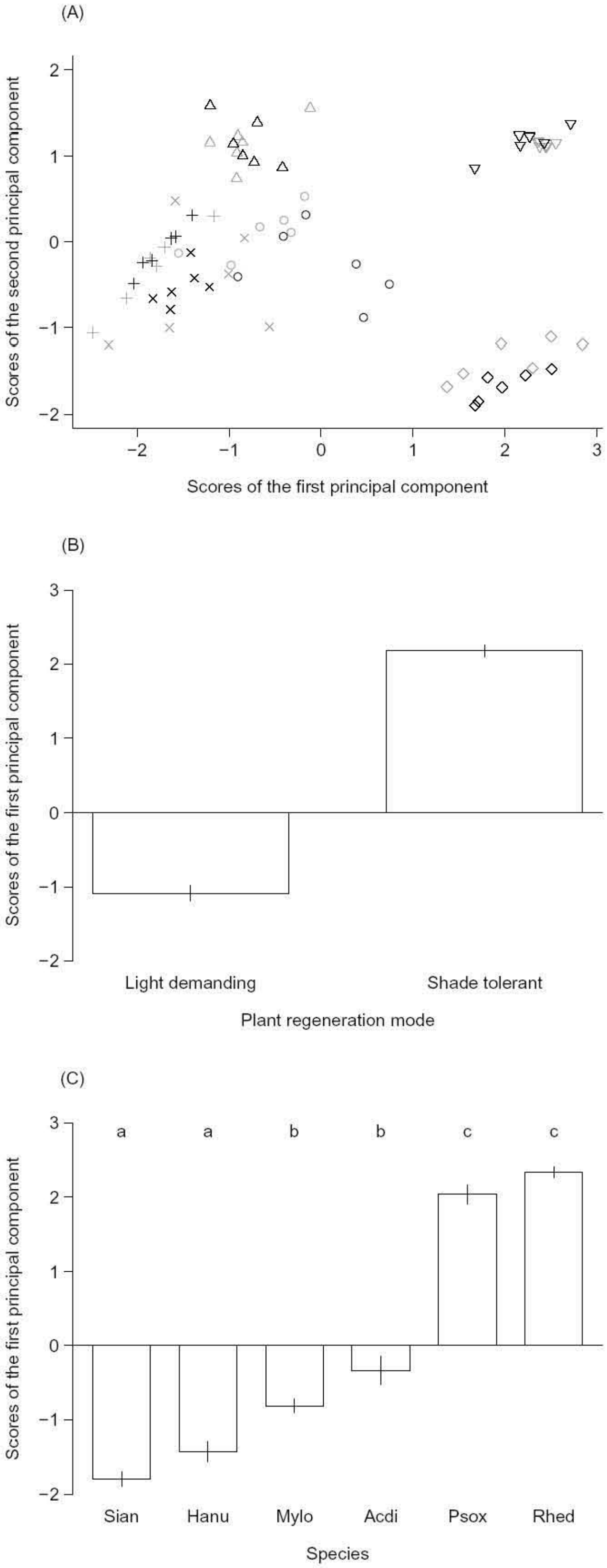
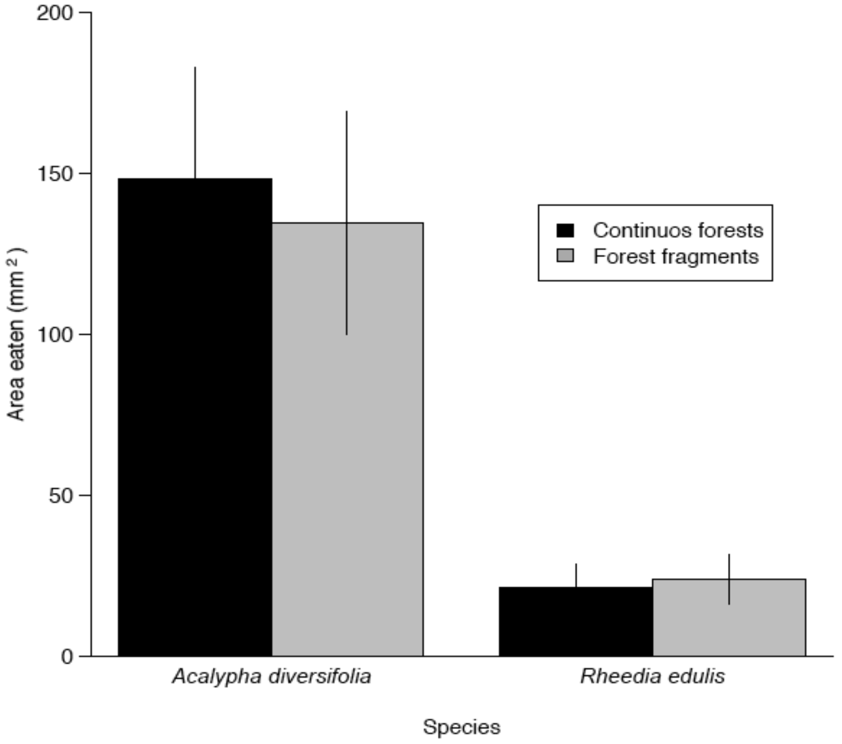

(A)
Scores of the second principal component
2
1
0
−1
−2
−2
−1
0
1
2
3
Scores of the first principal component
(B)
Scores of the first principal component
3
2
1
0
−1
−2
Light demanding
Shade tolerant
Plant regeneration mode
(C)
Scores of the first principal component
3
2
1
0
−1
−2
a
a
b
b
c
c
Sian
Hanu
Mylo
Acdi
Psox
Rhed
Species

Figure 3


200
150
100
50
0
Area eaten (mm²)
Continuos forests
Forest fragments
Acalypha diversifolia
Rheedia edulis
Species

Capítulo 4

Consecuencias de la fragmentación de la selva tropical sobre las comunidades de aves y la depredación de insectos.

LRH: Ruiz-Guerra, Renton, and Dirzo.

RRH: Bird Communities and Insect Predation in Forest Fragments

Consequences of Fragmentation of Tropical Rain Forest for Avian Communities and Their Role in Predation of Herbivorous Insects

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ABSTRACT

The consequences of habitat alteration on the role of understory insectivorous birds as predators of herbivorous insects in tropical forests are poorly understood. In order to examine if fragmentation may affect the top-down controls of herbivory, we compared the number of species, individuals, and the community structure of insectivorous birds between fragments and continuous tropical rain forest in Mexico. We also registered insect herbivore abundances and conducted a larvae predation experiment to evaluate the potential role of insectivorous birds as predators of herbivorous insects. We recorded 63 bird species in 22 families, 43 percent of which were insectivorous birds. The number of species and individuals of insectivorous birds did not differ between fragmented and continuous forest. The diversity of both the entire avian community and the community of insectivorous birds was higher in continuous forest. We found low similarity of insectivorous birds, with forest fragments presenting heavily dominated avian insectivore communities. Abundance of Lepidoptera was higher in continuous forest during the dry season, though abundance of Orthoptera or Coleoptera did not differ. Predation rates on artificial caterpillars were higher in forest fragments than in continuous forest during the dry season, and there was a significant negative correlation between predation levels on artificial caterpillars and Lepidoptera abundance. Hence, the decline in Lepidoptera abundance in forest fragments during the dry season may be due to predation by avian insectivores. We suggest that habitat fragmentation could disrupt predation rates on Lepidoptera and that this might drive changes in herbivory patterns in fragmented forests.

RESUMEN

Las consecuencias de la perturbación del hábitat sobre el papel de las aves insectívoras del sotobosque como depredadoras de insectos herbívoros han sido poco exploradas en sistemas tropicales. Para determinar si la fragmentación afecta los enemigos naturales de los herbívoros, comparamos el número de especies, individuos y la estructura de la comunidad de aves insectívoras entre fragmentos y bosque continuo en una selva tropical de México. Cuantificamos la abundancia de insectos y realizamos un experimento de depredación de larvas para evaluar el papel de los insectívoros como depredadores de insectos herbívoros. Registramos 63 especies de aves pertenecientes a 22 familias, 43 por ciento insectívoras. El número de especies e individuos de aves insectívoras no difirió entre fragmentos y bosque continuo. La diversidad de especies a nivel comunidad y de las insectívoras fue mayor en la selva continua. La similitud de aves insectívoras fue baja entre bosque continuo y fragmentos. La abundancia de lepidópteros fue mayor en el bosque continuo durante la estación seca. No encontramos diferencias en la abundancia de Ortópteros y Coleópteros. La depredación de larvas artificiales fue mayor en los fragmentos en secas. Encontramos una correlación negativa entre las tasas de depredación en larvas artificiales y la abundancia de Lepidópteros. La disminución en la abundancia de lepidópteros en fragmentos en las secas se puede deber a los altos niveles de depredación. Sugerimos que la fragmentación del hábitat puede alterar la depredación de lepidópteros, lo cual podría provocar cambios en los patrones de herbivoría en un bosque tropical fragmentado.

Keywords: avian species diversity; caterpillar predation; habitat fragmentation; Lepidoptera abundance; Los Tuxtlas; understory insectivorous birds.

THE RAPID EXPANSION OF CATTLE RANCHING AND AGRICULTURE OVER THE LAST FEW DECADES has created a highly fragmented landscape in the tropics (Achard *et al.* 2002, Dirzo & Raven 2003). As a consequence of this land-use change tropical species of plants and animals are becoming extinct, or their populations are in serious decline, with an associated loss of their functional role in natural ecosystems (Didham *et al.* 1996, Komonen *et al.* 2000, Koh *et al.* 2004, Sekercioglu *et al.* 2004, González-Gómez *et al.* 2006, Pimm *et al.* 2006). In particular, the loss of higher trophic groups from ecosystems can potentially affect the community dynamics of lower trophic groups such as herbivores and plants. For instance, insectivorous birds play an important role in regulating the abundance of herbivorous insects, and thus in an indirect way may influence their host plants (Van Bael *et al.* 2003, Van Bael and Brawn 2005, Boege and Marquis 2006).

Previous studies emphasize that habitat fragmentation may be particularly critical for forest understory birds given their high habitat specificity, near-ground nesting habits, low rates of dispersal abilities, their high dietary and foraging specialization and the combined effects of edge and gap-cross avoidance (Sherry 1984, Rosenberg 1993, Stouffer & Bierregaard 1995, Marra and Remsen 1997, Restrepo & Gomez 1998, Sekercioğlu *et al.* 2002, Laurance *et al.* 2004, Lees & Peres in press). Many understory species may avoid crossing even small forest gaps of 4-70 m (Lees & Peres in press), remaining confined to the forest interior. Given that the number of herbivorous insects depends on the presence of their predators (Hairston *et al.* 1960), a decrease in abundance and/or diversity of their natural enemies can trigger trophic cascading effects, releasing herbivorous populations, increasing their number and thus herbivory levels (González-Gómez *et al.* 2006, Valladares *et al.* 2006).

In the tropical rain forest of Los Tuxtlas, Mexico, human impacts of habitat fragmentation and hunting have caused the extinction of the King Vulture (*Sarcoramphus papa*), Harpy Eagle (*Harpia harpyja*), and Scarlet Macaw (*Ara macao*), while another 85 avian species are considered threatened or endangered, representing 16 percent of the total bird species registered for the region (Winker 1997). Of these threatened avian species, 77 percent include insects as part of their diet. Hence, the potential loss of these species, or a reduction in their populations, may impact their functional role as insect predators.

The consequences of habitat fragmentation on insectivorous birds remains poorly understood, and to date few studies have focused on the effects of habitat fragmentation on predation rates of insect herbivores by birds (Sekercioglu *et al.* 2002, González-Gómez *et al.* 2006). In the present study, we compared the number of species and individuals of insectivorous birds, as well as the diversity, similarity and dominance of the insectivorous bird community, between forest fragments and continuous forest. In addition, we evaluate insect herbivore abundance and the relative predation rates by birds on herbivorous insects in fragmented and continuous forest. The specific questions we aimed to answer were: (1) do the number of species, individuals, or the community structure of insectivorous birds vary between forest fragments and continuous forest? (2) to what extent do changes in the insectivorous bird community affect herbivore abundance? and (3) do larval predation rates by birds vary between fragmented and continuous forest? In addressing these questions and based on the negative impacts of forest fragmentation on insectivorous populations previously described, we hypothesized that the number of insectivorous birds would be lower in forest fragments than in continuous forest. Therefore we expected a decrease in predation levels and an increase in abundance of herbivorous insects in forest fragments.

