UNIVERSIDAD MICHOACANA DE
SAN NICOLÁS DE HIDALGO

PROGRAMA INSTITUCIONAL DE DOCTORADO
EN CIENCIAS BIOLOGICAS

Conservación y Manejo de Recursos Naturales

Facultad de Biología

“Estructura y composición de la comunidad de artrópodos del dosel asociados a *Quercus deserticola* en un paisaje fragmentado en la Cuenca de Cuitzeo, Michoacán”

Tesis

Que como requisito para obtener el grado académico de:

DOCTORA EN CIENCIAS BIOLÓGICAS

PRESENTA:

M.C. Silvia Ecaterina García Jain

DIRECTOR DE TESIS: Dr. Pablo Cuevas Reyes

CODIRECTORA DE TESIS: Dra. Yurixhi Maldonado López

Morelia, Michoacán, Febrero 2022

AGRADECIMIENTOS

Agradezco al CONACyT por la beca otorgada (305239) y a las instituciones que han hecho posible la realización del proyecto, CONACYT PDC2016-Project-3053 y la Coordinación de la Investigación Científica (UMSNH). Al Programa Institucional de Ciencias Biológicas (UMSNH), por formarme académicamente.

A mi asesor el Dr. Pablo Cuevas Reyes por sus comentarios y consejos. Por formar parte de su laboratorio desde la licenciatura. ¡Mi respeto y admiración!

A mi coasesora la Dra. Yurixhi por su tiempo y dedicación en la escritura de la tesis y de los manuscritos.

A los miembros de mi comité:

Dr. Antonio González

Dr. Luis Felipe Mendoza

Dr. Tiberio Monterrubio

Por las sugerencias para la realización del presente trabajo, sus consejos y el tiempo dedicado en las evaluaciones tutorales.

Al Dr. Edmundo por el gran apoyo en la identificación de los artrópodos.

A todos mis compañeros de trabajo con los que tuve la oportunidad de coincidir, por su amistad y compartir experiencias de vida. A todas y a cada una de las personas que directa o indirectamente apoyaron para realizar este proyecto.

A mis padres y hermano por motivarme y siempre confiar en mí. ¡Ser mi gran apoyo en la vida!

ÍNDICE

CAPÍTULO I. **Effects of forest fragmentation on plant quality, leaf morphology and herbivory of *Quercus deserticola*: is fluctuating asymmetry a good indicator of environmental stress?**

Silvia Ecaterina García-Jain[1], Yurixhi Maldonado-López[2], Ken Oyama[3], Marcílio Fagundes[4], Maurício Lopes de Faria[4], Mário M. Espírito-Santo[4] and Pablo Cuevas-Reyes[1]

[1]Laboratorio de Ecología de Interacciones Bióticas, Universidad Michoacana de San Nicolás de Hidalgo, Ciudad Universitaria, C.P. 58030, Morelia, Michoacán, México.
[2]CONACYT-Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Avenida San Juanito Itzícuaro SN, Nueva Esperanza, 58330 Michoacán, México.
[3]Escuela Nacional de Estudios Superiores Unidad Morelia, UNAM. Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-Hacienda de San José de la Huerta, Morelia, 58190 Michoacán, México.

RESUMEN GENERAL

Los bosques templados en México son dominados por distintas especies de encinos, y su manejo ha sido inapropiado teniendo altas tasas de deforestación y fragmentación. Particularmente, la Cuenca de Cuitzeo, Michoacán, ha sido altamente fragmentada debido a la expansión de la agricultura, el desarrollo urbano y la deforestación. La fragmentación de bosque puede influenciar la comunidad de artrópodos del dosel y modificar las interacciones bióticas, así como generar estrés ambiental en las plantas resultado de cambios en las condiciones abióticas (i.e. aumento en la intensidad de la luz, la velocidad del viento y la temperatura, disminuyendo la humedad y la fertilidad del suelo), siendo más intensos sus efectos en los fragmentos pequeños y en los bordes. El estrés ambiental en las plantas puede ser monitoreado utilizando la asimetría fluctuante (AF), ya que es una medida de la inestabilidad en el desarrollo de rasgos bilaterales o radialmente simétricos de los organismos. En el primer capítulo de esta tesis evaluamos el efecto de la fragmentación sobre la relación entre la AF y la herbivoría a través de cambios en la cantidad y la calidad de recursos (procesos ascendentes "bottom-up") de plantas de *Quercus deserticola* para los herbívoros en fragmentos de bosque templado de diferentes tamaños en la Cuenca de Cuitzeo, Michoacán y determinamos los cambios relacionados con la morfología de las hojas, AF, cantidad de recursos y la calidad de la planta entre los distintos tamaños de fragmento y el "efecto borde". Los resultados mostraron un mayor contenido de clorofila, área foliar, cobertura del dosel y tamaño de los árboles en fragmentos más pequeños en comparación de fragmentos grandes. Encontramos que las hojas de los individuos en fragmentos pequeños y en los bordes fueron más alargadas y anchas. Nuestros resultados también mostraron niveles más altos de AF y herbivoría en los pequeños fragmentos y los bordes. En el segundo capítulo evaluamos los cambios de la estructura y composición de la comunidad de artrópodos del dosel asociados a *Quercus deserticola* a lo largo de un gradiente de fragmentación en la Cuenca de Cuitzeo. Analizamos los cambios en la abundancia y riqueza, ordenes de artrópodos y gremios tróficos de la comunidad de artrópodos del dosel en fragmentos de bosque de distintos tamaños, borde e interior de los fragmentos en la Cuenca de Cuitzeo. Los resultados mostraron que tanto la abundancia como la riqueza de especies de artrópodos del dosel se incrementó en fragmentos pequeños y en el interior de los fragmentos. Los órdenes dominantes fueron Hemiptera, Hymenoptera y Coleoptera. El gremio trófico más abundante en todos los tamaños de fragmentos fue el de los fitófagos. De acuerdo a los resultados obtenidos en este estudio, *Q. deserticola* está asociada a una alta diversidad de especies de artrópodos, por lo tanto, es importante conservar los encinos a lo largo de los paisajes fragmentados.

PALABRAS CLAVE: Fragmentación, Encinos, Asimetría Fluctuante, Herbivoría, Diversidad de artrópodos.

GENERAL ABSTRACT

Temperate forests in Mexico are dominated by different species of oaks, and their management has been inappropriate, leading to high rates of deforestation and fragmentation. In particular, the Cuitzeo Basin, Michoacán, has been highly fragmented due to the expansion of agriculture, urban development, and deforestation. Forest fragmentation can influence the community of canopy arthropods and modify biotic interactions, as well as generate environmental stress on plants as a result of changes in abiotic conditions (i. e. increase light intensity, wind speed and temperature, decreasing soil moisture and fertility), its effects being more intense in small fragments and on the edges. Environmental stress in plants can be monitored using fluctuating asymmetry (FA), as it is a measure of the instability in the development of bilateral or radially symmetric traits of organisms. In the first chapter of this thesis we evaluated the effect of fragmentation on the relationship between FA and herbivory through changes in the quantity and quality of resources (bottom-up processes) of *Quercus deserticola* plants for the herbivores in temperate forest fragments of different sizes in the Cuitzeo Basin, Michoacán, and we determined the changes related to leaf morphology, FA, amount of resources and plant quality between the different fragment sizes and the "edge effect". Results showed higher chlorophyll content, leaf area, canopy cover, and tree size in smaller fragments compared to larger fragments. We found that the leaves of the individuals in small fragments and at the edges were more elongated and wider. Our results also showed higher levels of FA and herbivory in the small fragments and the edges. In the second chapter we evaluate changes in the structure and composition of the canopy arthropod community associated with *Quercus deserticola* along a fragmentation gradient in the Cuitzeo Basin.

We analyzed the changes in abundance and richness, arthropod orders and trophic guilds of the canopy arthropod community in forest fragments of different sizes, edge and interior of the fragments in the Cuitzeo Basin. The results showed that both the abundance and species richness of canopy arthropods increased in small fragments and within fragments. The dominant orders were Hemiptera, Hymenoptera, and Coleoptera. The most abundant trophic guild in all fragment sizes was the phytophagous. According to the results obtained in this study, *Q. deserticola* is associated with a high diversity of arthropod species, therefore, it is important to conserve oaks throughout fragmented landscapes.

INTRODUCCIÓN GENERAL

La fragmentación de bosques es un proceso dinámico en el que el bosque se reduce progresivamente en parches o fragmentos más pequeños de distintos tamaños, formas y grados de aislamiento, experimentando efectos de borde (Haddad et al. 2015; Fletcher et al. 2018). Los efectos de la fragmentación sobre aspectos bióticos son principalmente la reducción del tamaño poblacional de diferentes especies, la pérdida de especies de muchos taxa, la alteración de los patrones de dispersión y migración (Gibbs 2001), la modificación de las interacciones bióticas y la composición y estructura de artrópodos terrestres y del dosel (Bucher et al. 2010).

Una de las consecuencias de la fragmentación es la formación de bordes. El "efecto de borde" se produce en la interface entre entornos naturales y antropizados (Murcia 1995; Harper et al. 2005), existiendo una diferencia en la composición, estructura y función de las poblaciones (Ries et al. 2017). Los fragmentos pequeños de bosque tienen una mayor proporción de borde, con múltiples consecuencias para la biodiversidad y el funcionamiento del ecosistema (Jaeger et al. 2011). Según Haddad et al. (2015), aproximadamente el 20% de los bosques del mundo se encuentra a menos de 100 m del borde. En los bordes de los fragmentos existe una mayor incidencia de luz, velocidad del viento y temperatura, y una baja fertilidad y humedad del suelo en comparación con el interior del bosque (Laurance et al.2011; Delgado et al.2007; Arroyo- Rodríguez et al. 2017). Estos cambios abióticos de los bordes pueden tener una gran influencia en las comunidades biológicas, teniendo efectos diferenciales sobre las diferentes especies. El efecto de borde por actividades antropogénicas esta frecuentemente asociado con efectos adversos en los procesos ecológicos (Ries et al. 2004; Wirth et al. 2008) que favorecen la colonización y dominancia de especies invasoras y cambios drásticos en el funcionamiento de los ecosistemas (LeBrun et al. 2012; Lustig et al. 2017).

Específicamente, los artrópodos responden de diferentes maneras a la fragmentación del hábitat (Cagnolo et al.2009; Bagchi et al.2018), debido a diferencias en su capacidad de dispersión, requisitos del hábitat, ciclo de vida, patrones de distribución y adaptabilidad a las nuevas condiciones ambientales (Tscharntke et al. 2002; Nufio et al. 2011; Heidrich et al. 2020). Los artrópodos tienen roles ecológicos importantes, ya que participan en la regulación de la dinámica del dosel, afectando funciones del ecosistema como la descomposición, el ciclo de nutrientes, la transferencia de energía y la formación y mantenimiento del suelo (Yang y Gratton 2014; Maguire et al. 2015; Schowalter et al. 2018). Además, el dosel de los árboles tiene diversos conjuntos de artrópodos de diferentes niveles tróficos como fitófagos, depredadores, parásitos, parasitoides, polinizadores y detritívoros (Hamilton et al.2010; Nakamura et al.2017). La respuesta de las comunidades de artrópodos a la fragmentación del hábitat es muy variable, porque los cambios en el hábitat pueden aumentar los recursos para algunas especies o reducir los recursos para otras (Barberena-Arias y Aide 2002). Por lo tanto, las fuerzas “bottom-up” y “top-down” interactúan juntas moldeando y estructurando las comunidades de artrópodos (Castagneyrol et al.2014, 2017; Vaca-Sánchez et al.2021). Particularmente, los insectos herbívoros son muy sensibles a los cambios en las condiciones ambientales asociados con la fragmentación del bosque (Mooney et al. 2010; Maldonado-López et al. 2016). En general, los efectos de la fragmentación sobre la diversidad de herbívoros reflejan tanto los impactos directos sobre la dinámica poblacional de los herbívoros, como los impactos mediados a través de sus enemigos naturales “efectos top-down” (Holt 1996; Stone et al. 2002; Askew et al. 2013) y sus plantas hospederas “efectos bottom-up” (Tscharntke et al. 2002). En hábitats fragmentados, la abundancia de insectos herbívoros aumenta como resultado de una reducción de depredadores y parasitoides (efectos "top-down") (Schüepp et al. 2014; Pfeifer et al. 2017). Por el contrario, se ha observado que la calidad de la planta puede cambiar en los bordes del bosque y en pequeños fragmentos, disminuyendo la diversidad de insectos herbívoros (efectos "bottom-up") (Maguire et al. 2016; Maldonado-López et al. 2016). Por lo tanto, cambios en la cantidad de recursos para insectos herbívoros (e.g. cantidad de hojas, brotes, tamaño de la planta, cobertura del dosel) y en la calidad de la planta (e.g. contenido de nutrientes, contenido de clorofila, niveles de defensas químicas y físicas) pueden afectar la preferencia, abundancia y distribución de insectos herbívoros como consecuencia de la fragmentación del hábitat (Rautiainen et al. 2005; Endara y Coley 2010; Maldonado-López et al. 2016).