METHODS

STUDY SITE AND SELECTION OF FOREST FRAGMENTS.—The study was carried out in the tropical rain forest of Los Tuxtlas, located in the state of Veracruz, México. The region’s topography is complex, with elevation changes from sea level to 1,600 m asl. The mean annual temperature is 25ºC, with annual rainfall of 4,500 mm/year. The area experiences a dry season from March to May and a rainy season from June to February (Soto & Gama 1997). The predominant vegetation is tropical rain forest in the lowlands, with variations along the elevation range, including cloud forest and mixed forest at higher elevations (Ibarra-Manrriquez *et al.* 1997). The Los Tuxtlas region has one of the richest avifaunas of the northern Neotropics, composed of 561 species, 223 of which are Nearctic-Neotropical migrants (Winker 1997). Over the last decades, the landscape originally occupied by tropical rain forest has been converted to pasture lands, agricultural crops, and a large number of small fragments (< 10 ha) with only a few remaining areas of continuous forest (Dirzo & Garcia 1992). Most continuous forest occurs in the Los Tuxtlas Biological Research Station (18º34´- 18º36´N, 95º04´- 95º09´W), ca. 640 ha and its extension to the San Martin Volcano, encompassing an area of *ca.* 9,500 ha (Mendoza *et al.* 2005). The dramatic reduction of natural forest in the region is causing the disappearance of avian habitats and a reduction in the size of viable populations for many bird species (Estrada & Coates-Estrada 2005).

In this study we compared forest fragments and continuous forest. Based on direct exploration of the study area, and using aerial photographs as described by Aguirre and Dirzo (2008), we selected three fragments (0.3, 3 and 19 ha), characterized by their uniform vegetation of tropical rain forest, age of separation from the continuous forest (~20 yr), and a restricted elevation (15-150 m asl). The fragments were separated by distances of >1 km and surrounded by pastures. The continuous forest was represented by three independent sites located within Los Tuxtlas Research Station (640 ha). This site was considered as continuous forest due that the Los Tuxtlas, Research Station is connected, through an elevation gradient, with the San Martin Volcano, encompassing a total area of ca. 9, 500 ha. As in the case of the small fragment sites, the three continuous forest sites were considered as independent, since they were established at distances >1 km.

AVIAN SAMPLING PROTOCOL.—We applied two methodological approaches of mist-nets and point counts to evaluate bird assemblages (Blake & Loiselle 2001). Mist netting is a technique that can be readily standardized, is relatively free from observer biases and it is important for sampling species that are difficult to see and seldom vocalize (Ralph *et al.*1993). However, large species and species that seldom fly are under-represented by mist netting, as are birds that rarely descend to the understory (Karr 1981), thus excluding most canopy birds (Karr 1976, Rappole *et al.* 1998) and therefore, we also applied point counts. The combination of the two techniques was aimed at ensuring an effective evaluation of the avian community. We conducted bird counts from October to November after the arrival of migratory birds, as tropical migrants constitute 40 percent of the Los Tuxtlas avifauna (Winker 1997).

Mist-nets.—In October-November 2004, we mist-netted in the three forest fragments and in three sites of the continuous forest, with 12 x 2 m, 36 mm mesh nets. To avoid under- or over-sampling in areas of forest of differing sizes, we adjusted the number of mist-nets proportional to the fragment size (Bierregaard 1990, Stouffer & Bierregaard 1995). Hence, we set-up one mist-net in the 0.3 ha fragment, four mist-nets in the 3 ha fragment, eight mist-nets in the 19 ha fragment, and 16 mist-nets in each of the continuous forest sample sites. Mist-nets were opened from 0600 to 1400 h, and each site was sampled during three consecutive days. Birds captured were identified to species, marked with non- toxic paint, and released. Data included here are based on 17,568 net hours: 13,824 in continuous forest, and 3,744 in forest fragments.

Bird counts.— We used the fixed-radius point count procedure (Ralph & Scott 1981, Bibby *et al.* 2000) for bird surveys, recording all birds detected by sight and hear within a 25 m radius of the point-count centre, in November 2004. Each count lasted 5 min and at least 30 min elapsed between point counts. We sampled 8 points separated by 100 m intervals at each site, censuses were conducted during eight days for each site, giving a total of 24 points in each of fragmented and continuous forest. We conducted all bird counts between 0600 and 1300 h and avoided sampling on days of heavy rain. We identified birds to species level, and assigned species to foraging guilds according to Coates-Estrada and Estrada (1985).

INSECT HERBIVORE SURVEYS.— We established five transects of 100 m x 2 m at each site to record insect herbivore abundance. Transects were located at the centre of each site to avoid edge effects. We selected 15 points along each transect using random numbers. At each of these points we counted the number of herbivorous insects on all woody saplings with a height of 50 - 130 cm, rooted on the transect line, for a period of 3 min at each plant. Insect surveys were conducted in both the dry (April 2005) and rainy (November 2006) seasons, and individuals were grouped at order level (Orthoptera, Coleoptera, Lepidoptera).

LARVAL PREDATION RATES.—We conducted a larval predation experiment using plasticine caterpillars, as these have been used successfully to estimate predation levels in tropical systems (Loiselle & Farji-Brener 2002, Pin & Menge 2006, Fáveri *et al.* 2008). The caterpillar predation experiment was conducted in both the rainy (November 2006) and dry season (April 2005) at the same time as the insect herbivore surveys. We used non-toxic green plasticine for the caterpillar bodies and brown plasticine for the heads, constructing each caterpillar to a standard size of 3.5 cm long and 4.08 mm diameter. Plasticine caterpillars were then placed on leaves and tied up to the selected plants with a plastic thread. This insured that in those cases of predation that led to the caterpillars fall off the leaves, we were still able to record predation. We placed a total of 60 caterpillars at each site, with three caterpillars on the leaves of each plant, in 20 randomly selected woody plants (50 to 130 cm height). The plants were chose in the centre of the sites using random numbers. Predation attack by birds was registered by the peck marks left on plasticine caterpillars, and we calculated the average frequency of caterpillar attack for each plant.

STATISTICAL ANALYSES.—*Avian community*.-We analyzed separately the data obtained on the avian community from mist-nets and point-counts. For mist-nets, we estimated abundance using capture rate ratios (total captures of all nests in each site/net hours), and species number was estimated as number of species per net hours. For point counts, we estimated abundance as individuals per site, averaging the number of birds detected in each point count. Species richness was estimated averaging the number of species recorded at each site. We perform a comparison between both communities through statistical analysis of the potential biodiversity differences. We estimated Shannon index ($H' = - \sum p_i \ln p_i$, where p_i is the relative abundance of the *ith* species compared to all species identified in a sample). The statistical significance was assessed by bootstrap and permutation tests. The Shannon index of diversity is widely used to characterize species diversity in a community, and considers the number of species and the evenness of their abundance. Hence, the index may be increased either by the presence of additional unique species, or by greater evenness in the number of individuals representing each species. Then we conducted a multiresponse permutation procedure (MRPP) which is a class of non-parametric permutation method for distinguish possible differences among two o more groups in one or more dimensions. The analysis was preformed on squared root transformed abundance of birds for both methods, using Sorensen option for distance measure. The analyses were performed using PC-ORD (Ver 4.41) software.

Insectivorous bird community similarity and dominance.—Given that we were mainly interested in insectivorous birds, we estimated the proportion of insectivorous species shared between fragmented and continuous forest. We used the Sorensen quantitative index of similarity $C_N = (2jN)/ N_a + N_b$, where $2jN$ = the sum of the lower of the two abundances for species found in both sites; N_a = total number of individuals in site A; and N_b = total number of individuals in the site B (Magurran 2004). Values range from 0 when two samples have no species in common, to 1 when two samples are identical (Magurran 2004).

To visualize the relative abundance of insectivorous species in fragmented and continuous forest we constructed rank/abundance plots (Magurran 2004). We plotted the relative abundance of each species against the species rank, ordered from the most abundant to the least abundant species (Magurran 2004). We used a Kolmogorov-Smirnov two sample test to compare both dominance plots (Sokal & Rohlf 1995).

Insect herbivore abundance and predation rates.—We compared insect herbivore abundance and larval predation rates between fragmented and continuous forest in both the dry and rainy seasons, using a repeated one-way ANOVA. We also applied Pearson correlation analysis to determine whether predation levels at each site were correlated with Lepidoptera abundance.

The analyses were performed using JMP (Ver 6) software, and variables were tested for normality and homogeneity of variances prior to statistical analyses. Descriptive statistics are presented with mean ± standard error, and we applied the $P < 0.05$ significance level for statistical analyses.

RESULTS

AVIAN COMMUNITY.—We recorded a total of 463 individuals, comprising 63 bird species, and 22 families. These species represent 11 percent of the total avifauna reported for Los Tuxtlas. Thirty four of the 63 species were restricted to continuous forest, ten were found only in forest fragments, and nineteen in both. Insectivorous birds accounted with 27 species, while those that include insects plus at least plant based material and/or vertebrates in their diet comprise 20 species. The families with the greatest number of species were Emberizidae (13) and Tyrannidae (6). Three species:

the White-breasted Wood-Wren (*Henicorhina leucosticta*), Hooded Warbler (*Wilsonia citrina*) and the Red-throated Ant-tanager (*Habia fuscicauda*) accounted for 35 percent of all individuals.

Mist-nets.—We captured 160 birds in the mist-nets, 42 (26%) in forest fragments and 118 (74%) in continuous forest. These comprised 39 bird species from 15 families, and the most abundant bird family was Emberizidae (45 individuals). Insectivorous birds represented 53 percent of the mist-net captures (26 individuals in forest fragments and 59 individuals in continuous forest), comprising 23 species from 9 families (see Apendix). Avian diversity determined from mist-net captures differed significantly between fragmented and continuous forest for both the entire avian community, and the community of insectivorous birds (Table 1). The Shannon index of diversity was higher in continuous forest than in forest fragments whit nets and bird counts (1.2 times and 1.1 times respectively) (Table 1). However, we found no significant difference in insectivorous bird communities between fragmented and continuous captured in mist-nets (T = -0.86, *P* = 0.18).

Bird counts.—We recorded 303 birds in point-counts, representing 44 species and 20 families. Of all individuals counted, 186 of 303 individuals (61%) were recorded in continuous forest and 117 (39%) individuals in forest fragments. The most abundant bird family was Emberizidae (86 individuals). Of all birds recorded in point-counts, 140 were insectivorous (80 individuals in continuous forest and 60 individuals in forest fragments), representing 15 species and 6 families (see Apendix). Avian diversity from point-counts also varied between fragmented and continuous forest for both the entire avian community and the community of insectivorous birds, being higher in continuous forest than in forest fragments (Table 1). Further, the MRPP analysis showed significantly differences in insectivorous birds communities between fragments and continuous forest (T = 2.31, $P = 0.02$).

Avian community similarity and dominance.—There was low similarity in insectivorous bird species between fragmented and continuous forest (Sorensen value = 0.46). We found that 19 of the 63 species were shared across forest types, 34 were exclusive to continuous forest and 10 were present only in the forest fragments. The dominant avian species in both fragmented and continuous forest was the White-breasted Wood-Wren (Fig. 1). However, the pattern of species abundance-dominance in continuous forest was significantly different from that in forest fragments ($D_{0.05} = 0.16$, $P < 0.05$). In general, most of the species found in the continuous forest were absent from the forest fragment, while those species which occurred in both fragmented and continuous forest varied in their abundance distribution. The Red-throated Ant-tanager was the second most dominant species in continuous forest, though this species had low rank-abundance in forest fragments (Fig. 1). By comparison, forest fragments were more heavily dominated by three species: White-breasted Wood-Wren, Hooded Warbler, and Band-backed Wren, (Fig. 1).

INSECT HERBIVORE ABUNDANCE.—We counted a total of 604 herbivorous insects. Orthoptera were the most common herbivores, comprising about 52 percent of the individuals found, while Coleoptera and Lepidoptera accounted for 36 percent and 12 percent respectively. Forty eight percent of the herbivores counted were recorded in continuous forest, and 52 percent in forest fragments. Considering the three main orders of invertebrates, we found no significant differences in herbivore abundance between fragmented and continuous forest ($F_{1,4} = 0.12$, $P = 0.74$) or between seasons ($F_{1,4} = 3.37$, $P = 0.12$). There was a trend for higher insect abundance in forest fragments (78.3 ± 12.9 individuals) than in the continuous forest (44.3 ± 12.9 individuals) during the rainy season, while insect abundance in the dry season did not differ between continuous and fragmented forest. However, the interaction term of forest fragmentation x season was not significant ($F_{1,4} = 6.49$, $P = 0.06$).

When we separated data by insect orders, we found that overall Lepidoptera abundance did not differ between forest fragments (4.6 ± 2.1 individuals) and continuous forest (6.8 ± 2.2 individuals). Nevertheless, there was a significant interaction term in which Lepidoptera abundance differed between fragmented and continuous forest depending on the season ($F_{1,4} = 14.4$, $P = 0.012$). Lepidoptera abundance was higher in fragmented forests during the rainy season, declining in the dry season (Fig. 2), while in continuous forest Lepidoptera abundance was highest in the dry season and differed significantly from Lepidoptera abundance in fragmented forest (Fig. 2). By comparison, neither Coleoptera nor Orthoptera abundance differed significantly between fragmented and continuous forest (Coleoptera: $F_{1,4} = 2.74$, $P = 0.17$; Orthoptera: $F_{1,4} = 2.27$, $P = 0.20$), or between seasons (Coleoptera: $F_{1,4} = 0.13$, $P = 0.72$; Orthoptera: $F_{1,4} = 2.46$, $P = 0.19$). The interaction term was not significant in both cases (Coleoptera: $F_{1,4} = 0.08$, $P = 0.78$; Orthoptera: $F_{1,4} = 2.37$, $P = 0.19$).

LARVAL PREDATION RATES.—Predation levels on artificial caterpillars ranged from 15 to 32 percent of caterpillars attacked. Predation levels between fragmented and continuous forest and though season were not statistically significant ($F_{1,4} = 3.81$; $P = 0.12$; $F_{1,4} = 0.51$, $P = 0.51$). Nevertheless, the interaction of forest fragmentation x season was highly significant ($F_{1,4} = 27.9$, $P = 0.006$), with the frequency of caterpillar predation being 2.2 times higher in fragmented forest (32 ± 0.02%) than continuous forest (15 ± 0.02%) in the dry season (Fig. 3). In addition, there was a significant negative correlation ($r^2 = -0.69$, $P = 0.01$) between predation levels on artificial caterpillars and Lepidoptera abundance (Fig. 4).

DISCUSSION

Our results demonstrate that the diversity of both the entire avian community and the community of insectivorous birds was significantly higher in continuous forest than in forest fragments. This suggests that habitat fragmentation has negative impacts on avian communities through combined effects on the number of species and evenness of the communities. We also found a low similarity of insectivorous bird species between fragmented and continuous forest, suggesting that forest fragmentation creates changes in the species composition of insectivorous communities. Hence, although we found no significant difference in the number of species and individuals of insectivorous birds between fragmented and continuous forest, the variation in diversity, similarity, and dominance of the insectivorous bird community suggests that habitat fragmentation may alter avian community structure. In effect, communities of insectivorous birds in forest fragments were dominated by the White-breasted Wood-Wren, Hooded Warbler, and Band-backed Wren, all resident insectivorous species, common in the mid to low understory.

With regard to insect herbivores, Lepidoptera abundance was significantly higher in continuous forest than fragmented forest during the dry season, while predation levels on artificial caterpillars were significantly higher in forest fragments in the dry season. We also found a strong negative relationship between predation levels and Lepidoptera abundance. Thus high larval predation by insectivorous birds may be an important factor of reduced Lepidoptera abundance in forest fragments during the dry season.

BIRDS AND ARTIFICIAL CATERPILLAR PREDATION.—The reduction of avian diversity in forest fragments corresponds with several studies that have reported reduced bird species diversity in forest fragments (Stouffer & Bierregaard 1995, Sekercioglu *et al.* 2002, but see (Vergara & Simonetti 2004). In Los Tuxtlas, low species diversity has been correlated with high rates of nest predation in forest edges, and with habitat isolation (Estrada *et al.* 2002). We further demonstrated that this reduction in diversity specifically impacts the community of insectivorous birds in forest fragments. Hence, though the overall number of species or individuals of insectivorous birds may remain relatively similar between fragmented and continuous forest, there may still be significant effects on the biodiversity of avian communities. This was confirmed by the low similarity between fragmented and continuous forest in composition and dominance of the insectivorous bird community. The White-breasted Wood-Wren was the most dominant insectivorous bird species in both fragmented and continuous forest, which may be explained by its ability to use a wide variety of sites, such as the forest interior and more open areas on the forest edge (Winker 1997). Of the three most dominant avian insectivores in forest fragments, is know that Band-backed Wren is an edge species and occurs in disturbed habitats as well as Hooded Warbler. These changes in the composition and dominance of insectivorous bird communities in forest fragments could produce changes in insect predation levels.

In this context, we registered greater predation levels on artificial caterpillars in forest fragments than in continuous forest, and a decrease in Lepidoptera larvae in forest fragments, suggesting a top-down control. However, the artificial predation experiment may not reflect natural predation levels and therefore results should be viewed with caution. Previous studies have detected higher larval predation in small fragments than in continuous forest (Gónzalez-Gómez *et al.* 2006, but see Sekercioglu *et al.* 2002, Pin Koh & Menge 2006, and Fáveri *et al*. 2008). One explanation of the higher larval predation rates in forest fragments may be that caterpillars are more exposed to predators due to a reduction in the structural complexity of vegetation and a reduction in canopy cover in these sites (Aguirre 2008). Alternatively, the highly fragmented nature of the landscape in Los Tuxtlas may mean that insectivorous birds need to forage in a variety of alternative habitats in order to obtain sufficient food resources, resulting in greater exploitation of forest fragments. This supported to some extent by the fact that several insectivorous bird species recorded in our study have been observed in live fences and coffee groves (Estrada & Coates-Estrada 2005), as well as forest remnants (Graham & Blake 2001), which they use as stepping-stones to reach other habitats, or as temporal perching and foraging sites before returning to the continuous forest (Estrada *et al.* 2000).

INSECT HERBIVORES.—Of the three orders of insects recorded, only Lepidoptera populations were negatively affected by forest fragmentation, as found in other studies (Krauss *et al.* 2003). This may be related to differences in dietary requirements, and habitat requirements of the larvae (Thomas *et al.* 2002, Haynes *et al.* 2007). The abundance of herbivorous insects may be higher in areas where light-demanding plant species are abundant, such as in fragment edges or forest gaps (Brown and Southwood 1983). This may lead to increased abundance of generalist insect species given that light-demanding plants allocate fewer resources to herbivore defence, and therefore represent better food sources for generalist herbivores than the shade-tolerant plant species (Coley *et al.* 1985). Specialist insects such as Lepidoptera are more restricted to their particular host plants; therefore they may be confined to the interior of forest fragments or conserved sites, where they feed on shade-tolerant plant species (Rauguso & Llorente-Bousquets 1990, Rosenthal & Kotanen 1994, Barbosa *et al.* 2005, Novotny & Basset 2005). In this respect, overall Lepidoptera abundance was slightly higher in continuous forest, though this was not significantly different from Lepidoptera abundance in forest fragments.

Nevertheless, Lepidoptera abundance was significantly higher in continuous forest than in forest fragments particularly in the dry season. The decrease in Lepidoptera abundance in forest fragments during the dry season could be explained by microclimate changes, such as an increase in insect desiccation (Ledergerber *et al.* 2002), or by a decrease in their host plants (Groom 2001, Zenteno 2001, Arnold & Asquith 2002). In addition, it has been reported that dispersal rates of butterflies decrease with increasing habitat fragmentation (Mennechez *et al.* 2003). By contrast, we found no significant differences in Coleoptera and Orthoptera abundance between continuous forest and forest fragments. Other studies have reported that the abundances of these orders increase at edges or in disturbed sites whereas Lepidoptera was restricted to the interior (Barbosa *et al.* 2005).

In summary the reduced diversity of the avian community, and in particular the insectivorous bird community in forest fragments, suggests that forest fragmentation has complex effects on avian biodiversity. Forest fragments may be used as temporal foraging sites by a variety of resident and migratory bird species, particularly in a heavily fragmented landscape. However, although forest fragments contribute to the maintenance of avian species in the region they may not present appropriate structural and functional sites for the survival, reproduction, and maintenance of many avian species (Estrada *et al.* 2002). In particular, the differing composition of insectivorous bird communities between continuous and fragmented forest may disrupt ecological processes such as predation rates on Lepidoptera, which are one of the main herbivores in the tropical moist forest of Los Tuxtlas (de la Cruz & Dirzo 1987). This alteration may be translated to lower trophic levels, such as plants, and we have evidence that herbivory damage by insects is lower in forest fragments than in continuous forest in the same study site (Ruiz-Guerra *et al.* in press).

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TABLE 1. *Shannon index of diversity (H') determined from mist-net captures and point-counts for both the entire avian community and the community of insectivorous birds, in fragmented and continuous tropical moist forest in Los Tuxtlas, Mexico.*

Sampling protocol	Forest fragments (*H*´)	Continuous forest (*H*´)	Bootstrap *P*-value	Permutation *P*-value
Mist-net captures				
Avian community	2.56	3.08	0.036	0.094
Insectivorous bird community	1.82	2.57	0.001	0.003
Point-counts				
Avian community	2.41	2.88	0.001	0.004
Insectivorous bird community	1.20	1.68	0.009	0.027

FIGURE LEGENDS

FIGURE 1. Rank/abundance plots for insectivorous birds sampled in fragmented and continuous forest of Los Tuxtlas, Mexico, ordered from the most abundant to the least abundant species. Sp 1 White-breasted Wood-Wren (*Henicorhina leucosticta*), Sp 2 Red-throated Ant-tanager (*Habia fuscicauda*), Sp 3 Hooded Warbler (*Wilsonia citrina*), Sp 4 Wood Thrush (*Hylocichla mustelina*), Sp 5 Brown Jay (*Cyanocorax morio*) and Sp 6 Band-backed Wren (*Campylorhynchus zonatus*).

FIGURE 2. Lepidoptera abundance (mean individuals ± SE) in the dry and rainy season in forest fragments and continuous forest of Los Tuxtlas, Mexico. Different letters indicate significant differences.

FIGURE 3. Mean percent predation (± SE) on artificial caterpillars in fragmented and continuous forest during the dry and rainy season in Los Tuxtlas, Mexico.

FIGURE 4. Negative correlation of proportional predation on artificial caterpillars with Lepidoptera abundance in the tropical moist forest of Los Tuxtlas, Mexico. Points represent mean values per site in both seasons.

Figure 1

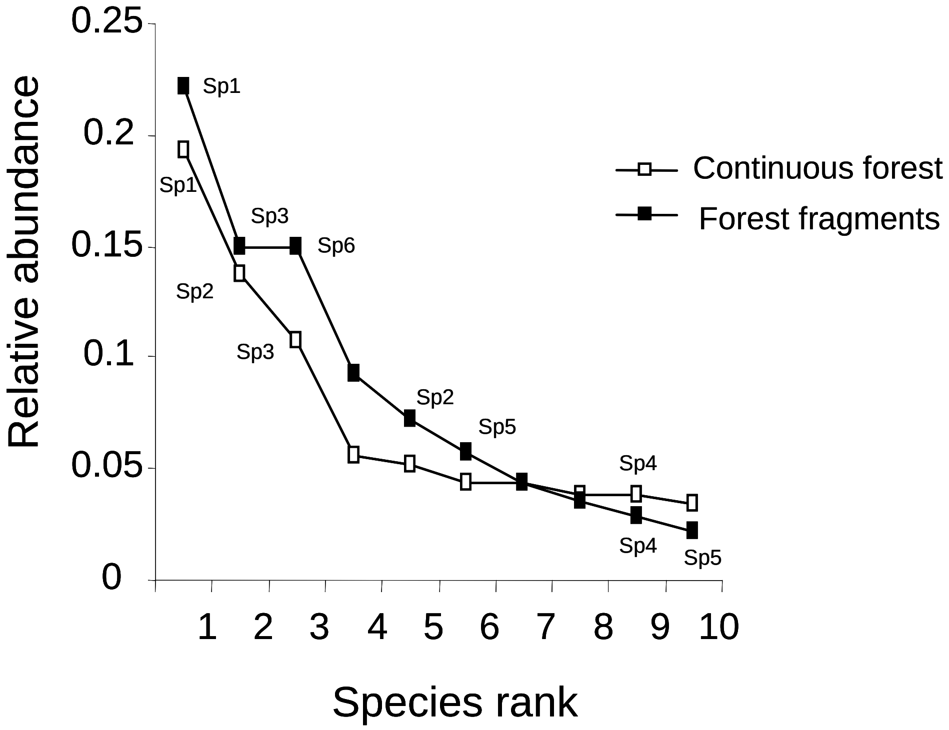

0.25
0.2
0.15
0.1
0.05
0
Relative abundance
1
2
3
4
5
6
7
8
9
10
Species rank
Continuous forest
Forest fragments
Sp1
Sp1
Sp3
Sp6
Sp2
Sp3
Sp2
Sp5
Sp4
Sp4
Sp5