Por otro lado, las condiciones ambientales en los fragmentos de bosque, pueden aumentar el estrés de las plantas y afectar negativamente su aptitud y supervivencia (Maldonado-López et al. 2019). Cuando las condiciones ambientales exceden el umbral de perturbación que las plantas pueden soportar, se presenta una inestabilidad en el desarrollo en diferentes órganos (Rozendaal et al. 2006; Cuevas-Reyes et al. 2018). Uno de los principales biomarcadores para medir la inestabilidad del desarrollo causado por el estrés genético y ambiental es la asimetría fluctuante (AF), que describe la variación aleatoria en tamaño y forma entre los dos lados de un carácter bilateral de un organismo (Cuevas-Reyes et al. 2011; Maldonado-López et al. 2019). La AF muestra la capacidad individual durante el desarrollo para mantener la homeostasis en condiciones estresantes (Møller y Swaddle 1997; Albarrán-Lara et al. 2010). En el caso de la morfología de la hoja, estas modificaciones pueden representar ajustes morfológicos causados tanto por cambios en las condiciones ambientales como la temperatura del aire, humedad, fertilidad del suelo (Freeman et al.2005) y por factores bióticos como la presencia de patógenos e insectos herbívoros (Cuevas-Reyes et al.2011; Aguilar-Peralta et al. 2020). Algunos estudios reportan una relación positiva entre la AF y el daño foliar generado por insectos herbívoros, lo que demuestra una mayor susceptibilidad de las plantas asimétricas a los herbívoros (i.e. Hipótesis del estrés de las plantas) (Cornelissen y Stiling 2011; Cuevas-Reyes et al. 2018). Plantas en condiciones de estrés aumentan la concentración de amino ácidos y disminuyen la producción de metabolitos secundarios en sus tejidos, por lo tanto, aumentan el rendimiento de los insectos y la susceptibilidad de la planta a la herbivoría (Torrez-Terzo y Pagliosa 2007; Cornelissen y Stiling 2011). Por el contrario, otros estudios sugieren que los herbívoros pueden actuar aumentando el nivel de estrés en las plantas y, en consecuencia, hacerlas más asimétricas (Gómez et al. 2003; Santos et al. 2013; Maldonado-López et al. 2019). Por lo tanto, los recursos de la planta huésped y su calidad podrían ser afectados por los cambios en las condiciones abióticas asociados a la fragmentación que afecta indirectamente la incidencia de herbívoros (Levey et al. 2016; Rossetti et al. 2017).

SISTEMA DE ESTUDIO

Los bosques templados en México están dominados por especies de encinos (Nixon 2006). México es uno de los centros de diversificación del género *Quercus* con más de 161 especies reportadas, de las cuales 109 son endémicas a nuestro país (Nixon 1993). Los encinares son importantes debido a que proveen servicios ambientales como el reciclaje de nutrientes, el balance hídrico y el secuestro de carbono (Lewington y Streeter 1993; Nixon 1993; Kappelle 2006), además de que mantienen un conjunto de interacciones complejas con otros organismos, como son hongos, insectos, vertebrados y otras plantas, por lo que se les puede considerar como especies clave que contribuyen significativamente a mantener la diversidad en las comunidades bióticas (Lewington y Streeter 1993; Nixon 1993; Kappelle 2006).

Los bosques de encinos han sido altamente degradados debido a su conversión en agrosistemas, actividades forestales, ganadería, turismo y desarrollo urbano (Lindenmayer y Fischer 2006). Esto ha transformado los bosques maduros a otros tipos de sistemas reduciendo su área total, afectando su distribución espacial y amenazando el mantenimiento de la biodiversidad en estos paisajes (Ortego et al. 2010). Particularmente, los bosques de encino en México han sido altamente fragmentados debido a la gran importancia económica de sus árboles para materia básica para construcción, elaboración de carbón, elaboración de muebles y artesanías (Bello y Labat 1987; Valencia-Avalos y Nixon 2004), agricultura, ganadería y desarrollo urbano. Los bosques de encinos han tenido una alta deforestación (11,156 ha por año) entre el 2007 y 2015 (Mas et al. 2017). La Cuenca de Cuitzeo alberga 16 especies de robles y ha sido muy fragmentada debido a la expansión de agricultura, desarrollo urbano y deforestación (Castillo-Santiago et al. 2013), por lo tanto, las grandes poblaciones continuas de los bosques de encinos se han reducido a muchos fragmentos pequeños de tamaño variable.

Se estima que la pérdida anual de bosques es de 668,000 ha/año, de las cuales 167,000 ha corresponden a los bosques templados y 501,000 ha son de bosques tropicales. De manera que las tasas de deforestación son realmente altas; siendo del 2 %/año para los bosques tropicales y del 0.64%/año para bosques templados (Masera et al 1997; Bocco et al. 2001, 2012). Aproximadamente, el 80% de la deforestación está concentrada en las zonas Centro y Sureste de México, siendo Michoacán el estado en donde se registran tasas altas de deforestación del 1.8%/año para bosques templados, por lo que la pérdida de bosque se estima en más de 50,000 ha/año (Masera et al.1997; Bocco et al. 2001, 2012). La Cuenca de Cuitzeo ha experimentado una fuerte fragmentación en las últimas décadas (López et al. 2006; Mendoza et al. 2011). Alrededor del 20 % de la cuenca está cubierta por bosques templados de pino-encino, el sotobosque subtropical ocupa alrededor del 15 %, los pastizales inducidos menos del 15 % y los cultivos ocupan alrededor del 40 % de la cuenca (López et al. 2006; Mendoza et al. 2011). Particularmente, la Cuenca de Cuitzeo ha sido altamente fragmentada (más de 1,200 fragmentos de diferentes tamaños) resultado de la deforestación, presencia de los incendios, y cambio de uso de suelo a cultivos (Mendoza et al. 2011). Las especies más comunes son *Quercus crassipes, Q. deserticola, Q. obtusata, Q. castanea, Q. glaucoides* y *Q. resinosa*. Estos bosques se desarrollan entre los 2, 000 y 2,600 msnm, en donde se intercala formando mosaicos con el pastizal, matorral subtropical y el bosque de pino (Mendoza et al. 2011; Bocco et al. 2012).

El género *Quercus* (Fagaceae) es un grupo muy diverso de árboles de bosques templados que sustenta una gran diversidad de artrópodos de dosel (Tovar-Sánchez y Oyama 2006; Maldonado-López et al. 2018). Los artrópodos del dosel de los bosques tropicales y templados constituyen una proporción importante de la biodiversidad mundial, estimándose 6.1 millones de especies de artrópodos en el mundo (Basset et al. 2007; Hamilton et al. 2013). Particularmente, el dosel está asociado a una comunidad única y rica de especies especializadas de artrópodos (Tovar-Sánchez et al. 2013; Stork et al. 2015, 2018). Los artrópodos tienen roles ecológicos importantes, ya que participan en la regulación de la dinámica del dosel, afectando funciones del ecosistema como la descomposición, el ciclo de nutrientes, la transferencia de energía o la formación del suelo (Yang y Gratton 2014; Maguire et al. 2015; Schowalter et al. 2018). Por ejemplo, los brotes de artrópodos fitófagos alteran los patrones de producción primaria y el ciclo biogeoquímico (Medvigy et al. 2012; Schowalter 2012). Además, el dosel tiene comunidades de artrópodos con diferentes niveles tróficos, ya que los artrópodos actúan como fitófagos, depredadores, parásitos, parasitoides, polinizadores y detritívoros (Hamilton et al.2010; Nakamura et al.2017).

PREGUNTA DE INVESTIGACIÓN

¿Cómo cambia la cantidad de recursos, calidad de la planta, morfometría, asimetría fluctuante, herbivoría y diversidad de especies en comunidades de artrópodos del dosel asociados a *Quercus deserticola* entre distintos tamaños de fragmentos y el efecto borde en la Cuenca de Cuitzeo?

HIPÓTESIS

La variación en la cantidad de recursos, calidad de la planta, morfometría, asimetría fluctuante y herbivoría se incrementará con los niveles de fragmentación, así como con el efecto borde.

El efecto de borde afectará negativamente la abundancia y riqueza de artrópodos, y estará relacionada positivamente con el tamaño de fragmento.

OBJETIVO GENERAL

Determinar los cambios en la cantidad de recursos, la calidad de la planta, morfometría, asimetría fluctuante foliar, herbivoría y diversidad de especies en comunidades de artrópodos del dosel asociados a *Quercus deserticola* a lo largo de un paisaje de fragmentación de bosque en la Cuenca de Cuitzeo, Michoacán.

OBJETIVOS ESPECÍFICOS

- Determinar los cambios en la cantidad de recursos, la calidad de la planta de *Quercus deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.
- Evaluar los efectos de borde sobre la cantidad de recursos, calidad de la planta de *Quercus deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.

- Determinar los cambios en la morfometría, asimetría fluctuante y herbivoría foliar de Q. *deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.
- Evaluar los efectos de borde sobre la morfometría, asimetría fluctuante y herbivoría foliar de Q. *deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.
- Evaluar los cambios en abundancia, riqueza y composición de artrópodos del dosel arbóreo de *Q. deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.
- Evaluar los efectos de borde sobre la riqueza, abundancia y composición de artrópodos del dosel de Q. *deserticola* a lo largo de un paisaje fragmentado en la Cuenca de Cuitzeo.

ESTRUCTURA DE LA TESIS

Esta tesis doctoral está formada por dos capítulos. En el primer capítulo evaluamos el efecto del tamaño de los fragmentos de bosque y los "efectos de borde" en la relación entre la AF y herbivoría foliar a través de cambios en la cantidad de recursos y la calidad de la planta hospedera para los herbívoros en la Cuenca de Cuitzeo, Michoacán. Analizamos la importancia de los procesos "bottom-up" (i.e., vigor de la planta, calidad de la planta) sobre la comunidad de herbívoros en un paisaje de fragmentación y determinamos los cambios relacionados con la morfología de las hojas, AF, cantidad de recursos y la calidad de la planta entre los distintos tamaños de fragmento y el "efecto borde". Suponemos que los pequeños fragmentos de bosque y los bordes de los fragmentos representan condiciones ambientales adversas para las plantas con temperaturas más altas y una menor humedad y disponibilidad de agua. Por lo tanto, predecimos que los individuos de *Q. deserticola* estarán más estresados en estos hábitats y tendrán una mayor calidad de recursos (es decir, mayor contenido nutricional y menos defensas), por lo que serán más atacadas por insectos herbívoros, y exhibirán niveles más altos de AF foliar en comparación con los individuos en que ocurren en grandes fragmentos y en el interior del bosque. Además, esperamos una relación positiva entre los niveles de AF foliar de individuos de *Q. deserticola* y sus niveles de herbivoría.

En el segundo capítulo evaluamos los cambios en la estructura y composición de la comunidad de artrópodos del dosel asociados a *Quercus deserticola* a lo largo de un gradiente de fragmentación en la Cuenca de Cuitzeo. Analizamos los cambios en la abundancia y riqueza, ordenes de artrópodos y los gremios tróficos, de la comunidad de artrópodos del dosel en fragmentos de bosque de distintos tamaños, borde e interior de los fragmentos en la Cuenca de Cuitzeo. Esperamos encontrar una mayor abundancia y riqueza de artrópodos en fragmentos de bosque más grandes y en el interior del bosque, debido a que los fragmentos grandes y el interior del bosque no presentan cambios bióticos y abióticos abruptos en comparación con los fragmentos pequeños y el borde del fragmento. Para los gremios tróficos, planteamos la hipótesis de que la fragmentación afectará negativamente a los detritívoros, parasitoides y depredadores, debido a la reducción del área, mientras que los fitófagos se verán favorecidos por la reducción de sus enemigos naturales.

Trees
https://doi.org/10.1007/s00468-021-02228-2

ORIGINAL ARTICLE

Effects of forest fragmentation on plant quality, leaf morphology and herbivory of *Quercus deserticola*: is fluctuating asymmetry a good indicator of environmental stress?

Silvia Ecaterina García-Jain[1] · Yurixhi Maldonado-López[2] · Ken Oyama[3] · Marcílio Fagundes[4] · Maurício Lopes de Faria[4] · Mário M. Espírito-Santo[4] · Pablo Cuevas-Reyes[1]

Received: 19 May 2021 / Accepted: 19 October 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Key message **Habitat fragmentation influences leaf morphology, quantity and quality of plant resources to herbivores, which in turn affects the patterns of fluctuating asymmetry and herbivory in *Quercus deserticola*.**

Abstract Forest fragmentation has negative effects on biodiversity by modifying environmental conditions, ecological processes and biotic interactions. We analyzed the effects of forest fragment size and habitat type (forest edge × interior) on the amount of plant resources and their quality for herbivores, leaf morphology, fluctuating asymmetry (FA) and herbivory on *Quercus deserticola* at the Cuitzeo Basin in Mexico. Six forest fragments, where *Q. deserticola* occurs were classified as (i) small (≤ 10 ha); (ii) medium (≥ 25 ha); and (iii) large (≥ 65 ha). In each forest fragment, four parallel transects of 5 × 50 m were sampled, two located at the edge and two in the interior of the fragments. Chlorophyll content, leaf area, canopy cover and tree size were greater in small than in larger fragments. Leaves of individuals in small fragments and in forest edges were more elongated and wider than in large and in the interior of fragments. Our results also showed higher levels of FA and insect herbivory in the small fragments and forest edges. Insect herbivory was positively correlated with FA in small forest fragments, indicating that the mechanisms driving their interaction are scale-dependent and vary among habitat types according to fragment size. Our findings do not support the idea that the fluctuating asymmetry is a reliable biomarker to detect environmental stress in *Q. deserticola* in fragmented habitats, but FA may be a good biomarker of plant stress caused by the amount of herbivory damage.

Keywords Edge effect · Fluctuating asymmetry · Forest fragmentation · Herbivory · Plant quality

Introduction

Anthropogenic activities such as deforestation and land cover change to crops and pasturelands are the main causes of habitat loss and forest fragmentation (Watson et al. 2016; Scanes 2018). Fragmentation is a dynamic process in which the forest is progressively reduced to patches with different sizes, perimeters and degrees of isolation undergoing rapid and abrupt abiotic and biotic changes (Haddad et al. 2015; Fletcher et al. 2018). Usually, a decrease in fragment area causes habitat loss, leading to declining population sizes of several species, inbreeding depression and local extinction,

---

Communicated by T. Koike.

* Pablo Cuevas-Reyes
pcragalla@gmail.com

[1] Laboratorio de Ecología de Interacciones Bióticas, Universidad Michoacana de San Nicolás de Hidalgo, Ciudad Universitaria, C.P. 58030, Morelia, Michoacán, Mexico

[2] CONACyT-Instituto de Investigaciones Sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Avenida San Juanito Itzícuaro SN, Nueva Esperanza, 58330 Morelia, Michoacán, Mexico

[3] Escuela Nacional de Estudios Superiores Unidad Morelia, UNAM, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-Hacienda de San José de la Huerta, 58190 Morelia, Michoacán, Mexico

[4] Programa de Pós-Graduação em Ciências Biológicas, Laboratório de Biologia da Conservação, Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Av. Ruy Braga s/n, Caixa postal 126, Montes Claros, Minas Gerais CEP 39.401-089, Brazil

Published online: 27 October 2021

reducing species diversity (Ibáñez et al. 2014). Furthermore, small forest fragments have a higher edge-to-core ratio, with multiple consequences to biodiversity and ecosystem functioning (Jaeger et al. 2011). According to Haddad et al. (2015), approximately 20% of the world's forests is situated at less than 100 m from a forest edge. Edge effects include a higher light incidence, wind speed and temperature, and a low soil fertility and humidity compared to forest interior (Laurance et al. 2011; Delgado et al. 2007; Arroyo-Rodríguez et al. 2017). The changes in habitat structure and ecosystem functioning in small forest patches caused by fragmentation also disrupt biotic interactions such as seed and fruits dispersal, predation and herbivory (Rossetti et al. 2017; Salomão et al. 2019). Although edge-to-core gradients are well documented (Haddad et al. 2015), the extent of this peripheral effect (the depth-of-edge influence; see Harper et al. 2005) depends on the parameter under analysis (e.g., species composition, vegetation structure, tree mortality and growth rates, leaf traits, among many others) and site characteristics, varying from 100 m to 1 km (Murcia 1995; Sálek et al. 2013; Bergès et al. 2016, Govaert et al. 2020).

Insect herbivores are very sensitive to changes in environmental conditions associated with forest fragmentation (Mooney et al. 2010; Maldonado-López et al. 2016). In fragmented habitats, the abundance of insect herbivores increases as a result of a reduction of predators and parasitoids (top-down forces) (Schüepp et al. 2014; Pfeifer et al. 2017). In contrast, it has been observed that plant quality can change in forest edges and in small fragments, decreasing the diversity of insect herbivores (bottom-up forces) (Maguire et al. 2016; Maldonado-López et al. 2016). Hence, changes in amount of resource for insect herbivores (i.e., quantity of leaves and shoots, plant size, canopy cover) and in host plant quality (i.e., nutrient and chlorophyll content, levels of chemical and physical defenses) can affect the preference, abundance and distribution of insect herbivores as a consequence of habitat fragmentation (Rautiainen et al. 2005; Endara and Coley 2010; Maldonado-López et al. 2016).

The harsh environmental conditions, observed in the edge of forest fragments, can increase plant stress and negatively affect their fitness and survival (Maldonado-López et al. 2019). When environmentally stressful conditions exceed the disturbance threshold that the molecular, physiological, cellular and morphological mechanisms of plants can support, a developmental instability appears in different organs (Rozendaal et al. 2006; Cuevas-Reyes et al. 2018a). One of the main biomarkers to measure developmental instability caused by genetic and environmental stress is the fluctuating asymmetry (FA), which describes the random variation in size and shape between the two sides of a bilateral character of an organism (Cuevas-Reyes et al. 2011; Maldonado-López et al. 2019). According to Freeman et al. (2003), FA can be caused by genetic or environmental factors that disrupt side-to-side communication, impairing an organism's capacity to maintain symmetry. For plants, leaf FA is usually considered an excellent indicator of subtle development instability, responding to low stress levels (Cornelissen and Stiling 2011; Cuevas-Reyes et al. 2018a; Mendes et al. 2018). In the case of leaf shape, these modifications may represent morphological adjustments caused both by changes in environmental conditions such as air temperature and humidity, and soil fertility (Freeman et al. 2005), and by biotic factors such as the presence of pathogens and insect herbivores (Cuevas-Reyes et al. 2011; Aguilar-Peralta et al. 2020).

Some studies reported a positive relationship between FA and leaf damage, demonstrating higher susceptibility of asymmetric plants to herbivores (the plant stress hypothesis) (Cornelissen and Stiling 2011; Cuevas-Reyes et al. 2018a; but see Bañuelos et al. 2004; Telhado et al. 2010). The mechanisms underlying such pattern may be related to the plant's nutritional quality and chemical defense levels (Cornelissen and Stiling 2011). Plants under stress conditions (i.e., with higher FA) increase the concentration of amino acids and decrease the production of secondary metabolites in their tissues, which in turn, increase insect performance and plant's susceptibility to herbivory (Torrez-Terzo and Pagliosa 2007; Cornelissen and Stiling 2011). On the other hand, the herbivory per se can also be a plant stressor and the attack by insect herbivores would directly increase the levels of FA on their hosts (herbivory-induced stress hypothesis) (Cuevas-Reyes et al. 2011; Alves-Silva and Del-Claro 2016; Cuevas-Reyes et al. 2018b). Anyway, it is possible that a stronger edge effect on small forest fragments would increase plant stress, resulting in higher FA and changes in plant quality and resource availability that positively affect herbivory levels in these habitats in comparison to large fragments.

In Mexico, temperate forests are dominated by oak species (Nixon 2006) that provide environmental services such as nutrient cycling, water balance and carbon sequestration, and maintain a great diversity of canopy arthropods (Tovar-Sánchez and Oyama 2006). However, due to their great economic importance, oak forests have had high deforestation rates (11,156 ha per year) between 2007 and 2015 (Mas et al. 2017). The Cuitzeo Basin harbors 16 oak species and has been highly fragmented due to the expansion of agriculture, urban development and deforestation (Castillo-Santiago et al. 2013). In the present study, we used the oak species *Quercus deserticola* to evaluate how the forest fragment's size (and edge effects) mediates the relationship between leaf FA and herbivory, via changes on the amount of resources to herbivores and plant quality. The following questions were addressed: (i) Does leaf morphology and size of *Q. deserticola* change in function of the size of forest fragments and edge proximity? (ii) Are host plant resources, plant quality and herbivory levels affected by forest fragmentation? (iii) Does leaf fluctuating asymmetry increase with habitat fragmentation and herbivory levels? We assume that small forest fragments and forest edges have harsher environmental conditions, with higher temperature and lower humidity and water availability. Thus, we predict that the stressed individuals of *Q. deserticola* in these habitats provide a lower amount of resources with higher quality (i.e., higher nutritional content and less defenses), being more attacked by herbivorous insects. They will also exhibit higher levels of leaf FA compared to individuals in large fragments and forest core areas. As a result, we expect to find a positive relationship between the levels of leaf FA of *Q. deserticola* individuals and their herbivory intensity.

Materials and methods

Study system

Quercus deserticola Trel. (Fagaceae) is a white oak which belongs to the section *Quercus*. It is a deciduous tree, growing up to 10 m and occuring in semitropical bushes and temperate forests. Leaves of *Q. deserticola* Trel. vary from oblong-oblanceolate to lanceolate, with a slightly shiny and rough dark green upper surface and a clear underside with abundant trichomes (Arizaga et al. 2009). *Q. deserticola* is a Mexican endemic oak that inhabits in high, cold and dry regions, around the foothills of the mountains in xerophytic areas (at altitudes between 2000 and 2800 m), with a geographical distribution in the Trans-Mexican Volcanic Belt (Arizaga et al. 2009).

Study site

This study was carried out in the hydrological basin of Cuitzeo lake that has an area of 4,026 km^2 and is located in the north of the state of Michoacán, Mexico (between 19° 30'–20° 05' north and 100° 35'–101° 30'west), where *Q. deserticola* is one of the dominant oak species (Maldonado-López et al. 2016). The climate is temperate with an annual mean temperature that ranges between 14 and 20 °C and annual rainfall between 646 and 1402 mm concentrated in the summer (Mendoza et al. 2006; Carlón-Allende et al. 2009). High rates of deforestation and forest degradation occurred throughout the basin during period of 2004–2014 (Mas et al. 2017). Due to human activities such as agriculture, livestock, urbanization and deforestation, oak populations have been reduced to fragments of different sizes and shapes that cover approximately 20% of the basin (López et al. 2006).

Sampling design

Survey sampling was conducted from October to December 2019. First, we selected six permanent forest fragments, where *Q. deserticola* occurs, categorized into three size classes as follows: (i) two small fragments ≤ 10 ha in El Tigre: (8 ha) (19° 37 'N, 101° 24' W) and La Concepción: (9 ha) (19 42' N, 101° 18' W), (ii) two medium fragments ≥ 25 ha in Capula: (30 ha) (19° 42 'N, 101° 24' W) and Las Canoas: (34 ha) (19° 51' N, 101° 14' W); and (iii) two large fragments ≥ 65 ha in Atécuaro: (71 ha) (19° 37' N, 101° 10' W) and El Remolino: (76 ha) (19° 37' N, 101° 20' W). An assessment of human occupation and land use history indicates that all fragments in the Cuitzeo Lake Basin have same age (López et al. 2006). In each forest fragment, four following parallel transects of 5 × 50 m were delimited: two located at the edge of the fragment and two inside of the fragment distant at 300 m from the edge. Therefore, 15 mature individuals of *Q. deserticola* were randomly collected in each transect, totaling 30 individuals at the edge and 30 in the interior of each fragment ($n = 60$ individuals per fragment). To assess the amount of resources to insect herbivores, plant quality, leaf morphology, FA and herbivory levels, we sampled leaves at the end of the rainy season (November) after the peak of herbivore activity. In each tree, three branches were randomly collected at each canopy stratum as follows: upper, middle and lower (Cuevas-Reyes et al. 2011). To analyze leaf morphology and FA, 30 fully expanded and undamaged leaves were collected per tree (10 leaves per canopy stratum) (Cuevas-Reyes et al. 2011). Another 30 leaves were randomly selected per tree to estimate herbivory levels, (also ten leaves per canopy stratum). In general, oak community composition was different between forest fragment sizes and among interior and edges of fragments. A full characterization of oak community composition is given in Supplementary Materials (Online Appendix 1).

Quantity and quality of plant resources

In each selected tree, we measured the following parameters to quantify plant resources and quality to herbivores: (i) diameter at breast height (DBH) as plant size estimator (Cuevas-Reyes et al. 2004); (ii) canopy cover (an indicator of leaf availability) (Maldonado-López et al. 2015) was estimated using the following two different methods: first, we used a spherical densimeter, which consists of a small wooden box with a convex or concave mirror, engraved with 24 squares. Canopy cover was estimated at four different points of the canopy (North, South, East and West in relation to the tree trunk) by calculating the number of squares (or quarters of the squares) covered by the canopy in the image generated by the densimeter (Korhonen et al. 2006). The second method consisted of using a luminous flux exposure meter (lux), which measures the intensity of light flux that passes through the tree canopy per unit of time. Therefore, a lower luminous flux represents a larger canopy tree. We assessed plant quality to herbivores indirectly by quantifying the chlorophyll content using SPAD 502 (Minolta) measurements from 15 random leaves per tree. Chlorophyll content can be used as an indicator of photosynthetic capacity, primary productivity and nutritional status, because most of the plant´s nitrogen is found in different chlorophyll types (Li et al. 2018; Santos et al. 2021).

Fluctuating asymmetry measurements

We used a digital image of each sampled leaf to measure the distance from the leaf edge to the midrib at the midpoint of the leaf, to the right side (Rw) and left side (Lw), corresponding to its widest part. Since asymmetry may be size-dependent, we calculated leaf FA as the absolute value of the difference between the distances from the midrib to the right and left margins of each leaf divided by the average distance: $(|Ai—Bi|)/(Ai + Bi/2)$ (Cornelissen and Stiling 2005; Cuevas-Reyes et al. 2011, 2018a). To control the measurement error in FA, we obtained a subsample of ten leaves to re-measure without reference to previous measurements. In this subsamples, we evaluated the degree of significance of FA relative to measurement error using a two-way mixed-model ANOVA. If the interaction individual × leaf × side is significant, it indicates that variation in FA is greater than expected by measurement errors ($F_{9,25} = 18.7$; $P < 0.0001$). It is also necessary to discriminate FA from other types of asymmetry, all of which are characterized by a different combination of mean and variance of the distribution of right-minus–left (R–L) differences (Palmer and Strobeck 1986). In the case of FA, the R-minus–L differences are normally distributed with a mean value of zero. In Directional asymmetry, the R-minus–L differences are also normally distributed, but the mean is significantly greater or less than zero. In Antisymmetry, a platykurtic or bimodal distribution of R-minus–L differences with a mean of zero is found. In this context, it was necessary to confirm that our data reflected only FA. To do this, we performed a Student's t test and Lilliefors' normality test to determine whether mean values of signed R-minus–L values differed significantly from zero (Telhado et al. 2010; Alves-Silva and Del-Claro 2016). Our results showed that R-minus–L measurements did not differ from zero ($t = 0.39$; $P > 0.05$), rejecting the presence of directional asymmetry in our data. The presence of antisymmetry was also rejected, because our data (R-minus–L) exhibited a normal distribution ($P > 0.05$).

Herbivory measurements

To estimate the leaf area consumed by insect herbivores, we obtained a digital image of each leaf to calculate the total leaf area and the area removed by insect herbivores using the software Image J v1.48 (Schneider et al. 2012). The percentage of leaf area removed by herbivores was calculated for each leaf by (leaf area consumed/total leaf area) × 100. Herbivory data were transformed as arc-sine square root to meet normality (Cuevas-reyes et al. 2018a).

Morphometric measurements of leaves

We used geometric morphometric techniques to determine the differences in leaf morphology and size between trees of *Q. deserticola* from different fragments size, forest edge and forest interior. In each leaf image used to assess FA, 32 anatomical marks were placed with two additional marks as size reference. All landmarks correspond to homologous loci, which are unambiguous and repeatable marks in all the leaves, representing their shape (i.e., 'landmarks' sensu Bookstein 1991; Cuevas-Reyes et al. 2018b). We used the TpsDig program (Rohlf 2015) to record the coordinates (x, y) of the 32 landmarks in each leaf image. A Procrustes superimposition analysis was performed with the CoordGen6 program in the Integrated Morphometrics Package (IMP series: http://www.canisius.edu/~sheets/morphsoft.html). We considered the average configuration of all leaves as reference, and then we calculated the shape variables (Procrustes distances) based on superimposition coordinates to eliminate the effect of leaf size (Cuevas-Reyes et al. 2018a). We applied a canonical variate analysis (CVA) and discriminant analysis (DA) to determine shape differences between different fragment size, habitat type (edge × interior) of all fragments, edge and interior by fragment size. The CVA test produces ordination plots indicating the differences in the shape of the leaves, whereas DA test provides reliable information on the classification of the leaf shape by calculating morphological classification tables with cross-validated. A DA was performed using cross-validated scores classification tables with T^2 statistics (P value for tests with 1000 permutations < 0.0001) while CVA, the statistical significance of pairwise differences in mean shapes was assessed with permutation tests (T^2 statistics; 10 000 permutations per test) using the Mahalanobis distance in the MophoJ v1.07a (Klingenberg 2011).