Figure 2

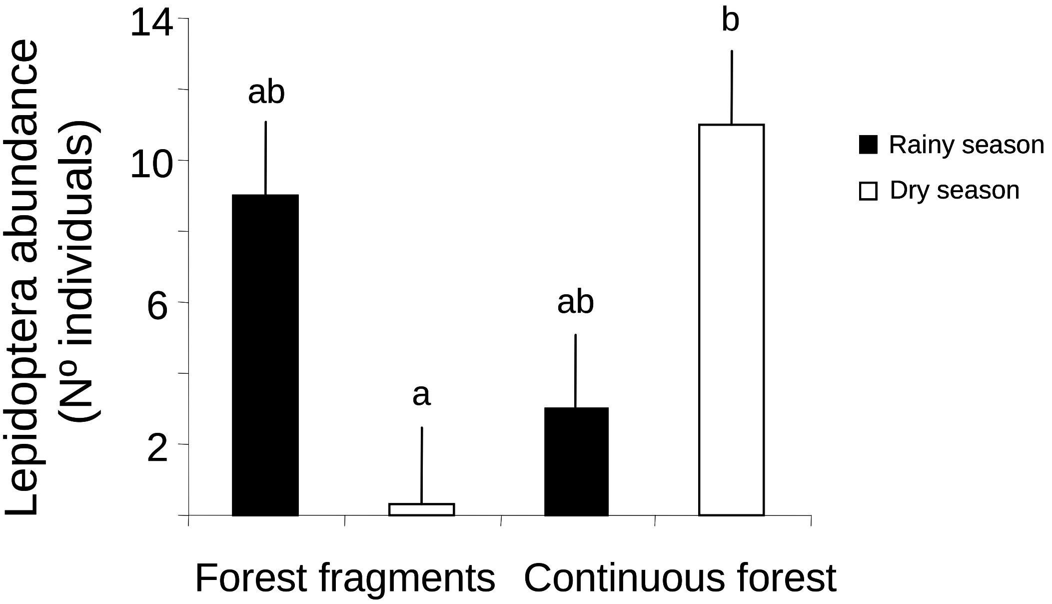

Lepidoptera abundance
(Nº individuals)
14
10
6
2
ab
a
ab
b
■ Rainy season
□ Dry season
Forest fragments
Continuous forest

Figure 3

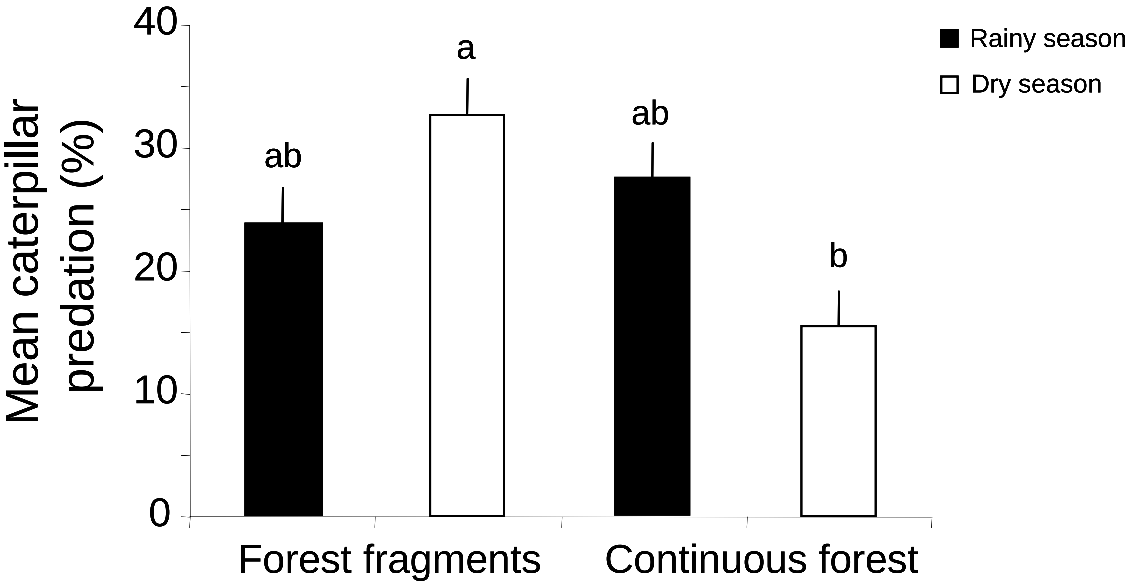
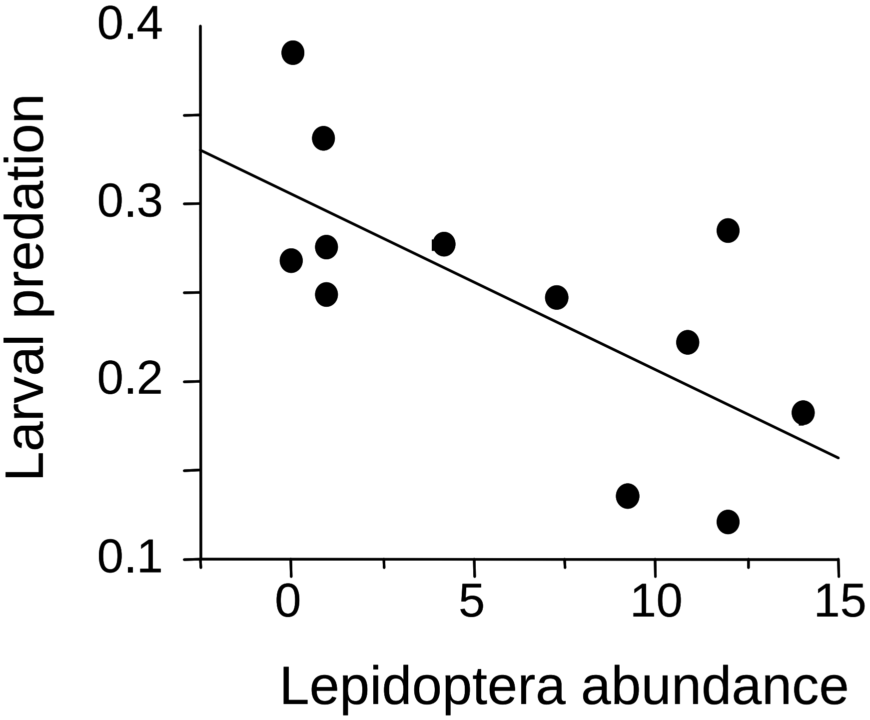

Mean caterpillar predation (%)
40
30
20
10
0
a
ab
ab
b
Rainy season
Dry season
Forest fragments
Continuous forest

Figure 4



Appendix

Bird species list according to their scientific names and below common names, in forest fragments (F) and Continuous forest (CF). Method refers to nets (N), birds counts (C) and both (NC). Foraging guild are represented by V = vertebrates, I = insectivores, S = seeds, F = frugivores, N = nectarivores.

Family	Method	Guild	F1	F2	F3	CF1	CF2	CF3
Accipitridae								
Spizaetus ornatos	C	V		X				
Ornate Hawk-Eagle								
Caprimulgidae								
Nyctidromus albicollis	C	I						X
Common Pauraque								
Cardinalidae								
Caryothraustes poliogaster	C	FI						X
Black-faced Grosbeak								
Cyanocompsa cyanoides	NC	S				X		
Blue-black Grosbeak								
Paserina cyanea	N	SI						X
Indigo Bunting								
Saltator atriceps	C	FI				X	X	
Black-headed Saltator								
Columbidae								
Geotrygon montana	NC	SF		X		X		
Ruddy Quail-Dove								
Leptotila plumbeiceps	C	FS		X	X			
Grey-headed Dove								
Corvidae								
Cyanocorax morio	C	IFV		X		X		X

Brown Jay								
Dendrocolaptidae								
Lepidocolaptes affinis Spot-crowned Woodcreeper	N	I			X		X	
Lepidocolaptes souleyetii Streak-headed Woodcreeper	N	I						X
Sittasomus griseicapillus Olivaceous Woodcreeper	N	I					X	X
Veniliornis fumigatus sanguinolentus Smoky-brown Woodpecker	N	I						X
Xiphorhynchus flavigaster Ivory-billed Woodcreeper	N	I					X	
Furnariidae								
Automolus ochrolaemus Buff-throated Foliage-gleaner	C	I				X		
Xenops minutus Plain Xenops	N	I						X
Icteridae								
Dives dives Melodious Blackbird	C	IS	X					
Icterus galbula Baltimore Oriole	C	IFN						X
Psarocolius montezuma Montezuma Oropendola	C	IFV		X	X	X		X

Family	**Method**	**Guild**	**F1**	**F2**	**F3**	**CF1**	**CF2**	**CF3**
Mimidae								
Dumetella carolinensis Gray Catbird	NC	I	X	X		X		X

Family	Method	Guild	F1	F2	F3	CF1	CF2	CF3
Momotidae								
Momotus momota Blue-crowned Motmot	NC	IFV						X
Emberizidae								
Basileuterus culicivorus Golden-crowned Warbler	NC	I			X		X	X
Dendroica magnolia Magnolia Warbler	N	I					X	
Geothlypis trichas Yellow Crowned	N	I			X			
Helmitheros vermivorus Worm-eating Warbler	N	I				X	X	
Mniotilita varia Black-and-white Warbler	NC	I				X	X	
Oporirnis formosus Kentucky Warbler	N	I		X	X	X	X	X
Seiurus aerocapillus Ovenbird	NC	I		X	X	X	X	X
Seiurus noveboracensis Northern Waterthrush	N	I		X				
Setophaga ruticilla American Redstart	C	I						X
Vermivora celata Orange-crowned Warbler	C	I						X
Vermivora peregrina Tennessee Warbler	C	IFN				X	X	
Vermivora ruficapilla Nashville Warbler	C	I						X
Wilsonia citrina Hooded Warbler	N	I	X	X	X	X	X	X

Picidae								
Melanerpes aurifrons	C	IF			X			
Goleen-fronted Woodpecker								
Pipridae								
Pipra mentales	N	FI				X	X	
Red-capped Manakin								
Psittacidae								
Amazona autumnalis	C	FS				X		
Red-lored Parrot								
Ramphastidae								
Pteroglossus torquatus	N	FIV						X
Collared Aracari								
Ramphastos sulfuratus	C	FIV			X	X		X
Keel-billed Toucan								
Thraupidae								
Euphonia gouldi	NC	FI					X	X
Olive-backed Euphonia								
Euphonia hirudinacea	NC	FI		X		X		
Yellow-throated Euphonia								

Family	**Method**	**Guild**	**F1**	**F2**	**F3**	**CF1**	**CF2**	**CF3**
Habia fuscicauda	NC	IF	X	X	X	X	X	X
Red-throated ant-tanager								
Trochilidae								
Amazilia candida	NC	NI			X		X	
White-bellied Emerald								
Phaethornis longuemareus	C	NI						X

Little Hermit								
Phaethornis superciliosus Long-tailed Hermit	NC	NI		X	X	X	X	X
Troglodytidae								
Campylorhynchus zonatus Band-backed Wren	C	I	X	X	X			
Henicorhina leucosticta White-breasted Wood-Wren	NC	I	X	X	X	X	X	X
Trogonidae								
Trogon collaris Collared Trogon	C	IF						X
Turdidae								
Catharus ustulatus Swainson´s Thrush	N	IF			X			
Hylocichla mustelina Word Thrush	NC	IF			X	X	X	
Turdus assimillis White-throated Robin	N	IF						X

Family	**Method**	**Guild**	**F1**	**F2**	**F3**	**CF1**	**CF2**	**CF3**
Turdus grayi Clay-colored Robin	NC	IF				X	X	X
Tyrannidae								
Leptopogon amaurocephalus Sepia-capped Flycatcher	N	I				X		
Attila spadiceus Bright-rumped Attila	N	IFV						X
Mionectes oleagineus Ochre-bellied Elaenia	N	IF				X	X	X

Platyrhinchus cancrominus Stub-tailed Spadebill	N	I	X		X	X	X
Rhynchocyclus b. brevirostris Eye-ringed Flatbill	N	I			X		
Tolmomyias sulphurescens Yellow-olive Flycatcher	N	IF		X			
Vireonidae							
Hylophilus ochraceiceps Tawny-crowned Greenlet	NC	I			X	X	X
Vireo flavifrons Yellow-throated Vireo	C	IF	X				
Vireo gilvus Warbling Vireo	C	IF					X
Vireo griseus White-eyed Vireo	N	IF	X		X		
Vireo olivaceus Red-eyed Vireo	NC	IF	X				X

Capítulo 5

La fragmentación del hábitat afecta la abundancia y riqueza de parasitoides icneumónidos en una selva tropical en México.

Con formato para: Biodiversity and Conservation

Running head: Forest fragmentation and ichneumonid parasitoids

Forest fragmentation affects abundance and richness of ichneumonid parasitoids in a Mexican tropical site

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Abstract

Because of the magnitude of land use currently occurring in tropical regions, the local loss of animal species due to habitat fragmentation has been widely studied, particularly in the case of vertebrate taxa. Many invertebrate groups and the ichneumonid wasps in particular, however, have been poorly study in this context, despite the fact that they are one of the most species-rich groups and play an important role as regulators of other insect populations. Here we recorded the taxonomic composition of ichneumonid parasitoids and assessed their species richness, diversity, abundance, similarity and dominance in the Los Tuxtlas tropical rain forest, Mexico. We assessed the effects of habitat fragmentation by comparing: continuous forest (640 ha) and a forest fragment (19 ha). We sampled ichneumonid species using four Malaise traps in each forest type during the dry (September-October) and rainy season (March-April). A total of 104 individuals of Ichneumonidae wasps belonging to 11 subfamilies, 18 genera and 42 species were collected in continuous forest, and 11 subfamilies, 15 genera and 24 species in the forest fragment. Species richness, abundance, and diversity of ichneumonid parasitoids were greater in the continuous forest than in forest fragment. We did not detect differences between seasons. Species rank/abundance curves showed that the ichneumonid community between forest types was different. Species similarity between forest types was low. The most dominant species in continuous forest was *Neotheronia* sp., whereas in the forest fragment it was *Orthocentrus* sp. Changes in the ichneumonid wasp community may compromise important tropical ecosystem processes.