Statistical analyses

Spatial autocorrelation

Spatial autocorrelation is a common phenomenon of ecological distributions, because closer geographic areas tend to be more similar than expected by random (Schiegg 2003).

Therefore, if there is spatial variation in the quality and quantity of plant resources, as well as in the levels of FA and herbivory, it is possible to expect that *Q. deserticola* individuals that occur in neighboring forest fragments have similar quality and quantity of plant resources, as well FA and herbivory levels regardless of their size. In this way, we performed a spatial autocorrelation analysis using the Moran's *I* coefficient, which measures the degree of correlation between the values of a particular variable as a function of spatial location (Deléglise et al. 2011). Thus, this coefficient indicates whether the data have a scattered, clustered or random spatial distribution pattern. In addition, the Moran's *I* values range from − 1 to 1, where values close to 1 and – 1 indicate high positive and negative spatial autocorrelation, respectively, and values close to 0 represent a random spatial distribution (i.e., no spatial relationship) (Fu et al. 2014). The values of Moran coefficient can be visualized in a scatterplot, where the *x*-axis is represented by the original variable studied, the *y*-axis represents the spatially lagged variable and the slope of the linear fit is the value of the Moran coefficient (Bonada et al. 2012). For this analysis, a distance-weight matrix with the variables of the x- and y-coordinates was used as the east and north coordinates, as well as a distance band estimated automatically from the inverse of the distance using the GeoDA 1.8 software (Fu et al. 2014).

Effects of fragment size and habitat type

We used general linear mixed models (GLMM) to analyze the differences in leaf area, diameter at breast height, chlorophyll content, canopy cover, FA and herbivory (a separate model for each of these response variables) among fragment size classes (small × medium × large) and habitat types (edge × interior). Fragment size and habitat type were considered as the independent variables and site as a random effect. For GLMM analysis luminous flux data were transformed to log values. Residuals were normally distributed in all cases. We also perform a Principal Component Analysis (PCA) to evaluate the variation in plant resources and quality, FA and herbivory between forest fragment size classes.

Effects of plant resources and quality on herbivory

A Spearman correlation was performed to determine the relationships between herbivory and leaf area, DBH, chlorophyll content, canopy cover, luminous flux and FA levels. All these analyses were performed in SAS ver. 11 (SAS 2000).

We conducted mixed-effect analyses of covariance (ANCOVA tests) to determine whether plant quality and FA covariate with herbivory among fragment size classes (small × medium × large) and habitat types (edge × interior) (Baskett and Schemske 2018). In a first set of ANCOVA tests, forest fragments, plant quality, FA and the interaction between forest fragments × plant quality or FA were considered as independent variables. Study site was considered as a random factor and herbivory as response variable (Baskett and Schemske 2018). In a second set of ANCOVA tests, habitat type (edge × interior), plant quality, FA and the interactions between habitat type × FA and plant quality × FA were considered as independent variables, study site as a random factor and herbivory as response variable (Baskett and Schemske 2018).

Results

Spatial autocorrelation

We detected values of the Moran's *I* coefficient were close to 0 to all parameters related to the quantity (leaf area = − 0.028; DBH = − 0.022; canopy cover = − 0.080; luminous flux = − 0.020) and quality (chlorophyll content = 0.035) of plant resources, as well as in the FA (− 0.060) and herbivory (− 0.032) of *Q. deserticola* individuals growing in different fragment sizes, indicating a random spatial distribution of our data. This confirms that all forest fragments can be considered independent data points in all statistical analyzes. The scatterplots of values of Moran's coefficient for each response variable analyzed were included in the Supplementary Materials (Online Appendix 1).

Effects of fragment size and habitat type

According to general linear models' analyses, leaf area, DBH, chlorophyll content, canopy cover, luminous flux, FA and herbivory varied between fragments of different size classes (Table 1). Individuals of *Q. deserticola* growing in small forest fragments had higher leaf area, chlorophyll content, canopy cover, FA and herbivory in comparison with those in medium and large fragments (Fig. 1). We also found differences in DBH, luminous flux, FA and herbivory between the edge and the interior of the forest fragments. However, no significant differences were found in leaf area, chlorophyll content and canopy cover among habitat types (Table 1). The DBH, luminous flux and chlorophyll content were higher in the interior of fragments compared with the edges. The opposite patter was observed for FA and herbivory (Fig. 1).

The effects of fragments size on plant resources and quality, FA and herbivory were reinforced by the PCA, which indicated that more than 58.8% of the variation among individuals was explained by the first two component axes. The first PCA axis accounted for 43.9% of overall variation and

Table 1 Summary of the results of mixed models testing the effects of fragment size class (small, medium and large fragments), habitat type (interior and edge) and their interaction on plant resources and quality, FA and herbivory.

Response variable	Explanatory variable	*d.f.*	*F*	*P* <
Leaf area (cm^2)	Fragment size	2	48.6	0.008*
	Habitat type	1	3.4	0.07
	Fragment size × Habitat type	2	0.3	0.76
DBH (cm)	Fragment size	2	10	0.04*
	Habitat type	1	11.4	0.0009*
	Fragment size × Habitat type	2	26.7	0.0001*
Chlorophyll (SPAD units)	Fragment size	2	13.3	0.02*
	Habitat type	1	1.3	0.25
	Fragment size × Habitat type	2	5.3	0.005*
Canopy cover (%)	Fragment size	2	23.2	0.01*
	Habitat type	1	0.23	0.63
	Fragment size × Habitat type	2	4.9	0.009*
Luminous flux (lux)	Fragment size	2	14.6	0.02*
	Habitat type	1	17.7	0.0001*
	Fragment size × Habitat type	2	5.1	0.006*
FA	Fragment size	2	42.8	0.006*
	Habitat type	1	36.9	0.0001*
	Fragment size × Habitat type	2	4.8	0.009*
Herbivory (%)	Fragment size	2	10.1	0.04*
	Habitat type	1	48.3	0.0001*
	Fragment size × Habitat type	2	3.2	0.04*

The asterisk indicates the plant variables that were significantly different

was associated to chlorophyll content, DBH, canopy cover, leaf area, herbivory and FA on the right side. The second PCA axis explained 14.9% of the total variation, with a substantial contribution of the luminous flux as observed by the high individual loadings (Fig. 2).

Effects of plant resources and quality on herbivory

In general, significant positive relationships were observed between herbivory and leaf area, FA, DBH, chlorophyll content and canopy cover (in descending order of R coefficient values). On the other hand, the herbivory and luminous flux were negatively correlated (Table 2). Thus, herbivory was higher on individuals of *Q. deserticola* with higher resource availability and quality at the fragment scale. A negative relationship was found between luminous flux with all variables analyzed (Table 2).

The results of mixed models ANCOVA showed that only leaf area and FA covaried with herbivory along forest fragment size classes (Table 3a). The covariation between leaf area and herbivory was positive in small ($R^2 = 0.17$, $P = 0.002$) and medium fragments ($R^2 = 0.23$, $P = 0.005$), but no significant relationship was detected in large forest fragments ($R^2 = 0.05$, $P = 0.10$). In the same way, FA covaried positively with herbivory in small ($R^2 = 0.33$, $P = 0.0001$) and large forest fragments ($R^2 = 0.23$, $P = 0.0003$), but not in medium fragments ($R^2 = 0.03$, $P = 0.23$). We found that only FA covaried positively with herbivory both in the edge ($R^2 = 0.39$, $P = 0.0001$) and the interior of the forest fragments ($R^2 = 0.37$, $P = 0.0001$) (Table 3b).

Leaf morphology

Leaf morphology of *Q. deserticola* individuals was different among forest fragments of different size classes and habitat types. The coordinate superimposition analysis showed that leaves of individuals of small fragments were more elongated and wider in comparison with leaves of individuals of medium and large fragments (Fig. 3a). The canonical variate analysis distinguished three groups, segregating individuals according to fragment size class. The CVA 1 explains 58.25% of total variance; (Axis 1 $\lambda = 0.853$ *d.f.* = 120 $P < 0.0001$, Axis 2 $\lambda = 0.935$ *d.f.* = 59 $P < 0.0001$) (Fig. 3b). The discriminant analysis revealed significant differences between fragments from different size classes. The Mahalanobis distances and the T^2 value were 0.74, 155.36 (small *vs.* large fragments), 0.68, 126.73 (small *vs.* medium) and 0.71, 145.05 (medium vs. large). All pairwise comparison tests T^2 were significant ($P < 0.0001$). Leaves of *Q. deserticola* individuals growing in forest edges were more elongated and wider than in the interior of the fragments (Fig. 1c), and the CVA 1 explained 52.27% of the total of variance ($\lambda = 0.880$ *d.f.* = 60 $P < 0.0001$) (Fig. 3d). The discriminant analysis indicated differences among the

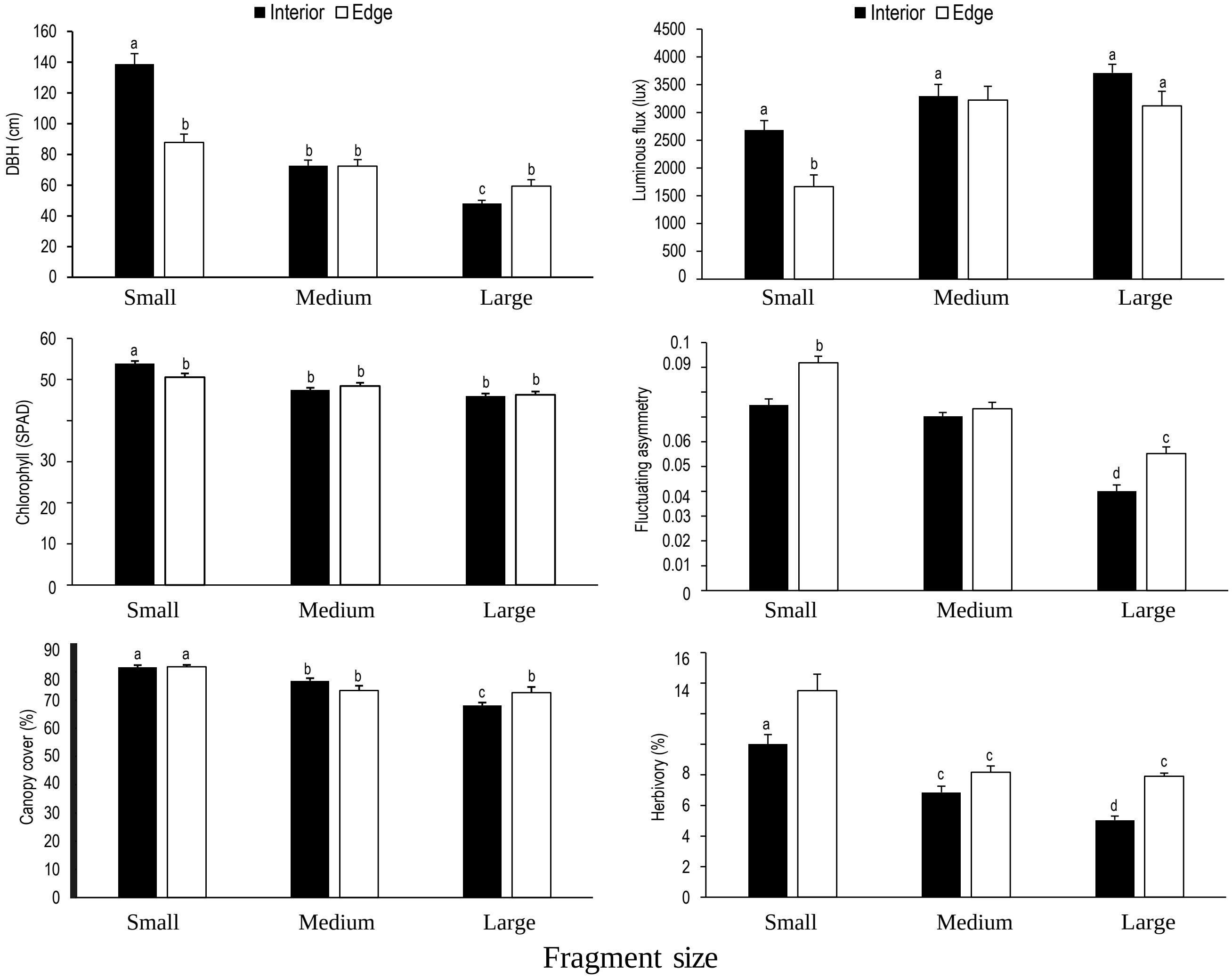


Fig. 1 Plant resources and quality, leaf FA and herbivory in *Quercus deserticola* in three forest fragments size classes and two habitat types (interior and edge of fragments). Different letters indicate statistically significant differences ($P < 0.05$). Untransformed herbivory data and standard error bars are show

interior and the edge of forest fragments (Mahalanobis distance = 0.73 and the $T^2 = 229.42$ for habitat type).