Keywords: habitat fragmentation, Ichneumonidae, Los Tuxtlas, parasitoids, tropical rain forest.

Introduction

Habitat fragmentation (habitat loss and the breaking apart of the habitat) represents one of the greatest threats to species survival in the tropics (Fahrig 2003; Laurance et al. 2008). Despite the great importance of habitat fragmentation, we are far from knowing its consequences on many organisms. The scenario is even worse for the insects, where a high number of species are unknown and several aspects of their biology still need to be discovered and described (Didham et al. 1996; Hanson and Gauld 2006). One group of insects that is particularly important in the functioning of tropical ecosystems, as enemies and therefore population controls of phytophagous insects, are the parasitic wasps (Hymenoptera). Among this group of insects one of the largest families is the Ichneumonidae, which includes more species than all vertebrates together (Townes 1969). It is not surprising therefore, that predatory and parasitic hymenopterans are linked, via complex food webs, to more species of insects than any other order of terrestrial arthropods (Schoenly 1990). Nevertheless, up to the present time, information on the consequences of habitat fragmentation on the diversity and abundance of parasitoids in the tropics is very limited (Tylianakis et al. 2005), though it has been argued that changes in abundance and diversity of natural enemies, such as parasitoids, could trigger trophic cascading effects, potentially affecting not only their host herbivores, but also the herbivore’s food plants (Tscharntke and Brandl 2004; Valladares et al. 2006).

Ichneumonidae, together with the Braconidae and Tachinidae (Diptera), represents the most species-rich group of parasitoids of two of the most important groups of tropical phytophagous insects, the Lepidoptera and Coleoptera. For instance, the diversity of this group of insects in the Neotropics is estimated to be of the order of

30 000 species (Hanson and Gauld 2006). However, we know close to nothing about the impacts of fragmentation on these parasitoids in the tropics, and this prevents our understanding of the potential impacts of fragmentation on the ecological processes in which they are involved, and their consequences on the rest of the trophic chain, including patterns of herbivory, known to be affected by fragmentation in our study site (Ruiz-Guerra et al. in press).

Previous studies have emphasized that habitat fragmentation may be particularly critical for parasitoids, due to their low densities, high variability in population size, and their dependence on hosts from lower trophic levels (Kareiva 1987; Kruess and Tscharntke 1994; Gibb and Hochuli 2002; Kondoh 2003; Cronin 2004; Valladares et al. 2006). Moreover, many parasitic wasps are expected to be particularly vulnerable to habitat fragmentation because of their susceptibility to increased temperature and reduced humidity; and therefore increased risks of insect desiccation associated with fragments and their edges (Valladares et al. 2006). The study of Neotropical parasitic wasps is important not only in the context of forest fragmentation, but also as basic biodiversity information dealing with one of the most representative groups of insects. In Mexico, for example, the basic inventory of this group has been restricted to the genus level (Ruiz 1988).

Here we present data on the richness and abundance of ichneumonid wasps in both continuous and fragmented forest at Los Tuxtlas, in southeast Mexico. As a first approximation to the long-term consequences of fragmentation and controls of herbivory in the Los Tuxtlas rain forest, we recorded the ichneumonid parasitoids. Given that the taxonomy of this group is poorly studied we first surveyed this group and sorted specimens to subfamily level. We also made an effort to separate the specimens into morphospecies and in some cases to named species, to quantify metrics of richness, diversity and species similarity. We repeated our surveys in forest fragment and continuous forest and in two seasons of the year, rainy and dry. The rationale for the latter was that Lepidoptera, one of the main herbivores at the study site (see de la Cruz and Dirzo 1987), and major hosts of Ichneumonidae, show some seasonality, with greater abundance of larvae in the rainy season (Rauguso and Llorente-Bousquets 1990).

The specific questions we aimed to answer were: i) what is the taxonomic composition, at the subfamily and (morpho) species level, of ichneumonid parasitoids in these forests? ii) is there variation in ichneumonid species richness and abundance between forest fragment and continuous forest, and across seasons? According to the trophic-level hypothesis of island biogeography, species at higher trophic levels in a community are more prone to the effects of habitat fragmentation than species at lower levels (Holt et al. 1999), and therefore we hypothesized that the number of ichneumonid parasitoids would be lower in forest fragment than in continuous forest. To our knowledge this is the first study that attempts to survey the community of ichneumonid parasitoids in the context of habitat fragmentation and seasonality in Mexico. This is not surprising given the limited taxonomic information on this group in most Neotropical sites. For example, no study is known on the Hymenoptera that operate as parasitoids from the otherwise well studied region of Los Tuxtlas (see González-Soriano et al.1997)

Methods

Study site

The study was conducted in Los Tuxtlas region, located in the state of Veracruz, Mexico, representing the current northernmost point of the distribution of tropical rainforest in the Americas (Dirzo and Miranda 1992). The topography is complex, with elevation ranges from sea level to 1 600 m a.s.l. The mean annual temperature is 25ºC and rainfall averages 4,700 mm/year (Soto and Gama 1997). The area experiences a dry season from March to May and a rainy season from June to February. The predominant vegetation is tropical rain forest in the lowlands, with variations along the elevational range, including cloud forest and mixed forest at higher elevations (Dirzo et al. 1997) Characteristics of the region's physical environment, flora, fauna and natural history are described in detail in González-Soriano et al. (1997).

In the last decades, the landscape that originally was occupied by tropical rain forest was converted to pasture lands, field crops, and a large number of small fragments (< 10 ha) with a few remaining extensive forests. The latter correspond to the Los Tuxtlas Research Station, ca.640 ha, and their extension to the San Martin Volcano, encompassing an area of ca. 9,500 ha (Mendoza et al. 2005). In this study we compare two habitat types: a forest fragment and continuous forest (hereafter referred to as forest types). Our comparison is based on a survey of these parasitoids in a 19-ha fragment and the continuous forest located within the Los Tuxtlas Research Station.

Parasitoid sampling protocol

We placed four Malaise traps in a 19-ha fragment (FF) and four in continuous forest (CF). These traps were separated by at least 100 m at each site in order to avoid interference between traps. Trapping bottles were collected and replaced every five days. Sampling was undertaken from September 10 to 5 October 2006, and March 29 to April 22, 2007, corresponding to the rainy and dry seasons respectively.

We used Malaise traps (BioQuip product no.2875A) with a modification in the collecting head in order to use 90% alcohol. Samples were stored in 90% alcohol, and specimens of Ichneumonidae were subsequently separated from the remaining insects. The material was identified to subfamily level using identification keys (Hanson and Gauld 2006) and was identified to species level by Dr. D. Kasparyan, ZIP (Zoological Institute, St. Petesburg). Specimens were deposited in the Entomological Collection of the Instituto de Biología, UNAM (Universidad Nacional Autónoma de México) and ZIP.

Diversity metrics

Species richness and diversity

Species richness was determined by the total number of different species/morphospecies captured in each Malaise trap. A repeated measures one-way ANOVA test was used to test for differences in parasitoid richness between forest types, each malaise trap was considered as a replicate. The analyses were preformed using JMP (Ver 6) software. In addition, we assessed differences in the species richness of Ichneumonidae between continuous forest and the forest fragment by constructing a species rarefaction curve without randomizations. The curve was developed for individuals collected in each Malaise trap in each season, using the EstimateS (Ver. 8) program (Colwell 2006).

Species abundance

The effects of habitat fragmentation (CF vs. FF) on ichneumonid abundance were examined using repeated measures one-way ANOVA. All analyses were performed using JMP (Ver 6). The variables were tested for normality and homogeneity of variances prior to the statistical analysis.

Species similarity

To describe the taxonomic similarity between seasons and forest types we used the Sorensen quantitative index of similarity (C_N) as $C_N = (2jN)/N_a + N_b$ where $2jN$ = the sum of the lower of the two abundances for species found in both sites; N_a= the total number of individuals in site A; and N_b = the total number of individuals in site B (Magurran 2004). The index reflects differences in total abundance. A higher value indicates greater similarity between sites. The value ranges from 0, when two samples have no species in common, to 1.0 when two samples are identical (Magurran 2004).

Species dominance

To visualize species relative abundance in the forest fragment and in continuous forest we constructed rank/abundance plots for the ichneumonid community (Magurran 2004). For each forest type we plotted the relative abundance of each species against the species rank, ordered from the most abundant to the least abundant species (Magurran 2004). We used a Kolmogorov-Smirnov (KS) two sample test to compare both dominance plots (Sokal and Rohlf 1995).

Results

Parasitoids assemblage

Overall, we collected a total 104 individuals of Ichneumonidae, 56 of which were present in the rainy season and 48 in the dry season. These individuals belong to a total of 11 subfamilies, 18 genera and 42 species in the continuous forest, whereas in the forest fragment 11 subfamilies, 15 genera and 24 species were represent (see Appendix).

Fifty seven percent of the subfamilies are recorded to be parasitoids of Lepidoptera; 20% are parasitoids of Coleoptera; one subfamily uses both Lepidoptera and Coleoptera as hosts; two subfamilies use both Coleoptera and Apoidea (Hymenoptera); one subfamily is known to be composed of hyperparasitoids, one uses Diptera, one parasitizes spiders, while only one of the subfamilies has unknown hosts (Table 1). Thirteen of the 14 subfamilies were recorded in the rainy season and 9 in the dry season; therefore, there was an overlap of six subfamilies in the dry season and five in the rainy season (Fig. 1).

Species richness and diversity

A total of 52 morphospecies were collected ranging from two to eleven morphospecies per sampling unit (Malaise trap). The effect of forest type was highly significant ($F_{(1,6)} = 34.93$, $P = 0.001$), while season and the interaction forest type x season were not statistically significant ($F_{(1,6)} = 1.04$; $P = 0.346$; and $F_{(1,6)} = 2.34$; $P = 0.176$ respectively). The continuous forest had 2.5 times more species than forest fragment sampling sites (Fig. 2a).

According to the species rarefaction curve, species richness was not completely recorded with our sampling effort in either the continuous forest or the forest fragment (Fig. 3). A tendency of higher species richness in continuous forest than in the forest fragment was also observed though there is great variation in the data. However, Shannon's diversity index confirmed that the continuous forest was 20% more diverse (H = 3.6) than the fragmented forest (H = 3.0), and this difference is highly significant ($t = 6.28$; df = 90.9; $P < 0.001$).

Species abundance

Comparing parasitoid abundance, the effect of forest type was highly significant (Fig. 2b) ($F_{(1,6)} = 36.28$; $P = 0.0009$), whereas season and the interaction term were not significant ($F_{(1,6)} = 0.57$; $P = 0.476$; and $F_{(1,6)} = 1.98$; $P = 0.208$ respectively). Ichneumonid species abundance was 2.4 times greater in continuous forest than in the forest fragment (Fig. 2b).

Species similarity

In general, species similarity between continuous forest and the forest fragment was low. We found that only nine of the 57 species were shared across forest types, 33 were exclusive to continuous forest and 15 were present only in the forest fragment (see Appendix). These numbers translate into relatively low similarity coefficients (overall Sorensen value = 0.25). The highest similarities were between continuous forest in the two seasons and between the forest fragment and continuous forest in the dry season

(Table 2). The lowest similarity was that of the comparison of continuous forest in the dry season against forest fragment in the rainy season (Table 2).

Species dominance

The low similarity across sites is consistent with and complementary to the observed changes in the dominant species. In continuous forest the dominant species was *Neotheronia* sp., whereas in the forest fragment it was *Orthocentrus* sp. (Fig. 4). In continuous forest the pattern of species abundance-dominance is significantly different from the pattern in the forest fragment ($D_{0.05} = 0.98$, $P < 0.05$). Most of the species found in the continuous forest were absent in the forest fragment (Fig. 4), and the most abundant species shared between forest types, *Orthocentrus* sp., Ichneumoninae morphospecies 6, and ichneumonid morphospecies 1, differ in their abundance distribution. For instance, while in the forest fragment *Orhtocentrus* sp. is the most abundant species, in the continuous forest this species occupies the fifth place (Fig. 4).