Discussion

Effects of fragment size and habitat type on quantity and quality of plant resources

The present study detected signifi fragment size and edge eff on the amount and quality of resources for herbivorous insects, and also on FA and herbivory intensity. Abiotic changes associated with forest fragmentation,

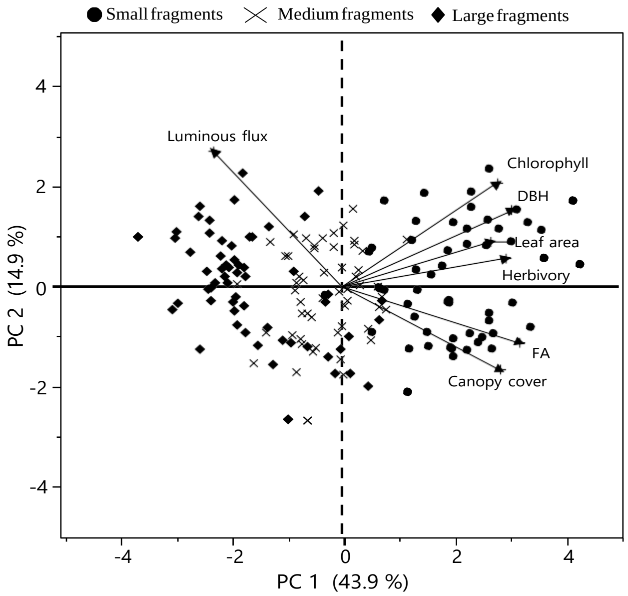


Fig. 2 Biplot showing the results of principal component analysis (PCA) of plant resources and quality, FA and herbivory in *Quercus deserticola* for fragments from different size classes

such as increasing wind speed, light availability and temperature, and decreasing soil moisture and nutrients, can directly affect plant quality (Tuff et al. 2016; Arroyo-Rodríguez et al. 2017; Schmidt et al. 2019). For example, Maldonado-López et al. (2015) showed that individualls of *Q. castanea* and *Q. deserticola* had higher DBH, height and canopy cover in small fragments and in the forest edge in comparison to conspecifics in larger fragments, as a consequence of higher solar radiation and temperature. Our results show that chlorophyll content was higher in individuals of *Q. deserticola* in small than in medium and large fragments. The chlorophyll content is related to a higher photosynthetic capacity per unit of leaf area (Souza et al. 2004), and depends on environmental factors such as the incidence of light, temperature and precipitation (Bielinis et al. 2015). Therefore, more light incidence in plants that grow in small fragments or the edge of the fragments can represent a higher photosynthetic capacity and carbon fixation in the form of carbohydrates, which in turn, increase plant growth rate (Thompson et al. 2017; Killi et al. 2018; Ghorbanzadeh et al. 2020). This idea

Table 2 Spearman's correlation coefficients of the pairwise relations between all variables related to plant resource availability and quality, FA and herbivory, considering all forest fragments regardless of their size ($P < 0.05$)

	Leaf area	DBH	Chlorophyll content	Canopy cover	Luminous flux	FA	Herbivory
Leaf area		0.33*	0.32*	0.24*	– 0.22*	0.32*	0.45*
DBH			0.52*	0.42*	– 0.22*	0.47*	0.35*
Chlorophyll content				0.30*	– 0.17*	0.25*	0.34*
Canopy cover					– 0.62*	0.46*	0.24*
Luminous flux						– 0.39*	– 0.31*
FA							0.43*
Herbivory							

* Significant values of the correlations

Table 3 Results of the mixed-effects ANCOVA testing the effects of fragment size (small vs. medium vs. large), leaf area, FA and their interaction (fragment size × leaf area and fragment size × FA) on herbivory (a), and the effects of habitat type (edge × interior), FA and their interaction (habitat type × FA) on herbivory (b)

Response variable	Explanatory variable	*df*	*F*	*P* <
(a) Effects of fragment size				
Herbivory (%)	Fragment size	2	1.49	0.04*
	Leaf area	1	33.38	0.0001*
	Fragment size × Leaf area	2	3.76	0.0103*
Herbivory (%)	Fragment size	2	3.05	0.03*
	FA	1	16.17	0.0001*
	Fragment size × FA	2	10.59	0.0002*
(b) Effects of habitat type				
Herbivory (%)	Habitat type	2	27.49	0.0001*
	FA	1	13.36	0.0004*
	Habitat type × FA	2	0.12	0.72

Only models with significant results are shown

*Significant values

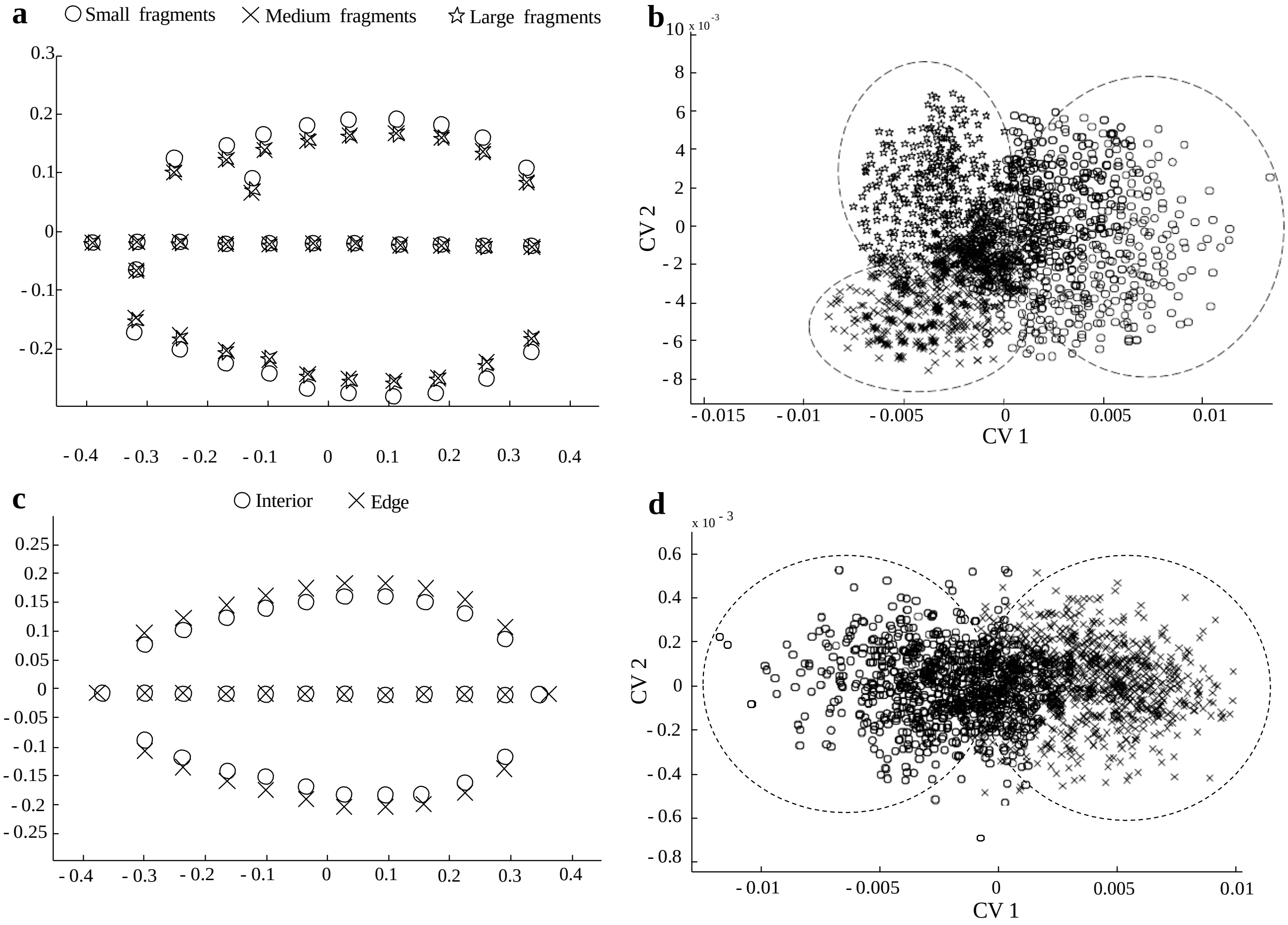


Fig. 3 Leaf morphological variation of *Quercus deserticola*. **a** Morphological differences among fragments from different size classes. The shape shows the average of the coordinates of the configuration of the leaves; **b** differences in leaf shape morphology among fragments from different size classes according to the canonical variate analysis (CVA); **c** morphological differences among the forest interior and edge. The shape shows the average of the coordinates of the configuration of the leaves; and **d** differences in leaf shape morphology between forest interior and edge according to the canonical variate analysis (CVA)

agrees with our results, since individuals of *Q. deserticola* in small fragments had higher DBH, chlorophyll content and canopy cover. In addition, individuals that occur in the edge of the fragments had lower DBH and luminous fl that passes through its canopy. One possible explanation for these results is that abiotic conditions in small fragments and the edge of the fragments change more abruptly than in large fragments and the interior of fragments (Silva and Simonetti 2009), affecting the plant growth by increasing canopy cover and leaf production.

Allometric theories suggest that size and shape of organisms follow universal rules assuming that mean values of plant branching traits characterize the network architecture and providing a mechanistic basis for scaling physiological processes such as metabolic rate with plant size (Mäkelä and Valentine 2006). Shinozaki et al. (1964a, b) proposed the pipe model theory that it suggests that a unit quantity of leaves is supported by a unit pipe that has a constant cross-sectional area and connects the leaves down with the base of the stem, obtaining an estimation of number of leaves, photosynthesis and respiration rates. In addition, Shinozaki et al. (1964a, b) find that a constant relationship between foliage mass and wood area, that which governs the degree of carbon gain by photosynthesis and loss of water by transpiration. In our study, we found a positive relationship between leaf area with DBH, canopy cover and chlorophyll content, suggesting that individuals of *Q. deserticola* that grow in small fragments and at the edge of the fragments would have a greater carbon gain by photosynthesis which is expressed in a higher chlorophyll content in the leaves according to the pipe model theory proposed by Shinozaki et al. (1964a, b).

Some studies have documented that forest fragmentation aff quantity and quality of plant resources to herbivores (Ruíz-Guerra et al. 2010; Maldonado-López et al. 2015). Microclimatic conditions at forest fragments are characterized by high incidence of solar radiation and temperature, low relative humidity and water availability and soil fertility (Murcia 1995; Bernaschinia et al. 2019), which in turn can reduce plant nutritional quality and increase chemical defense (Cuevas-Reyes et al. 2013; Maldonado-López et al. 2015). For example, in conditions of a low water availability that is typically associated with both high temperatures and the incidence of UV radiation (Xu et al. 2010; Ramakrishna et al. 2011), plant growth is affected and thus, plants tend to decrease both the absorption and the use of nitrogen and carbon, reducing the nutritional quality of the leaves and generating a surplus of carbohydrates available for the synthesis of carbon-based defenses, accumulating secondary metabolites such as terpenes, alkaloids and phenolic compounds (de Matos Nunes et al. 2014, Niinemets 2015; Piasecka et al. 2017). Therefore, biosynthetic pathways of primary metabolism are affected when plants tend to decrease the absorption and use of nitrogen and carbon, reducing leaf nutritional quality and increasing chemical defenses (Ramakrishna and Ravishankar 2011; Brunner et al., 2015). In addition, temperature can influence the regulation, permeability and intracellular reactions rate of secondary metabolites, increasing terpenoid biosynthesis, as it was detected in *Quercus rubra* and *Q. alba* (Hanson & Sharkey 2001). Thus, plants are able to respond to high solar radiation increasing the production and accumulation of secondary metabolites such as phenolic compounds, triterpenoids, and flavonoids (Ghosh et al. 2018; Isah & Umar 2018). For example, the accumulation of flavonoids is due in many cases to UV-exposure, which giving protection to leaves (Hectors et al 2012). These facts affect insect herbivores preference and performance (Kolb et al., 2016).

Effects of quantity and quality of plant resources on herbivory

Our results indicated that herbivory levels were higher on *Q. deserticola* individuals that occur in small fragments and in the edges of the fragments, where the amount of plant resources and their nutritional quality was higher (i.e., chlorophyll content, DBH and canopy cover). This pattern agrees with the findings of Maldonado-López et al. (2016), who reported that oak quality and herbivory levels were higher in small fragments compared to large fragments. Therefore, we propose that abiotic conditions in small fragments and the edge of fragments change more abruptly than in larger fragments and in the interior of the fragments, increasing plant quality (i.e., canopy cover, chlorophyll content and plant size), which in turn increases the herbivory levels (Trombulak and Frissell 2000; Karban 2007; Silva and Simonetti 2009). Our results support "the plant vigor hypothesis" (Price 1991) that proposes that herbivorous insects preferentially feed on large and more vigorously growing plants, because their higher nutritional quality increases offspring performance. A meta-analysis involving 161 independent comparisons confirmed that herbivorous insects were significantly more abundant on more vigorous plants (Cornelissen et al. 2008). In accordance with this idea, we propose that individuals of *Q. deserticola* growing in small fragments and in fragment edges are more vigorous, representing resources of higher nutritional content and low concentration of chemical defenses for insect herbivores.

We demonstrated that individuals of *Q. deserticola* exhibited significantly higher levels of FA and herbivory in small fragments and in the fragment edges, as well as a positive relationship between FA and herbivory. These results agree with other studies (Lempa et al. 2000; Maldonado-López et al 2019) and can be explained in two different ways. The first is that insect herbivory directly causes stress on host plants, resulting in higher levels of FA (Gómez et al. 2003; Santos et al. 2013; Maldonado-López et al. 2019). It has been shown that herbivory damage can lead to alterations in the developmental instability (i.e., ability of a genotype to develop the same phenotype regardless of environmental conditions, where leaves damaged by insects show small deviations from perfect symmetry, indicating high levels of stress expressed in higher levels of fluctuating asymmetry compared to undamaged leaves (Møller & Shykoff 1999; Alves-Silva & Del-Claro 2016). Alternatively, plants with higher FA might be more susceptible to herbivory as results of chemical or nutritional differences between symmetric and asymmetric leaves (Lempa et al. 2000; Ribeiro et al. 2013). For example, studies performed in *Quercus laevis* and *Q. geminata*, as well as in *Epirrita autumnata* indicated that asymmetric leaves had higher nitrogen and sugar concentrations, respectively, and lower concentrations of secondary metabolites such as tannins and gallotannins than symmetric leaves (Lempa et al. 2000; Cornelissen & Stiling 2005). In this way, host plant resources and their quality could be affected by changes in abiotic conditions associated to forest fragmentation indirectly affecting herbivore incidence (Levey et al. 2016; Rossetti et al. 2017). However, since herbivory was measured at the end of the rainy season (accumulated herbivory) it was not possible to detect whether asymmetric leaves were present before herbivore attack or whether herbivores preferentially attack asymmetric leaves. This limitation can be overcome by conducting experimental studies of insect herbivores exclusion under controlled conditions and/or field studies that consider measurements of FA, nutritional quality and secondary metabolites before leaves are damaged by insect herbivores (Lempa et al. 2000; Cornelissen and Stiling 2011; Alves-Silva and Del-Claro 2016).