Discussion

This study represents the first attempt to assess changes in ichneumonid parasitoids resulting from reduction in forest size in a Mexican tropical forests. Overall, our results suggest that a decrease in forest size led to a significant decline in species richness, diversity and abundance of ichneumonid species. These alterations are associated with concomitant changes in species composition in the forest fragment. The most salient trend in such compositional changes is the shift towards a community dominated by fewer species. Furthermore, the fragment did not support a subset of the continuous forest species, but rather a markedly different ichneumonid wasp fauna. Differences in species abundance between forest types reflect the fact that several species may be more common in certain environments, and that others can withstand the environmental changes prevalent in a forest fragment, whereas others decreased or disappeared. For instance, *Orthocentrus* sp. was the most abundant species, although the possibility that there is more than one cryptic species masquerading under this name can not be ruled out. In other studies it has been reported that species of this genus are extremely numerous and in some cases comprise 30 percent of the ichneumonoids in a Malaise trap. Unfortunately very little is known about their biology other than that they are koinobiont endoparasitoids (i.e those parasitoids which allow their host to continue developing after being parasitized) of the larvae of Mycetophilidae (Diptera) and related families (Hanson and Gauld 2006). Species of *Neotheronia* are idiobiont endoparasitoids (i.e. those parasitoid species that permanently paralyse their hosts during parasitism, causing the cessation of host growth and development) of the prepupae and pupae of Lepidoptera and some species may be obligate hyperparasitoids. This genus includes some of the most abundant ichneumonids encountered in any locality, although some are rare species (Hanson and Gauld 2006).

Decline in parasitoid species richness in forest fragments has been reported in other study systems (Kruess and Tscharntke 1994; Golden and Crist 1999; Valladares et al. 2006; but see Gibb and Hochuli 2002). However, this is the first report for Mexico. In other systems, this pattern has been attributed to the degree of habitat specificity, space-use requirements and the range of tolerance to abiotic factors (Golden and Crist

1999). The number of hosts available in the forest fragment can also explain the changes in abundance and richness of parasitoids (Dubbert et al. 1998). In general, the number of insects associated with their respective host plants is known to increase with the area of the host patches (McGarvin 1982). This could be the case in Los Tuxtlas where host availability (mainly Lepidoptera) was also found to decrease in the forest fragment (B. Ruiz-Guerra unpublished data). In this context, the higher species richness in the continuous forest could be attributed to the specialization of some parasitoid groups to specific insect herbivores. More specialized species could be more susceptible to habitat fragmentation since they are more closely associated with their hosts or habitat, and are less flexible with respect to environmental changes (Tscharntke and Brandl 2004).

Abiotic factors, such as negative microclimatic changes near edges can alter the development of insects. For example, an increase in temperature and a decrease in humidity can increase desiccation rates at the edges (Valladares et al. 2006). An additional explanation for the lower abundance and species richness in the forest fragment is habitat isolation, as has been found in several studies. For example, Dubbert et al. (1998) showed that habitat connectivity caused an increase in parasitism of 4.9% in a continuous habitat compared to isolated habitats. Kruess and Tschanke (2000) found that on isolated plants parasitoid attack of *Oxystoma ochropus* (Coleoptera: Curculionidae) was 50% lower in isolated sites than in the control area. In addition, composition of the surrounding matrix also has an important effect on parasitoid populations due principally to primary and secondary effects of agricultural pesticides on insect populations (Cronin 2004).

Ichneumonid individuals were present in both seasons, but contrary to our expectation, there were no seasonal differences either in abundance or in species richness. This lack of response could be attributed to the high precipitation at the study site (4 700 mm) where there is not a marked differences in availability of leaf tissue between seasons (García-Guzmán and Dirzo 2001), and it is possible that there are no significant differences in abiotic conditions needed by parasitoid wasps.

We do not know whether the decline in abundance and richness of ichneumonids in Los Tuxtlas will translate into changes in parasitism rates, given that a decline in abundance and richness does not always result in a concomitant increase in parasitism levels. Instead, a few species (one or two) can account for most of the parasitism (Hawkins, 1994). An examination of parasitism rates between forest types is needed to further evaluate the effect of habitat loss in trophic processes. In addition, given that we compared continuous forest with sites in a fragment that was excised 20 years ago, it remains to be seen whether the biased ichneumoinid assemblages we detected in the fragmented habitat have reached some stable condition or are still undergoing temporal changes. This is an aspect that warrants further research.

Although our study was limited by a lack of fragment replication, the information generated here may be of significance to conservation efforts since the taxonomic and distribution records for this group of parasitoids represent the first steps in their conservation. Large forest remnants such as the UNAM reserve play an important role in the conservation of parasitic wasp communities. However our study also underscores that forest fragments may host different species assemblages of these parasitoids and therefore may also have complementary, conservation value.

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Appendix

Contingent of species of ichneumonid parasitoids found in continuous forest (CF) and in a forest fragment (FF), and their seasonal variation at Los Tuxtlas. Msp = morphospecies.

		CF		**FF**	
Subfamily	**Species**	**Dry**	**Rainy**	**Dry**	**Rainy**
Anomaloninae					
	AnMsp.1		1		
	Podogaster sp.			2	
Banchinae					
	BaMsp. 1		1		
	Lissonota sp.				2
	Meniscomorpha sp.		1		
Campopleginae					
	Cymodusa sp.		2		
	Dusona sp.	1	1		
	Hyposoter sp.	2	2		
	Venturia sp.			1	
	Xanthocampoplex sp.			1	
Cryptinae					
	Baltazaria sp.	1		1	
	Cestrus admotus (Cresson, 1873)		3		
	Digonocryptus propodeator Kasparyan and Ruiz, 2005		1		
	Lymeon sp.	1	2		

Appendix Continued

		CF		FF	
Subfamily	**Species**	**Dry**	**Rainy**	**Dry**	**Rainy**
Cryptinae					
	Lymeon cf. *rufinotum* Kasparyan and Ruiz, 2004		2	1	
	Lymeon tantillus (Cresson, 1874)		1		
	Photocryptus ater Cushman, 1931			1	
	Messatoporus sp.		2		
	Messatoporus cf. *propodeator* Kasparyan and Ruiz, 2005	1			
	Polycyrtus melanoleucus (Brullé, 1846)		1		
	Ptilobatus sp.		1		
	Whymperia sp.				1
Ichneumoninae					
	IcMsp. 1		1		
	IcMsp. 2		2		1
	IcMsp. 3		2		
	IcMsp 4				1
	IcMsp 5				1
	IcMsp 6.	4		3	

Appendix Continued

		CF		FF	
Subfamily	**Species**	**Dry**	**Rainy**	**Dry**	**Rainy**
Labeninae					
	Apechoneura pelucida Gauld, 2000				1
Mesochorinae					
	MesoMsp 1				1
Metopiinae					
	Exochus sp.	4			
	Exochus sp. 1	1			
	Exochus sp. 2	1			
	Exochus urzus Gauld & Sithole, 2002		2		
	Hypsicera sp.			1	
	Lemus sp.				1
	Metopiinae sp.	1			
Nesomesochorinae					
	Nonnus sp.	1			1
Ophioninae					
	Enicospilus sp.	1			
Orthocentrinae					
	OrMsp. 2		2		1
	OrMsp. 3		1		
	OrMsp. 4				1

Appendix Continued

		CF		FF	
Subfamily	**Species**	**Dry**	**Rainy**	**Dry**	**Rainy**
	OrMsp. 1		1		1
	Orthocentrus sp.	4		4	
Pimplinae					
	Neotheronia sp.	2	4	1	
	Neotheronia sp. 1	1			
	Neotheronia sp. 2	1			
	PiMsp1				2
	Zaglyptus sp.	1	1		
	Zatypota sp.		1		
Poemeninae					
	Ganodes matai Gauld, 1991		1		
Tersilochinae					
	TerMsp.1		1		
Total		31	41	17	15

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Figure legends, Ruiz-Guerra et al.

Figure 1. Relative representation of ichneumonid subfamilies recorded in a) rainy season and b) dry season in continuous forest (CF) and forest fragment (FF).

Figure 2. a) Ichneumonid species richness (mean ± SE) and b) ichneumonid abundance (individuals mean ± SE) in forest fragment and continuous forest.

Figure 3. Species rarefaction curve for ichneumonid individuals collected in 8 Malaise traps, in continuous forest (CF) and forest fragment (FF) in two seasons (dry and rainy).

Figure 4. Rank/abundance plots for the Ichneumonidae community sampled in continuous forest (CF) and forest fragment (FF) in Los Tuxtlas, México. For each forest type we plotted the relative abundance of each species against the species rank, from the most abundant to the least abundant species. Sp 46 (*Orthocentrus* sp.), Sp 38 (*Neotheronia* sp.), Sp 15 (Ichneumoninae morphospecies 6), Sp 19 (Ichneumoninae morphospecies 1).

Table 1. The main hosts of the ichneumonid parasitoids found in continuous forest and forest fragment during two seasons at Los Tuxtlas. Hosts taken from Hanson and Gauld (2006).

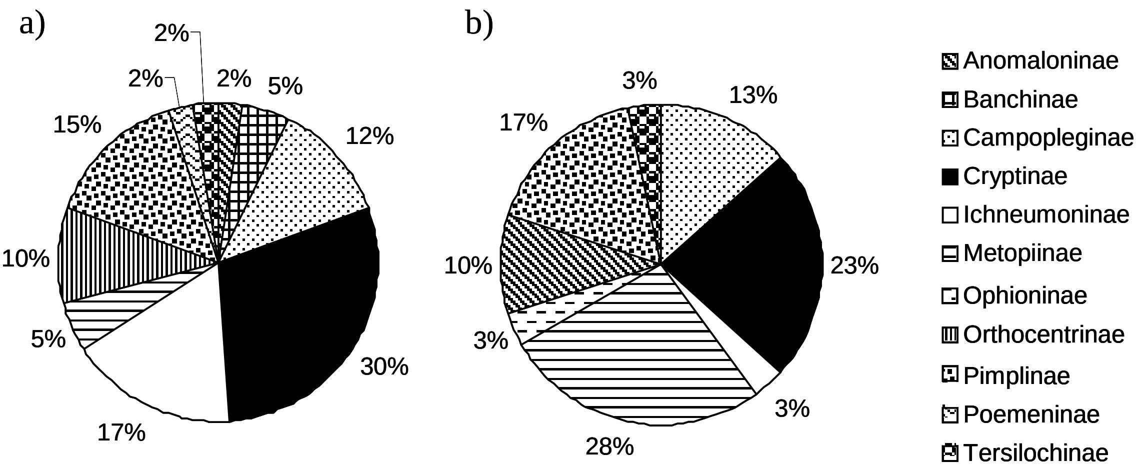
		CF		**FF**	
Subfamily	**Main hosts**	**Rainy**	**Dry**	**Rainy**	**Dry**
Anomaloninae	Lepidoptera				x
Banchinae	Lepidoptera			x	
Campopleginae	Lepidoptera	x	X	x	x
Cryptinae	Lepidoptera, Hymenoptera	x	X		x
Icheneumoninae	Lepidoptera	x	X	x	x
Labeninae	Coleoptera, Apoidea			x	
Mesochorinae	Other parasitoids			x	
Metopiinae	Lepidoptera	x	X	x	x
Nesomesochorinae	Unknown			x	
Ophioninae	Lepidopera		X		
Orthocentrinae	Diptera	x	X	x	x
Pimplinae	Araneae, Lepidoptera	x	X	x	x
Poemeninae	Coleoptera, Apoidea	x			
Tersilochinae	Coleoptera	x	X		
Total		**10**	**8**	**9**	**7**

Table 2. Sorensen's quantitative similarity index comparing sites in continuous and fragmented forest during two seasons at Los Tuxtlas.

	CF Rainy	**CF Dry**	**FF Rainy**	**FF Dry**
CF Rainy	—			
CF Dry	0.25	—		
FF Rainy	0.07	0.04	—	
FF Dry	0.06	0.25	0	—

Figure 1.

Continuous forest



Forest Fragment

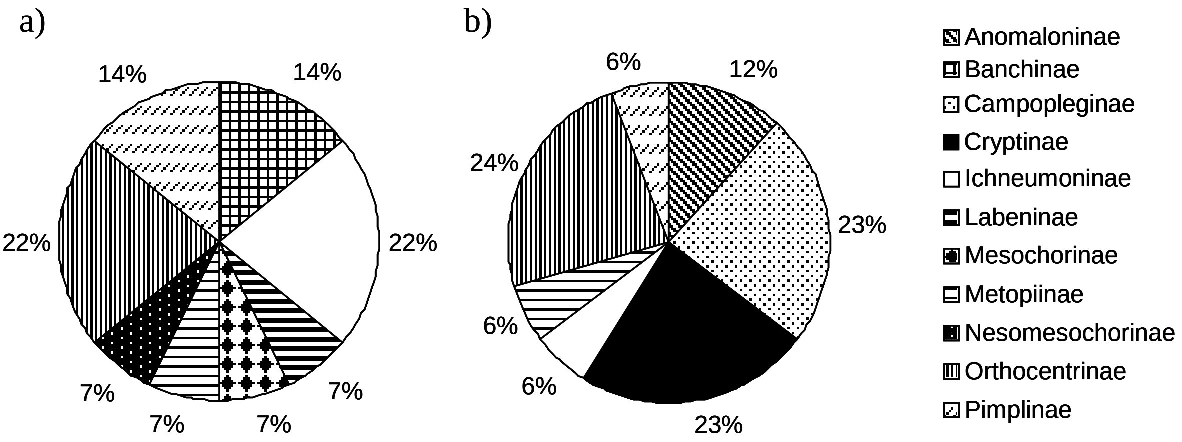


Figure 2.

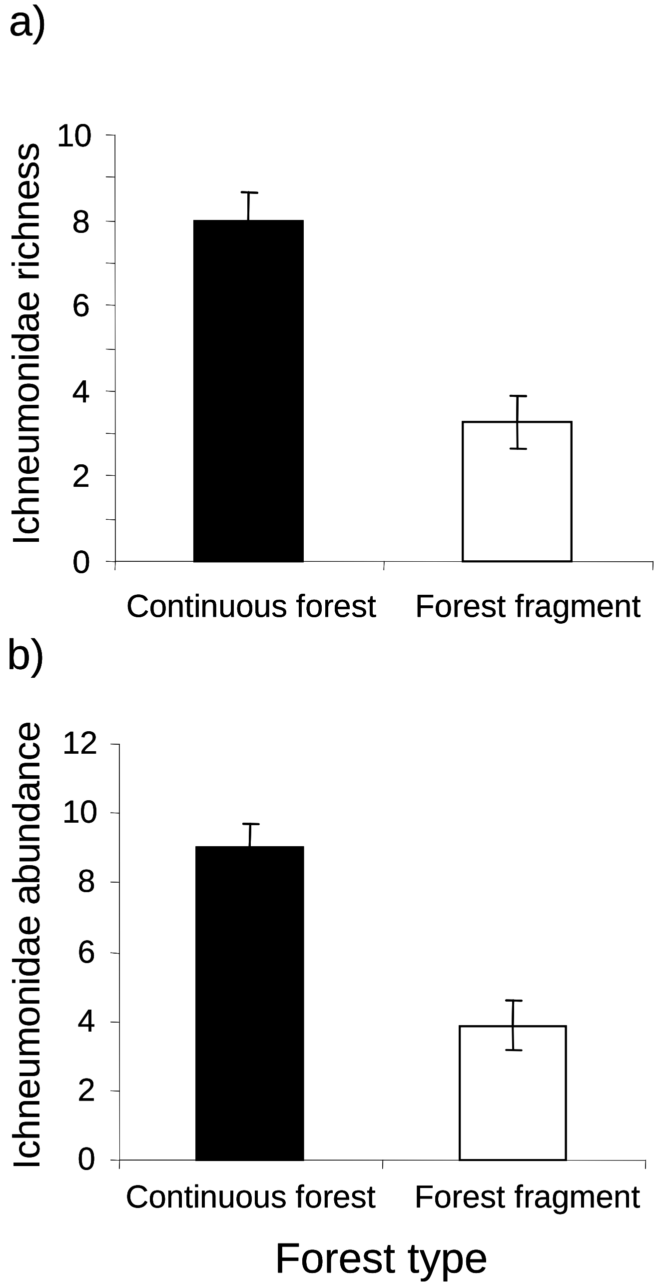

a)
Ichneumonidae richness
10
8
6
4
2
0
Continuous forest
Forest fragment
b)
Ichneumonidae abundance
12
10
8
6
4
2
0
Continuous forest
Forest fragment
Forest type

Figure 3

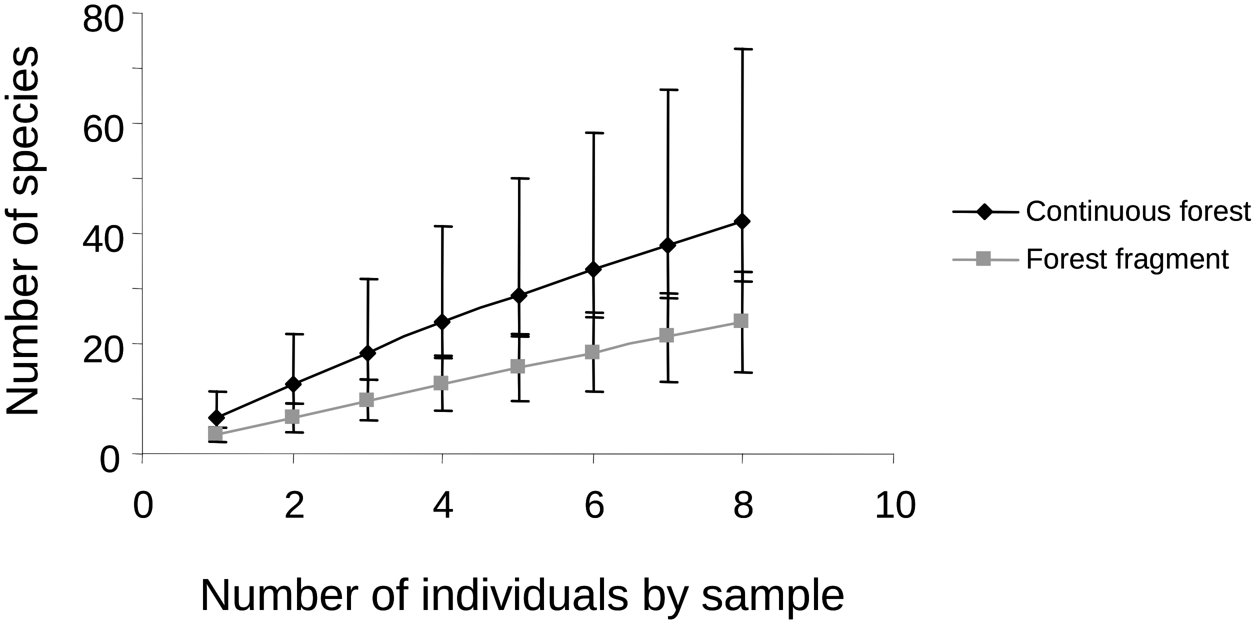
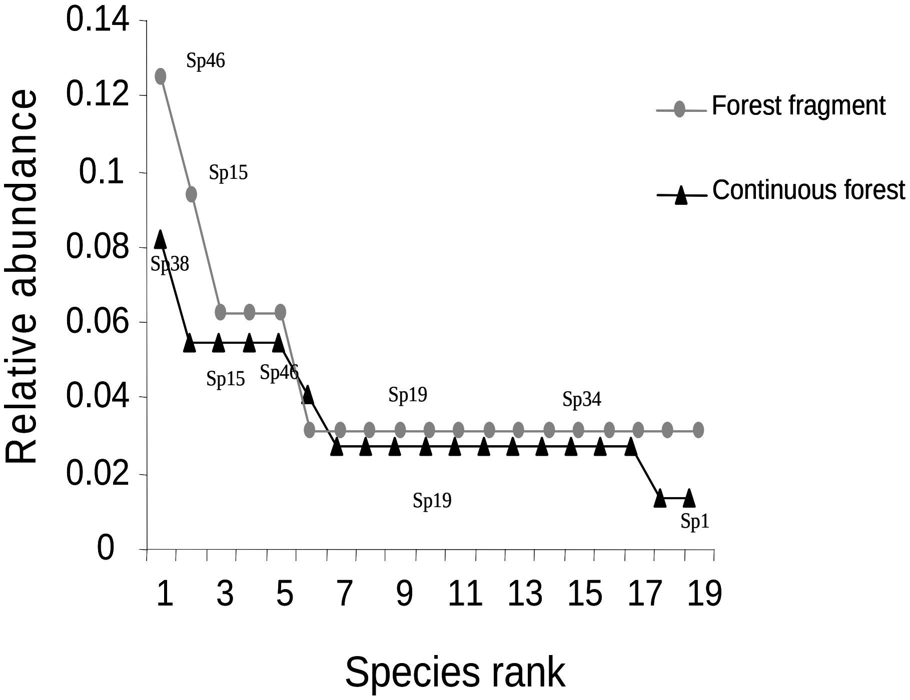

80
60
40
20
0
0
2
4
6
8
10
Number of species
Number of individuals by sample
Continuous forest
Forest fragment

Figure 4



Relative abundance
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Species rank
1
3
5
7
9
11
13
15
17
19
Forest fragment
Continuous forest
Sp46
Sp15
Sp38
Sp15
Sp46
Sp19
Sp34
Sp19
Sp1

DISCUSION GENERAL

Los resultados de este estudio muestran que la fragmentación del hábitat reduce los niveles de herbivoría a nivel comunidad (97 especies de brinzales) y en las especies compartidas. En primer término se detectó que los cambios en los niveles de herbivoría debidos a la fragmentación del hábitat covarían con la estrategia de regeneración (demandantes de luz *vs.* tolerantes a la sombra), la identidad de la especie y el método de medición utilizado (daño acumulado vs. mediciones puntuales). Cuando se midió el daño acumulado en seis meses, se encontró que la disminución en los niveles de herbivoría fue consistente en las especies tolerantes a la sombra. En contraste, las especies pioneras mostraron respuestas especie-específicas, dos de ellas (*Hampea nutricia* y *Myriocarpa longipes*) presentaron una reducción de los niveles de herbivoría en los fragmentos, mientras que las otras dos (*Acalypha diversifolia* y *Siparuna andina*) presentaron un aumento. Estos resultados son contrarios a la hipótesis inicial de este estudio. Los niveles de herbivoría detectados parecen estar determinados por el control descendente o por factores del ambiente fragmentado que afectan al herbívoro directamente, más que por el control ascendente.

Los niveles de herbivoría que una planta puede sufrir en un sistema fragmentado pueden ser el resultado de una gran cantidad de factores abióticos y/o bióticos. Los primeros están en función del ambiente físico y se relacionan principalmente con la tolerancia fisiológica de cada especie a distintas variables ambientales. Los efectos bióticos que afectan la dinámica poblacional de los herbívoros, y por tanto determinan los niveles de herbivoría, pueden actuar desde la base de la cadena trófica (control ascendente) y tienen que ver con la cantidad y/o calidad del recurso vegetal disponible, así como de niveles tróficos superiores (control descendente) representados por los enemigos naturales de los herbívoros.

Control ascendente

La cantidad y calidad del tejido vegetal disponible para los herbívoros puede ser decisiva para las poblaciones de fitófagos (Price, 1992). Los cambios en el microclima derivados del efecto de borde pueden afectar la disponibilidad y la calidad de las plantas para los herbívoros y por lo tanto alterar los niveles de herbivoría (Ayres, 1993; Coley, 1998). Entre los cambios microclimáticos sobresalen un aumento en la temperatura, en la incidencia lumínica y del viento y una disminución en la humedad relativa del aire y del suelo en los fragmentos con respecto a la selva continua (Murcia, 1995; Ferreira y Laurance, 1997; Ruiz-Guerra, 2003). Estas variaciones en el entorno abiótico pueden provocar cambios morfológicos, bioquímicos y fisiológicos en las plantas. Por ejemplo, Repetto-Giavelli y colaboradores (2007) reportan que las hojas de *Aristotelia chilensis* presentan un menor porcentaje de nitrógeno en el follaje de los fragmentos, que en bosque continuo. Esta misma especie disminuye la pérdida de agua en fragmentos reduciendo su superficie foliar, engrosando sus hojas, y aumentando la cantidad de capas de parénquima esponjoso. En contraste, en el bosque continuo *A. chilensis* produce hojas más delgadas pero de mayor área que las de los fragmentos, aumentando con ello el área disponible para captar la radiación solar. Contrario a estos hallazgos, en el presente trabajo las características defensivas (fenoles totales, taninos condensados y dureza) y nutritivas (carbono, nitrógeno y contenido de agua) de las plantas no fueron afectadas por la fragmentación del hábitat. Esta carencia de cambio entre fragmentos y selva continua, fue reforzada por el experimento de palatabilidad en el que el herbívoro generalista *Spodoptera fugiperda* no mostró preferencia entre tejido proveniente de fragmentos o selva continua pero sí entre estrategias de regeneración, siendo más consumida la especie pionera (*Acalypha diversifolia*) que la especie tolerante (*Rheedia edulis*). Este resultado no es sorprendente dada la calidad nutritiva (alta concentración de nitrógeno y contenido de agua) y los bajos niveles de defensa, de las hojas de la especie pionera comparada con la tolerante a la sombra. Las diferencias en la calidad nutritiva entre especies pioneras y tolerantes han sido reportadas en otras selvas tropicales (Coley y Barone, 1996). Sin embargo, este trabajo es uno de los primeros que comparan dichas características en un sistema fragmentado (ver Fáveri *et al*., 2008; Repetto-Giavelli *et al.*, 2007). En general, los resultados de este estudio son indicativos de que los atributos nutritivos y defensivos evaluados no son afectados por la fragmentación del hábitat y por lo tanto, los cambios en los niveles de herbivoría encontrados no se deben a cambios en las características del follaje. Otros estudios tampoco han encontrado una relación entre la fragmentación del hábitat y las características defensivas y nutritivas de las plantas (Zenteno, 2001; Fáveri *et al*., 2008). Por ejemplo, Fáveri y colaboradores (2008) reportan que el contenido de agua, nitrógeno y concentración de fenoles totales en las hojas de *Henriettella caudata* no fue diferente entre fragmentos y selva continua en Amazonia central. Por su parte, Zenteno (2001) reporta que la dureza y la aceptabilidad de la palma *Chamaedorea alternans* fue similar entre fragmentos y selva continua en Los Tuxtlas, México. La ausencia de cambio en las características defensivas y nutricionales de las especies evaluadas en este estudio puede ser atribuida a dos factores. Primero, es probable que las plantas no fueran influenciadas por el efecto de borde dado que fueron colectadas en parcelas ubicadas en el centro de cada uno de los sitios. Segundo, la variación intra en inter específica en la producción de metabolitos secundarios fue considerable, lo que pudo enmascarar el efecto de la fragmentación del hábitat sobre estos atributos defensivos. Otros estudios han atribuido la variación intra e inter específica en la cantidad de metabolitos secundarios a una combinación de factores genéticos, ambientales y de desarrollo (Lambers *et al.*, 1998; Agrell *et al.*, 2000; Tharall *et al*., 2001; Brenes-Arguedas y Coley, 2005).