Leaf morphology

We found that leaves of individuals from sites exposed to greater intensity of light (i.e., small fragments and the edge of the fragments) had wider and elongated leaves compared to leaves of individuals growing in medium and large fragments, and inside the fragments. Plants respond to biotic and abiotic changes generated by habitat fragmentation through morphological, physiological and chemical adjustments, according to their ability to tolerate environmental stress (Schöb et al. 2013; Cuevas-Reyes et al. 2018a). These adjustments imply changes such as expansions or reductions in leaf shape and size (Cuevas-Reyes et al. 2018a; Derroire et al. 2018), according to both the degree of phenotypic plasticity and the tolerance of individuals to environmental stress imposed by forest fragmentation (Møller and Shykoff 1999; Agrawal 2001; Viscosi 2015). Plants in small fragments and fragment edges are subject to greater environmental stress due to changes in abiotic conditions (Murcia 1995), which influences the shape of the leaves (Graham et al. 2010). A general pattern was reported by Steinger et al. (2003), where exposure to low light intensities induces leaf elongation to maximize the absorption of light to meet the demands of photosynthesis, while exposure to high intensities of light causes a reduction in leaf area (Givnish et al. 2004; Kromdijk et al. 2016). Our results were opposite to the general pattern, and may be explained by the resources availability hypothesis (Coley et al. 1985), which predicts that plants develop grow faster and produce larger leaves in sites with higher resource availability (i.e., incidence of light and nitrogen). Therefore, increased light intensity in small fragments and fragment edges can be associated with high photosynthetic rates, faster growth, and larger leaves (Lohbeck et al. 2015).

Some studies have shown that leaf shape can affect the choice of feeding and oviposition sites for insect herbivores, as a result of visual appearance that can delay feeding time, limit access to other areas, or cause non-selection of the leaves (Rivero-Lynch et al. 1996; Campitelli et al. 2008; Higuchi and Kawakita 2019). For example, in Heliconius butterflies it was observed that the preference for oviposition sites is determined by the leaf shape, resulting from a visual selection by females, suggesting that insect herbivores are capable of distinguish leaf shape traits related to palatability (Williams and Gilbert 1981 Dell'Aglio et al. 2016). In our study, more elongated and wider leaves of individuals in small fragments had higher herbivory levels in comparison with shorter and narrower leaves of *Q. deserticola* individuals that occurred in medium and large fragments. However, further studies are necessary to determine the role of leaf shape on the observed differences in herbivory on *Q. deserticola* among fragment sizes and habitat types.

In conclusion, our results showed that habitat fragmentation, which creates small fragments with intense edge effects causes changes in *Q. deserticola* traits related to leaf morphology and FA, as well as in the amount of resources and their quality to insect herbivores. Such changes make the host plants more susceptible to the attack by insect herbivores, suggesting that bottom-up forces driving plant–herbivore interactions are affected by forest fragmentation. More vigorous plants in the highly fragmented habitats may represent key resources for insect herbivores due to their high nutritional quality and low concentration of chemical defenses. Since many insect species are associated to *Q. deserticola* and the oak species, it is important to conserve Mexican oaks throughout the fragmented landscapes. Our findings do not support the idea that the fluctuating asymmetry is a reliable biomarker to detect environmental stress in *Q. deserticola* in fragmented habitats, but FA may be a good biomarker of plant stress caused by the amount of herbivory damage. In addition, our study shows how the complex relationship between FA and herbivory is modified by forest fragmentation because of the several abiotic and biotic factors involved that can affect plant–herbivore interactions. More investigation, possibly using experimental approaches, is fundamental to unravel the effects of abiotic factors on *Q. deserticola* chemistry and physiology, to determine the stress conditions driving FA and herbivory in this species.

Author contribution statement Conceptualization: SEGJ, YML, KO and PCR. Methodology: YML, MF, MLF and PCR. Formal analyses: SEGJ, MF, MLF and PCR. Writing—original draft: SEGJ, YML, KO, MMES and PCR. Writing—review and editing: SEGJ, YML, KO, MF, MLF, MMES and PCR.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00468-021-02228-2.

Acknowledgements García-Jain is a doctoral student from the Programa de Doctorado Institucional en Ciencias Biológicas, Universidad Michoacana de San Nicolás de Hidalgo (UMSNH) and was supported by CONACyT (scholarship no. 305239) and PFCTI/ICTI/2019/A/315. The study was funded by Coordination of Scientific Research (UMSNH), as part of research project 002. This project was supported by CONACYT PDC2016-Project-3053.

Data availability Data will be made available upon request.

Declarations

Conflict of interest All authors declare that they have no conflict of interest. The work represents an original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

References

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. Science 294:321–326. https://doi.org/10.1126/science.1060701

Aguilar-Peralta JS, González-Rodríguez A, Maldonado-López Y, Fagundes M, Faria ML, Ávila-Cabadilla LD, Álvarez-Añorve MY, Cuevas-Reyes P (2020) Contrasting patterns of morphology, fluctuating asymmetry and leaf herbivory in three plant species of different successional stages of a tropical dry forest. Trees 34:1075–1086. https://doi.org/10.1007/s00468-020-01982-z

Alves-Silva E, Del-Claro K (2016) Herbivory causes increases in leaf spinescence and fluctuating asymmetry as a mechanism of delayed induced resistance in a tropical savanna tree. Plant Ecol Evol 149:73–80. https://doi.org/10.5091/plecevo.2016.1093

Arizaga S, Martínez-Cruz J, Salcedo-Cabrales M, Bello-González MA (2009) Manual de la biodiversidad de encinos michoacanos. Secretaría de Medio Ambiente y Recursos Naturales, México. D.F.

Arroyo-Rodríguez V, Saldaña-Vázquez RA, Fahrig L, Santos BA (2017) Does forest fragmentation cause an increase in forest temperatura? Ecol Res 32:81–88. https://doi.org/10.1007/s11284-016-1411-6

Bañuelos MJ, Sierra M, Obeso JR (2004) Sex, secondary compounds and asymmetry: effects on plant–herbivore interaction in a dioecious shrub. Acta Oecol 25:151–157. https://doi.org/10.1016/j.actao.2004.01.001

Baskett CA, Schemske DW (2018) Latitudinal patterns of herbivore pressure in a temperate herb support the biotic interactions hypothesis. Ecol Lett 21:578–587. https://doi.org/10.1111/ele.12925

Bergès L, Avon C, Arnaudet L, Archaux F, Chauchard S, Dupouey JL (2016) Past landscape explains forest periphery-to-core gradient of understorey plant communities in a reforestation context. Divers Distrib 22:3–16

Bernaschinia ML, Trumper E, Valladares G, Salvo A (2019) Are all edges equal? Microclimatic conditions, geographical orientation and biological implications in a fragmented forest. Agr Ecosyst Environ 280:142–151. https://doi.org/10.1016/j.agee.2019.04.035

Bielinis E, Jozwiak W, Robakowski P (2015) Modelling of the relationship between the SPAD values and photosynthetic pigments content in *Quercus petraea* and *Prunus serotina* leaves. Dendrobiology 73:125–134

Bonada N, Dole´S, Statzner, (2012) Spatial autocorrelation patterns of stream invertebrates: exogenous and endogenous factors. J Biogeogr 39:56–68. https://doi.org/10.1111/j.1365-2699.2011.02562.x

Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology. Cambridge University Press, New York

Brunner I, Herzog C, Dawes M, Arend M, Sperisen C (2015) How tree roots respond to drought Front. Plant Sci 6:547. https://doi.org/10.3389/fpls.2015.00547

Campitelli BE, Simonsen AK, Wolf AR, Manson J, Stinchcombe J (2008) Leaf shape variation and herbivore consumption and performance: a case study with *Ipomoea hederacea* and three generalists. Arthropod-Plant Int 2:9–19. https://doi.org/10.1007/s11829-007-9028-x

Carlón-Allende T, Mendoza ME, López-Granados E, Morales-Manilla LM (2009) Hydrogeographical regionalization an approach for evaluating the effect of land cover change in watersheds A case study in the Cuitzeo lake watershed, central Mexico. Water Resour Manag 23:2587–2803. https://doi.org/10.1007/s11269-008-9398-6

Castillo-Santiago MA, Ghilardi A, Oyama K, Hernández-Stefanoni JL, Torres I, Flamenco-Sandoval A, Fernández A, Mas JF (2013) Estimating the spatial distribution of woody biomass suitable for charcoal making from remote sensing and geostatistics in central Mexico. Energy Sustain Dev 17:177–188. https://doi.org/10.1016/j.esd.2012.10.007

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899. https://doi.org/10.1126/science.230.4728.895

Cornelissen T, Stiling P (2005) Perfect is best: Low leaf fluctuating asymmetry reduces herbivory by leaf miners. Oecologia 142:46–56. https://doi.org/10.1007/s00442-004-1724-y

Cornelissen T, Stiling P (2011) Similar responses of insect herbivores to leaf fluctuating asymmetry. Arthropod Plant Int 5:59–69. https://doi.org/10.1007/s11829-010-9116-1

Cornelissen T, Fernandes GW, Vasconcellos-Neto J (2008) Size does matter: Variation in herbivory between and within plants and the plant vigor. Oikos 117:1121–1130. https://doi.org/10.1111/j.0030-1299.2008.16588.x

Cuevas-Reyes P, Quesada M, Hanson P, Dirzo R, Oyama K (2004) Diversity of gall-forming insects in a Mexican tropical dry forest the importance of plant species richness, life forms, host plant age and plant density. J Ecol 92:707–716. https://doi.org/10.1111/j.0022-0477.2004.00896.x

Cuevas-Reyes P, Oyama K, González-Rodríguez A, Fernandes GW, Mendoza-Cuenca L (2011) Contrasting herbivory patterns and leaf fluctuating asymmetry in *Heliocarpus pallidus* between different habitat types within a Mexican tropical dry forest. J Trop Ecol 27:383–391. https://doi.org/10.1017/S026646741100006X

Cuevas-Reyes P, Gilverti L, González-Rodríguez A, Fernándes GW (2013) Patterns of herbivory and fluctuating asymmetry in *Solanum lycocarpum* St. Hill (Solanaceae) along an urban gradient in Brazil. Ecol Indic 24:557–561. https://doi.org/10.1016/j.ecolind.2012.08.011

Cuevas-Reyes P, Canché-Delgado A, Maldonado-López Y, Fernandes GW, Oyama K, González-Rodríguez A (2018a) Patterns of herbivory and leaf morphology in two Mexican hybrid oak complexes: Importance of fluctuating asymmetry as indicator of environmental stress in hybrid plants. Ecol Indic 90:164–170. https://doi.org/10.1016/j.ecolind.2018.03.009

Cuevas-Reyes P, Pereira GC, Gélvez-Zúñiga I, Fernandes GW, Venâncio H, Santos JC, Maldonado-López Y (2018b) Effects of ferric soils on arthropod abundance and herbivory on *Tibouchina heteromalla* (Melastomataceae): is fuctuating asymmetry a good indicator of environmental stress? Plant Ecol 219:69–78. https://doi.org/10.1007/s11258-017-0778-y

de Matos Nunes J, Bertodo LOO, Da Rosa LMG, Von Poser GL, Rech SB (2014) Stress induction of valuable secondary metabolites in *Hypericum polyanthemum* acclimatized plants. S Afr J Bot 94:182–189. https://doi.org/10.1016/j.sajb.2014.06.014

Deléglise C, Loucougaray G, Alard D (2011) Spatial patterns of species and plant traits in response to 20 years of grazing exclusion in subalpine grassland communities. J Veg Sci 22:402–413. https://doi.org/10.1111/j.1654-1103.2011.01277.x

Delgado JD, Arroyo NL, Arévalo JR, Fernández-Palacios JM (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landsc Urban Plan 81:328–340. https://doi.org/10.1016/j.landurbplan.2007.01.005

Dell'Aglio DD, Losada ME, Jiggins CD (2016) Butterfly learning and the diversification of plant leaf shape. Front Ecol Evol 4:81. https://doi.org/10.3389/fevo.2016.00081

Derroire G, Powers JS, Hulshof CM, Varela LEC, Healey JR (2018) Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica. Sci Rep 8:285. https://doi.org/10.1038/s41598-017-18525-1

Endara MJ, Coley PD (2010) The resource availability hypothesis revisited: a meta-analysis. Func. Ecol. 25:389–398. https://doi.org/10.1111/j.1365-2435.2010.01803.x

Fletcher JR, Didham RJ, Banks-Leite RK, Barlow C, Ewers J, Rosindell RM, Holt J, Gonzalez RD, Pardini A, Damschen R, Melo EI, Ries FPL, Prevedello L, Tscharntke JA, Laurance T, Lovejoy WF, Haddad NM (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15

Freeman DC, Brown ML, Dobson M, Jordan Y, Kizy A, Micallef C, Hancock LC, Graham JH, Emlen JM (2003) Developmental instability: measures of resistance and resilience using pumpkin (*Cucurbita pepo* L.). Biol J Linn Soc 78:27–41. https://doi.org/10.1046/j.1095-8312.2003.00123.x

Freeman DC, Brown ML, Duda JJ, Graraham JH, Emlen JM, Krzysik AJ, Balbache H, Kovacicf DA, Zak JC (2005) Leaf fluctuating asymmetry, soil disturbance and plant stress: a multiple year comparison using two herbs, *Ipomoea pandurata* and *Cnidoscolus stimulosus*. Ecol Ind 5:85–95

Fu WJ, Jiang PK, Zhou GM (2014) Zhao KL (2014) Using Moran's I and GIS to study the spatial pattern of forest litter carbon density in a subtropical region of southeastern China. Biogeosciences 11:2401–2409. https://doi.org/10.5194/bg-11-2401-2014

Ghorbanzadeh P, Aliniaeifard S, Esmaeili M, Mashal M, Azadegan B, Seif M (2020) Dependency of growth, water use efficiency, chlorophyll fluorescence, and stomatal characteristics of lettuce plants to light intensity. J Plant Growth Regul 1:17. https://doi.org/10.1007/s00344-020-10269-z

Ghosh S, Watson A, González-Navarro OE et al (2018) Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. Nat Protoc 13:2944–2963. https://doi.org/10.1038/s41596-018-0072-z

Givnish TJ, Montgomery RA, Goldstein G (2004) Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. Am J Bot 91:228–246. https://doi.org/10.3732/ajb.91.2.228

Gómez JM, García D, Zamora R (2003) Impact of vertebrate acorn and seedling predators on a Mediterranean *Quercus pyrenaica* forest. For Ecol Manag 180:125–134

Govaert S, Meeussen C, Vanneste T, Bollmann K, Brunet J, Cousins SA, Diekmann M, Graae Bente J, Hedwall P, Heinken T, Iacopetti G, Lenoir J, Lindmo S, Orczewska A, Perring MP, Ponette Q, Plue J, Selvi F, Spicher F, Tolosano M, Vermeir P, Zellweger F, Verheyen K, Vangansbeke P, De Frenne P (2020) Edge influence on understorey plant communities depends on forest management. J Veg Sci 31:281–292

Graham JH, Raz S, Hel-Or H, Nevo E (2010) Fluctuating asymmetry: methods, theory, and applications. Symmetry 2:466–540

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:2. https://doi.org/10.1126/sciadv.1500052

Hanson DT, Sharkey TD (2001) Effect of growth conditions on isoprene emission and other thermotolerance-enhancing compounds. Plant Cell Environ 24:929–936. https://doi.org/10.1046/j.1365-3040.2001.00744.x

Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19:768–782

Hectors K, van Oevelen S, Guisez Y, Jansen PE, MAK, (2012) The phytohormone auxin is a component of the regulatory system that controls UV-mediated accumulation of flavonoids and UV-induced morphogenesis. Phys Plant 145:594–603. https://doi.org/10.1111/j.1399-3054.2012.01590.x

Higuchi Y, Kawakita A (2019) Leaf shape deters plant processing by an herbivorous weevil. Nat Plants 5:959–964. https://doi.org/10.1038/s41477-019-0505-x

Ibáñez I, Katz DSW, Peltier D, Wolf SM, Barrie BTC (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess– multiresponse dynamics. J Ecol 102:882–895. https://doi.org/10.1111/1365-2745.12223

Isah T, Umar S (2018) Infl in vitro clonal propagation of *Chonemorpha fragrans* (moon) Alston by culture media strength, plant growth regulators, carbon source and photoperiodic incubation. J for Res 31:27–43. https://doi.org/10.1007/s11676-018-0794-3

Jaeger JAG, Soukup T, Madriñán LF, Schwick C, Kienast F (2011) Landscape fragmentation in Europe. Joint EEA-FOEN report No2/2011. EEA Publications, Copenhagen

Karban R (2007) Deciduous leaf drop reduces insect herbivory. Oecologia 153:81–88. https://doi.org/10.1007/s00442-007-0709-z

Killi D, Bussotti F, Gottardini E, Pollastrini M, Mori J, Tani C, Papini A, Ferrini F, Fini A (2018) Photosynthetic and morphological responses of oak species to temperature and [CO2] increased to levels predicted for 2050. Urban for Urban Green 31:26–37. https://doi.org/10.1016/j.ufug.2018.01.012

Klingenberg CP (2011) MorphoJ: an integrated software pack- age for geometric morphometrics. Mol Ecol Resour 11:353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecol Management 380:321–334

Korhonen L, Korhonen KT, Rautiainen M, Stenberg P (2006) Estimation of forest canopy cover: a comparison of field measurement techniques. Silva Fenn 40:577–588

Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP (2016) Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. Science 354:857–861. https://doi.org/10.1126/science.aai8878

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimmd SL, Bruna EM, Stouffer FC, Williamson GB, Benítez-Malvido J, Vasconcelos GL, Van Houtan KS, Zartman CE, Boyle SA, Didhamm RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest fragments: a 32-year investigation. Biol Conserv 144:56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Lempa K, Martel J, Koricheva J (2000) Covariation of fl asymmetry, herbivory and chemistry during birch leaf expansion. Oecologia 122:354–360. https://doi.org/10.1007/s004420050041

Levey DJ, Caughlin TT, Brudvig LA, Haddad NM, Damschen EI, Tewksbury JJ, Evans DM (2016) Disentangling fragmentation eff on herbivory in understory plants of longleaf pine savanna. Ecology 97:2248–2258. https://doi.org/10.1002/ecy.1466

Li Y, He N, Hou J, Xu L, Liu C, Zhang J, Wang Q, Zhang, Wu (2018) Factors influencing leaf chlorophyll content in natural forests at the biome scale. Front Ecol Evol 6:64. https://doi.org/10.3389/fevo.2018.00064

Lohbeck M, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Poorter L, Bongers F (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. PLoS ONE 10:e0123741. https://doi.org/10.1371/journal.pone.0123741

López E, Bocco G, Mendoza M, Velázquez A, Aguirre-Rivera R (2006) Peasant emigration and land use change at the watershed level: a GIS-based approach in central Mexico. Agric Syst 90:62–78. https://doi.org/10.1016/j.agsy.2005.11.001

Maguire DY, Buddle CM, Bennett EM (2016) Within and among patch variability in patterns of insect herbivory across a fragmented forest landscape. PLoS ONE 11:e0150843. https://doi.org/10.1371/journal.pone.0150843

Mäkelä A, Valentine HT (2006) Crown ratio infl allometric scaling in trees. Ecology 87:2967–2972. https://doi.org/10.1890/0012-9658(2006)87[2967:CRIASI]2.0.CO;2

Maldonado-López Y, Cuevas-Reyes P, Stone GN, Nieves-Aldrey JL, Oyama K (2015) Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees. Ecosphere 6:31. https://doi.org/10.1890/ES14-00355.1

Maldonado-López Y, Cuevas-Reyes P, Oyama K (2016) Diversity of gall wasps (Hymenoptera: Cynipidae) associated with oak trees (Fagaceae: Quercus) in a fragmented landscape in Mexico. Arthropod Plant Int 10:29–39. https://doi.org/10.1007/s11829-015-9404-x

Maldonado-López Y, Vaca-Sánchez MS, Canché-Delgado A, García-Jain SE, González-Rodríguez A, Cornelissen T, Cuevas-Reyes P (2019) Leaf herbivory and fluctuating asymmetry as indicators of mangrove stress. Wetlands Ecol Manag 27:571–580. https://doi.org/10.1007/s11273-019-09678-z

Mas JF, Lemoine-Rodríguez R, González R, López-Sánchez J, Piña-Garduño A, Herrera-Flores E (2017) Evaluación de las tasas de deforestación en Michoacán a escala detallada mediante un método híbrido de clasifi de imágenes SPOT. Madera Bosques 23:2. https://doi.org/10.21829/myb.2017.2321472

Mendes G, Boaventura MG, Cornelissen T (2018) Fluctuating asymmetry as a bioindicator of environmental stress caused by pollution in a pioneer plant species. Environ Entomol 47:1479–1484

Mendoza ME, Bocco G, Bravo M, López-Granados E, Osterkamp WR (2006) Predicting water-surface fluctuation of continental lakes: ARS and GIS based approach in central Mexico. Water Resour Manag 20:291–311. https://doi.org/10.1007/s11269-006-8199-z

Møller A, Shykoff JA (1999) Morphological developmental stability in plants: patterns and causes. Int J Plant Sci 160:135–146

Mooney KA, Halitschke R, Kessler A, Agrawal AA (2010) Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science 237:1642–1644. https://doi.org/10.1126/science.1184814

Murcia C (1995) Edge eff in fragmented forests: application for conservation. Trends Ecol Evol 10:58–62. https://doi.org/10.1016/S0169-5347(00)88977-6

Niinemets Ü (2015) Uncovering the hidden facets of drought stress: secondary metabolites make the difference. Tree Physiol 36:129–132. https://doi.org/10.1093/treephys/tpv128

Nixon KC (2006) Global and neotropical distribution and diversity of oak (genus *Quercus*) and oak forest. In: Ecology and conservation of neotropical montane oak forest, pp 3–13. https://doi.org/10.1007/3-540-28909-7_1

Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, patterns. Annu Rev Ecol Syst 17:391–421. https://doi.org/10.1146/annurev.es.17.110186.002135

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Ewers RM (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191. https://doi.org/10.1038/nature24457

Piasecka A, Sawikowska A, Kuczyńska A, Ogrodowicz P, Mikołajczak K, Krystkowiak K, Gudyś K, Guzy-Wróbelska J, Krajewski P, Kachlicki P (2017) Drought-related secondary metabolites of barley (*Hordeum vulgare* L.) leaves and their metabolomic quantitative trait loci. Plant J 89:898–913. https://doi.org/10.1111/tpj.13430

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251. https://doi.org/10.2307/3545270

Ramakrishna A, Ravishankar GA (2011) Infl of abiotic stress signals on secondary metabolites in plants. Plant Signal Behav 6:1720–1731. https://doi.org/10.4161/psb.6.11.17613

Rautiainen M, Stenberg P, Nilson T (2005) Estimating canopy cover in Scots pine stands. Silva Fenn 39:137–142

Ribeiro VA, Silva RN, Sousa-Souto L, Neves FD (2013) Fluctuating asymmetry of and herbivory on *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae) in pasture and secondary tropical dry forest. Acta Bot Brasilica 27:21–25. https://doi.org/10.1590/S0102-33062013000100003

Rivero-Lynch AP, Brown VK, Lawton JH (1996) The impact of leaf shape on the feeding preference of insect herbivores: experimental and field studies with Capsella and Phyllotreta. Philos Trans Biol Sci 351:1671–1677. https://doi.org/10.1098/rstb.1996.0149

Rohlf FJ (2015) The tps series of software. It J Mamm 26:9–12

Rossetti MR, Tscharntke T, Aguilar R, Batáry P (2017) Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecol Lett 20:264–272. https://doi.org/10.1111/ele.12723

Rozendaal DMA, Hurtado VH, Poorter L (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Func Ecol 20:207–216

Ruíz-Guerra B, Guevara R, Mariano NA, Dirzo R (2010) Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: evidence from a Mexican tropical rain forest. Oikos 119:317–325. https://doi.org/10.1111/j.1600-0706.2009.17614.x

Salomão RP, Brito LC, Iannuzzi L, Lira AF, Albuquerque CMR (2019) Effects of environmental parameters on beetle assemblage in a fragmented tropical rainforest of South America. J Insect Conserv 23:111–121. https://doi.org/10.1007/s10841-018-00120-y

Sálek L, Zahradníka D, Marušák R, Jeřábková L, Merganiča J (2013) Forest edges in managed riparian forests inthe eastern part of the Czech Republic. For. Ecol. Manag. 305:1–10. https://doi.org/10.1016/j.foreco.2013.05.012

Santos JC, Alves-Silva E, Cornelissen TG, Fernades GW (2013) The effect of fluctuating asymmetry and leaf nutrients on gall abundance and survivorship. Basic Appl Ecol 14:489–495. https://doi.org/10.1016/j.baae.2013.06.005

Santos JC, de Almeida WR, Cuevas-Reyes M-López Y, P, Santos JC, (2021) Variation in the co-occurrence of pathogen and herbivores between ontogenetic stages of *Miconia albicans*. Trees. https://doi.org/10.1007/s00468-021-02097-9

SAS (2000) Categorical data analysis using the SAS system. SAS Institute, Cary

Scanes CG (2018) Human activity and habitat loss: destruction fragmentation and degradation. Anim Hum Soc. https://doi.org/10.1016/B978-0-12-805247-1.00026-5

Schiegg K (2003) Environmental autocorrelation: curse or blessing? Trends Ecol. Evol 18:212–214. https://doi.org/10.1016/S0169-5347(03)00074-0

Schmidt M, Lischeid G, Nendel C (2019) Microclimate and matter dynamics in transition zones of forest to arable land. Agric for Meteorol 268:1–10. https://doi.org/10.1016/j.agrformet.2019.01.001

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675

Schöb C, Armas C, Guler M, Prieto I, Pugnaire FI (2013) Variability in functional traits mediates plant interactions along stress gradients. J Ecol 101:753–762. https://doi.org/10.1111/1365-2745.12062

Schüepp C, Uzman D, Herzog F, Entling MH (2014) Habitat isolation affects plant-herbivore-enemy interactions on cherry trees. Biol Control 71:56–64. https://doi.org/10.1016/j.biocontrol.2014.01.007

Shinozaki K, Yoda J, Hozumi K, Kira T (1964a) A quantitative analysis of plant form-the pipe model theory I. Basic analyses. Jap. J. Ecol. 14:97–105. https://doi.org/10.18960/seitai.14.3_97

Shinozaki K, Yoda J, Hozumi K, Kira T (1964b) A quantitative analysis of plant form-the pipe model theory: ii. Further evidence of the theory and its application in forest ecology. Jap J Ecol 14:133–139. https://doi.org/10.18960/seitai.14.4_133

Silva CA, Simonetti JA (2009) Inquiring into the causes of depressed folivory in a fragmented temperate forest. Acta Oecol 35:458–461. https://doi.org/10.1016/j.actao.2009.01.001

Souza GM, Ribeiro RV, Santos MG, Ribeiro HL, Oliveira RF (2004) Functional groups of forest succession as dissipative structures: an applied study. Braz J Biol 64:707–718. https://doi.org/10.1590/S1519-69842004000400020

Steinger T, Roy B, Stanton M (2003) Evolution in stressful environments II: adaptive value and costs of plasticity in response to low light in *Sinapis arvensis*. J Evol Biol 16:313–323. https://doi.org/10.1046/j.1420-9101.2003.00518.x

Telhado C, Esteves D, Cornelissen T, Fernandes GW, Carneiro MAA (2010) Insect herbivores of *Coccoloba cereifera* do not select asymmetric plants. Environ Entom 39:849–855. https://doi.org/10.1603/EN09179

Thompson M, Gamage D, Hirotsu N, Martin A, Seneweera S (2017) Effects of elevated carbon dioxide on photosynthesis and carbon partitioning: a perspective on root sugar sensing and hormonal crosstalk. Front Physiol 8:578. https://doi.org/10.3389/fphys.2017.00578

Torrez-Terzo G, Pagliosa PR (2007) Fluctuating asymmetry as a useful biomarker of Environmental stress: a case of study with *Avicennia schaueriana* Stapf and Leechm. Ex moldenke (Acanthaceae). Insula 33:75–94