La otra posibilidad de cambio en los niveles de herbivoría debido al control ascendente se refiere a una mayor concentración de especies pioneras en los fragmentos que en la selva continua, debido a que estas especies en general crecen es sitios muy abiertos y/o perturbados, como las condiciones encontradas en los fragmentos. Un estudio previo realizado en los mismos fragmentos utilizados en este trabajo confirmó que la abundancia de especies pioneras con respecto a las tolerantes a la sombra es mayor en los fragmentos que en la selva continua (Aguirre, 2008). Sin embargo, en este trabajo no se encontró un incremento en los niveles de herbivoría en los fragmentos como lo indicaría la distribución de especies en estos sitios. Estos resultados aunados a la ausencia de respuesta de las características defensivas y nutritivas de las plantas indican que la disminución en los niveles de herbivoría en los fragmentos no se debe a cambios en el control ascendente.

Control descendente

Si el follaje no representa restricciones para los herbívoros, entonces es posible argumentar que la variación en la herbivoría en la selva de Los Tuxtlas se puede explicar mejor por efectos del tercer nivel trófico. Diversos estudios han mostrado que tanto las tasas de depredación y parasitismo, como la diversidad y abundancia de aves insectívoras y de parasitoides disminuyen en fragmentos pequeños y aislados (Lovejoy *et al*., 1986; Kruess y Tscharntke, 1994; Stouffer y Bierregaard, 1995; Golden y Crist, 1999; Valladares *et al*., 2006). Al igual que estos estudios, este trabajo reporta una disminución en la riqueza, abundancia y diversidad de avispas parasitoides (Ichneumonidae). Estos cambios se reflejan en la composición y dominancia de especies. En general, las especies encontradas en el fragmento no son una sub-muestra de las encontradas en la reserva sino que representan un grupo de especies ausentes o no colectadas en la reserva. En otras palabras, el impacto de la pérdida del hábitat difiere entre especies de parasitoides. Estas diferencias pueden ser el reflejo de las diversas capacidades de las especies para soportar las características ambientales. Otra explicación a estos resultados es simplemente por efecto de la disminución en el área, dado que en un área pequeña existen menos sitios de refugio y hospederos disponibles. En este contexto, es reconocido que el número de insectos asociados con sus plantas hospederas disminuyen conforme el área (Tscharntke y Brandl, 2004). Este es el caso de los Tuxtlas, donde la disponibilidad de hospederos (principalmente lepidópteros) también se ve mermada por la pérdida del hábitat. El aumento en la diversidad de parasitoides reportada en la reserva de Los Tuxtlas, puede estar correlacionada con la especialización de los parasitoides a sus hospederos. En general, se ha documentado que las especies especialistas son mas susceptibles a la fragmentación del hábitat que las generalistas debido a su estrecha relación con el hospedero y a su poca flexibilidad ante las variaciones ambientales (Tscharntke y Brandl, 2004). Es importante señalar que estos resultados deben ser tomados con precaución debido a que tienen la limitante de carencia de replicación de los sitios. Sin embargo, estos datos representan una primera aproximación a las consecuencias de la pérdida del hábitat sobre las poblaciones de Icneumónidos de Los Tuxtlas y son de relevancia en términos de conservación dado que los registros taxonómicos y de distribución de las especies representan el primer paso en su conservación.

Por otra parte, aunque la riqueza y la abundancia de aves insectívoras no cambiaron entre fragmentos y selva continua, la composición de especies (similitud y dominancia) encontrada en los fragmentos sugiere que la pérdida del hábitat puede alterar la estructura de la comunidad de aves. Estudios previos tampoco han detectado diferencias en la abundancia de aves entre fragmentos y continuo en Los Tuxtlas (Graham y Blake, 2001), la explicación de esto radica en el hecho de que las aves utilizan los fragmentos, las cercas vivas, y los árboles de cítricos establecidos en los potreros como hábitats temporales para perchar, obtener alimento o pasar de un fragmento a otro y después regresan a la selva continua (de la Vega, 2005; Estrada *et al*., 2000; Estrada y Coates-Estrada, 2005). La presencia y abundancia de las aves estudiadas en los fragmentos hacen evidente el potencial de estos para operar como atractores de animales, en este caso aves, lo cual puede tener implicaciones importantes para la restauración del ecosistema y aporta argumentos para su conservación (de la Vega, 2005).

La diversidad de aves insectívoras del sotobosque fue menor en los fragmentos que en la selva continua. Sin embargo, y contrario a este patrón encontramos que la tasa de depredación, evaluada mediante el uso de larvas artificiales fue mayor en los fragmentos pero únicamente durante la temporada de secas, lo que a su vez, se tradujo en la disminución de lepidópteros en la misma temporada. Esto también, ha sido reportado en otros estudios (Gónzalez-Gómez *et al*., 2006; pero ver: Sekercioglu *et al*., 2002; Pin Koh y Menge, 2006; Fáveri *et al.*, 2008). Estos resultados pueden estar relacionados con el hecho de que en los fragmentos las larvas quedan más expuestas a los depredadores debido a la reducción en la complejidad estructural de la vegetación y del dosel en los fragmentos (Aguirre, 2008).

Otra explicación a la disminución en los niveles de herbivoría reportados en este estudio, es que la fragmentación del hábitat afecta directamente y de manera negativa a las poblaciones de herbívoros. Por ejemplo, las condiciones de altas temperaturas y baja humedad impuesta por el efecto de borde afectan considerablemente el desempeño de los insectos herbívoros (Klein, 1989; Rauguso y Llorente Bousquets, 1990; Didham *et al.*, 1996; Brown y Hutchins, 1997; Pinheiro *et al.*, 2001; Barbosa *et al.*, 2005; Valladares *et al.* 2006). En este trabajo encontramos que la abundancia de los lepidópteros, los principales consumidores de follaje de Los Tuxtlas (de la Cruz y Dirzo, 1987), disminuyó en los fragmentos y sólo en la temporada de secas, donde las condiciones microclimáticas impuestas por el efecto de borde se acentúan (Ries *et al.*, 2004). Sin embargo, la abundancia de ortópteros y coleópteros no difirió entre fragmentos y selva continua. Estas diferencias entre órdenes de insectos pueden ser explicadas por el grado de especialización a sus plantas hospederas. En general se ha mostrado que las especies especialistas son más afectadas por la fragmentación del hábitat. Zabel y Tscharntke (1998) mencionan que para los herbívoros monófagos la fragmentación del hábitat es más crítica por que estos dependen de condiciones que son menos probables de ocurrir en los fragmentos, pero sobre todo por que la matriz circundante constituye un hábitat con características físicas estresantes y carentes de recursos alimenticios de los cuales depende el herbívoro. En un estudio realizado en Los Tuxtlas, Zenteno (2001), encontró que la abundancia del coleóptero *Calyptocephala marginipennis*, que solamente se alimenta de la palma *Chamaedorea alternans* fue menor en fragmentos que en selva continua. En el mismo sentido, Arnold y Asquith (2002) reportan que la disminución en los niveles de herbivoría en especies del género *Protium* en islas pequeñas en Barro Colorado, Panamá se debe principalmente a la disminución de sus herbívoros especialistas (lepidópteros).

En síntesis, los efectos de la fragmentación a través del impacto sobre la calidad del recurso alimenticio (follaje) parecen jugar un papel despreciable o nulo en la disminución de los niveles de herbivoría en fragmentos. Al parecer, los patrones de herbivoría detectados en Los Tuxtlas, se explican mejor por un aumento en la depredación de lepidópteros en los fragmentos o por factores del ambiente fragmentado que afectan al herbívoro directamente. Por lo tanto, este estudio sugiere que el mecanismo determinante de la herbivoría en este sistema puede estar operando en modo descendente (“top down”). Aunque este trabajo tiene la limitante de que la evaluación de la tasa de depredación fue estimada mediante el uso de orugas artificiales y no se evaluaron las tasas de parasitismo, representa la primera aproximación de las consecuencias de la fragmentación sobre los enemigos naturales de los herbívoros en Los Tuxtlas. Además, constituye un campo promisorio en el estudio de las interacciones planta-herbívoro en paisajes fragmentados. Así mismo, es el primer estudio que evalúa los efectos de la fragmentación del hábitat sobre la comunidad de brinzales en una selva tropical. Este estadio es donde la herbivoría por insectos puede tener efectos negativos en los componentes de la adecuación de las plantas (Dirzo, 1984; Marquis, 1984). Dado que los brinzales representan el futuro de las comunidades de plantas, resulta prioritario realizar estudios detallados y a largo plazo para entender las consecuencias de la fragmentación del hábitat sobre el desempeño de las plantas, principalmente las tolerantes a la sombra, la cuales representan las especies típicas de la selva tropical húmeda (Dirzo y Boege, 2008). Finalmente, los resultados de este trabajo hacen evidente que la fragmentación del hábitat debido a los patrones actuales de uso de la tierra, tienen un efecto negativo en la abundancia, riqueza y diversidad de especies de insectos y la diversidad aves insectívoras, lo que a su vez se refleja en modificaciones de interacciones interespecíficas, tales como la herbivoría y la depredación de insectos.

Perspectivas

El estudio de los efectos de la fragmentación de las selvas tropicales es de particular interés debido a la condición actual de estos ecosistemas. Sin embargo, resulta evidente que todavía quedan muchas preguntas que deben ser contestadas para tener un panorama general de dichos efectos. A pesar de los trabajos que describen como son los patrones de herbivoría en sistemas fragmentados, el desarrollo de este campo está en su infancia. A lo largo de esta tesis se han hecho evidentes algunos de los vacíos en esta área de la Ecología tropical. Por ejemplo, la taxonomía y la biología de avispas parasitoides de las regiones tropicales de México han sido prácticamente ignoradas. Otro aspecto que ha recibido poca atención son respuestas fisiológicas de las plantas en sistemas fragmentados y en general a las interacciones que consideran tres niveles tróficos. Por otra parte, es necesario realizar estudios a largo plazo que nos permitan entender la dinámica de la interacción planta-herbívoro para tener una mayor claridad sobre el papel que juega la herbivoría en la dinámica de los brinzales tropicales en un sistema fragmentado. En este contexto sería importante investigar si la composición de plantas cambiaría en los fragmentos, donde de acuerdo con los resultados de este trabajo las especies tolerantes son favorecidas (menos herbivoría). Otras preguntas que restan por contestar son: ¿Qué pasa con las plántulas, la respuesta a la fragmentación es la misma? ¿La disminución en la abundancia riqueza y diversidad de avispas parasitoides se traduce en una reducción en las tasas de parasitismo? ¿Estos niveles de herbivoría pueden afectar el desempeño reproductivo de las plantas? ¿Las plantas están respondiendo a través de la tolerancia en lugar de mecanismos de resistencia? Igualmente, es necesario determinar el efecto que tienen las actividades que ocurren en la matriz circundante en la supervivencia y comportamiento de los insectos herbívoros.

La deforestación y la fragmentación del hábitat no son problemas exclusivos de las selvas tropicales húmedas, sino de la mayoría de los ecosistemas de México. Considerando que el deterioro de éstos, además de la pérdida de especies también implica la reducción de suministros irremplazables para el bienestar de la humanidad (*e.g.*, purificación del aire, abastecimiento de agua, regulación del clima, provisión de alimentos, entre otros), es importante crear mecanismos que vinculen el conocimiento generado en el país, a todos los sectores sociales. Esto se puede generar a través de la difusión del conocimiento en diferentes medios de divulgación tales como la televisión, revistas, talleres y exposiciones. En la medida que el conocimiento se difunda podremos encontrar más soluciones y recursos para la conservación de los ecosistemas del país.

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