Tovar-Sánchez E, Oyama K (2006) Community structure of canopy arthropods associated to *Quercus crassifola* × *Quercus crassipes* complex. Oikos 112:370–381. https://doi.org/10.1111/j.0030-1299.2006.14029.x

Trombulak SC, Frissell CA (2000) Review of ecological eff of roads on terrestrial and aquatic communities. Conserv Biol 14:18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Tuff KT, Tuff T, Davies KF (2016) A framework for integrating thermal biology into fragmentation research. Ecol Lett 19:361–374. https://doi.org/10.1111/ele.12579

Viscosi V (2015) Geometric morphometrics and leaf phenotypic plasticity: assessing fl asymmetry and allometry in European white oaks (Quercus). Bot J Linn Soc 179:335–3348. https://doi.org/10.1111/boj.12323

Watson JEM, Shanahan DF, Di Marco M, Allan J, Laurance WF, Sanderson EW, Mackey B, Venter O (2016) Catastrophic declines in wilderness areas undermine global environment targets. Curr Biol 26:2929–2934. https://doi.org/10.1016/j.cub.2016.08.049

Williams KS, Gilbert LE (1981) Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. Science 212:467–469. https://doi.org/10.1126/science.212.4493.467

Xu Z, Zhou G, Shimizu H (2010) Plant responses to drought and rewatering. Plant Signal Behav 5:649–654. https://doi.org/10.4161/psb.5.6.11398

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

SUPPORTING INFORMATION

Effects of forest fragmentation on plant quality, leaf morphology and herbivory patterns of *Quercus deserticola*: importance of fluctuating asymmetry as an indicator of environmental stress

Silvia Ecaterina García-Jain[1], Yurixhi Maldonado-López[2], Ken Oyama[3], Marcílio Fagundes[4], Maurício Lopes de Faria[4], Mário M. Espírito-Santo[4] and Pablo Cuevas-Reyes[1]

1) Forest composition:

To describe the structure and richness of the oak communities, in each forest fragment, four parallel transects of 5 x 50 m were delimited: two located at the edge of the fragment and two inside of the fragment distant at 300 m from the edge. Within each transect, the species identity of all oak trees with a diameter at breast height (DBH) ≥ 10 cm was determined and the number of individuals per species was counted. We calculated the oak species richness, as well as the total abundance of oaks individuals per forest fragment, including all oak species.

A generalized linear model (GLM) using a Poisson error distribution and a log link function was performed to determine the differences in the structure of oak community between forest fragments with different sizes. The model used fragment size (small vs medium vs large fragments) and oak species (*Q. deserticola* vs *Q. castanea* vs *Q. obtusata* vs *Q. magnoliifolia*) as independent variables. The abundance per hectare was used as the dependent variable. Similarly, to evaluate the structure of oak community between forest interior and forest edges, a GLM was performed sing a Poisson error distribution and a log link function. The model considered forest interior and forest edges, and oak species as independent variables. The abundance per hectare was used as the dependent variable (SAS, 2000). Non-Metric Multidimensional Scaling (NMDS) was performed to characterize Quercus community structure between fragments with different size. NMDS was performed using the Bray-Curtis distance in the software PAST 4.03 (Hammer et al., 2001).

We found variation of the composition of the oak community along gradient of forest fragmentation in the Cuitzeo Basin. Larger forest fragments had greater oak abundance species in comparison to medium and small fragments ($\chi^2 = 11.01$; d.f. = 2; $P < 0.004$). A similar pattern was observed with oak species richness, larger fragments had greater oak species richness than medium and small forest fragments ($\chi^2 = 1867.7$; d.f. = 3; $P < 0.0001$). The interaction of fragment size and oak species was significant ($\chi^2 = 108.6$; d.f. = 6; $P < 0.0001$) (Fig. 1a). In general, the oak abundance species was greater in the interior of forest fragments than in fragment edges ($\chi^2 = 140.9$; d.f. = 1, $P < 0.0001$); Similarly, oak species richness was higher in the interior than in edges of fragments ($\chi^2 = 2007.9$; d.f. =3, $P < 0.0001$). The interaction of forest interior and forest edges with oak species was significant ($\chi^2 = 199.3$; d.f. = 3; $P < 0.0001$) (Fig. 1b). We found three oak species in small fragments: *Quercus deserticola* was predominant with 74 %, followed by *Q. obtusata* (18 %) and *Q. castanea* (8 %). In medium fragments we registered three species: *Q. deserticola* that represented the 82 %, followed by *Q. castanea* (14%) and *Q. obtusata* (4%), and in larger fragments four species were found: *Q. deserticola* with 88 %, followed by *Q. castanea* (8 %), *Q. obtusata* (2 %) and *Q. magnoliifolia* (2 %) (Fig. 1c). The NMDS was adjusted to two dimensions with Bray-Curtis distance. The results of similarity in oak community showed that NMDS ordination explained 83 % of the variance between sampling points (axis 1 = 70 % and axis 2 = 13 %). Each point was a two-dimensional representation of the composition of oaks species based on global NMDS. We found that the composition of oaks species varied between forest fragments (ANOSIM r =0.49; n =12; P < 0.02). The results of post-hoc pairwise ANOSIM tests showed that the small and medium fragments were similar in composition of oak species, but different to large fragments. This fact was corroborated by the observed superimposition between small and medium fragments and the separation of the larger fragments according to the composition of the oak community (Fig. 1d).

Figure 1. Analysis of oak community structure, a) Differences in oak species abundance between forest fragments sizes. b) Differences in oak species abundance between the interior and edge of fragments. c) Proportion of oak species by fragment size. d) Ordination plot of oak abundance in fragments with different size along non-metric multidimensional scaling (NMDS). The three size are small, medium and large.

Figure 1

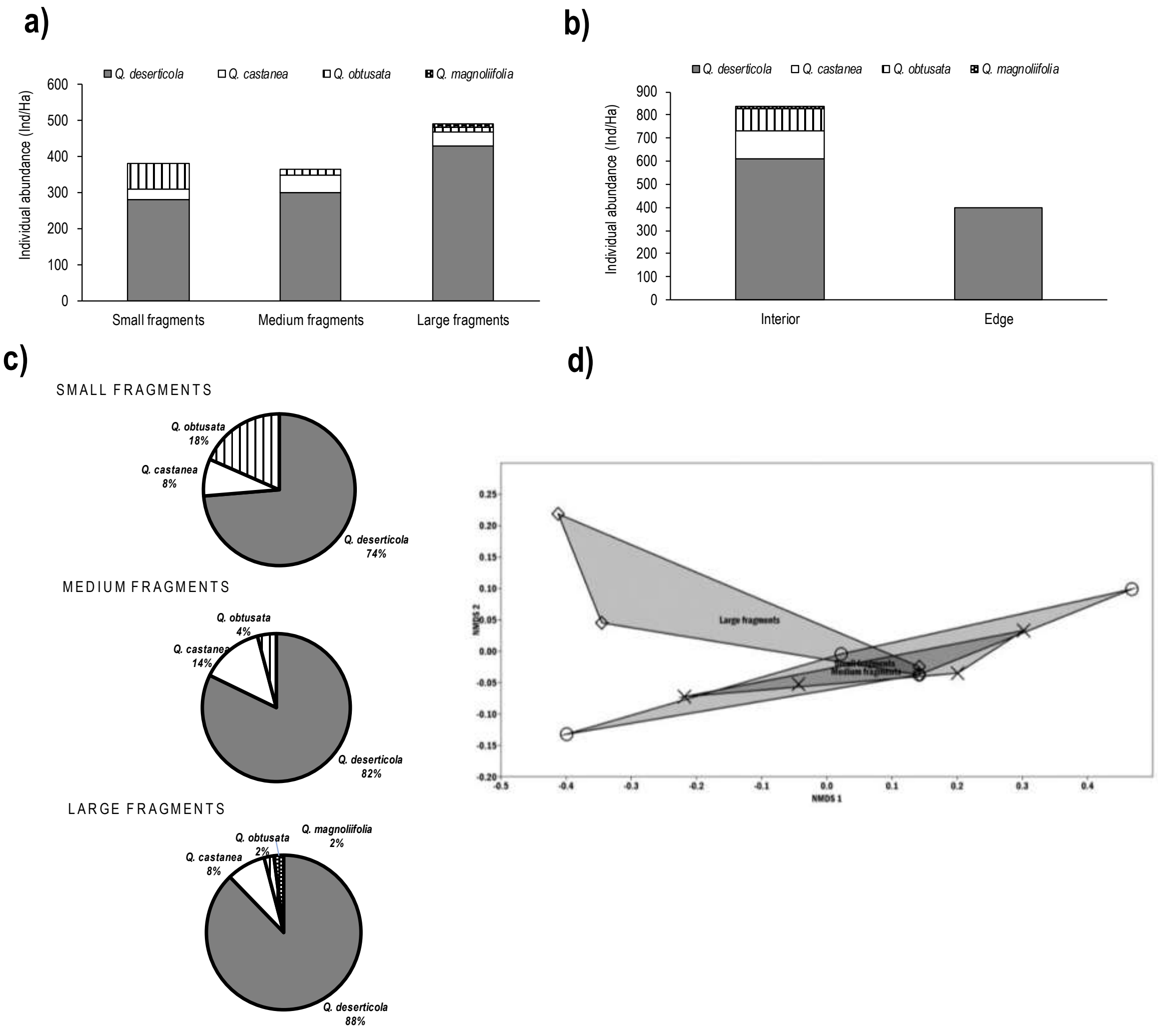
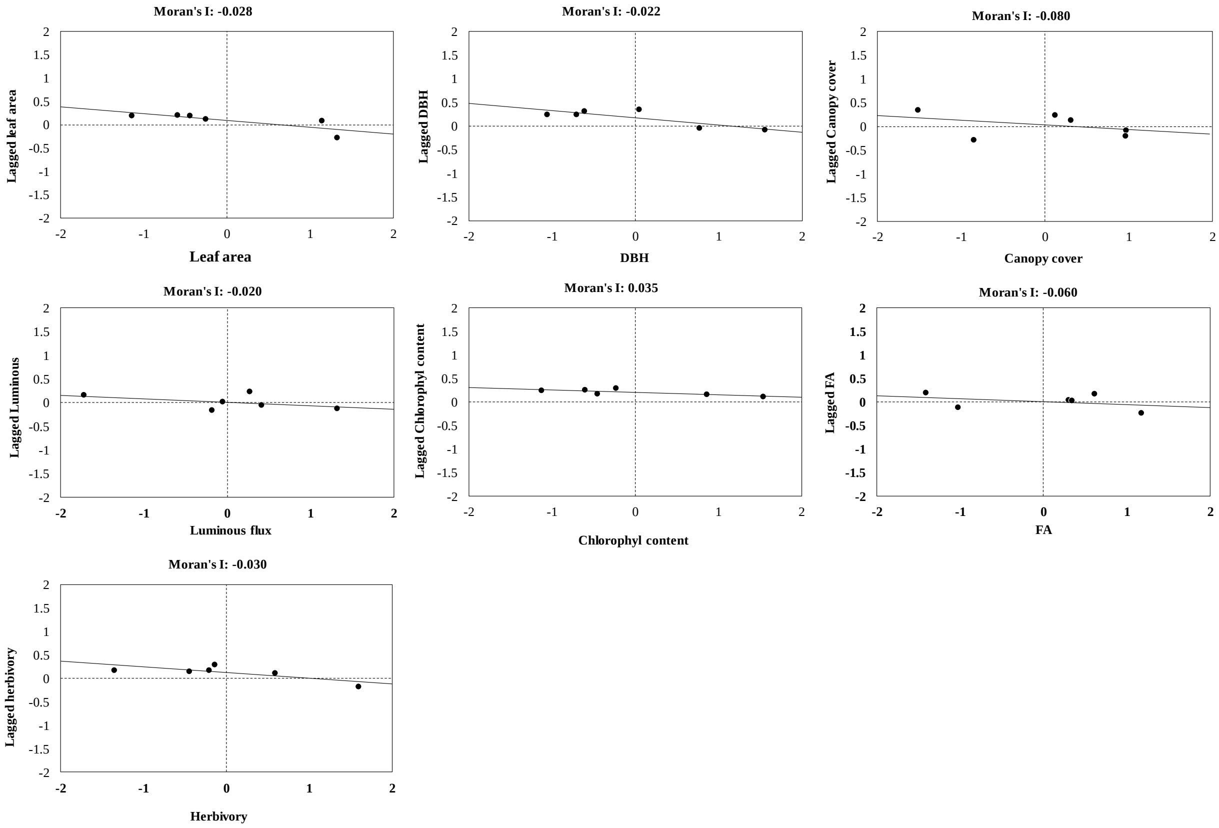

a)
Q. deserticola
Q. castanea
Q. obtusata
Q. magnoliifolia
Individual abundance (Ind/Ha)
0
100
200
300
400
500
600
Small fragments
Medium fragments
Large fragments
b)
Q. deserticola
Q. castanea
Q. obtusata
Q. magnoliifolia
Individual abundance (Ind/Ha)
0
100
200
300
400
500
600
700
800
900
Interior
Edge
c)
SMALL FRAGMENTS
Q. obtusata 18%
Q. castanea 8%
Q. deserticola 74%
MEDIUM FRAGMENTS
Q. obtusata 4%
Q. castanea 14%
Q. deserticola 82%
LARGE FRAGMENTS
Q. magnoliifolia 2%
Q. obtusata 2%
Q. castanea 8%
Q. deserticola 88%
d)
Large fragments
Small fragments
Medium fragments
NMDS 2
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
NMDS 1
-0.5
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4

Figure 2. Scatter plots of values of Moran index of each response variable analyzed in all forest fragments



CAPITULO II.

Forest fragmentation increases canopy arthropod diversity in *Quercus deserticola*

Silvia Ecaterina García-Jain[1], Yurixhi Maldonado-López[2], Ken Oyama[3], Edmundo Carlos López- Barbosa[4], Marcílio Fagundes[5], Maurício Lopes de Faria[5], Mário M. Espítito-Santo[5] and Pablo Cuevas-Reyes[1*]

[1]Laboratorio de Ecología de Interacciones Bióticas, Universidad Michoacana de San Nicolás de Hidalgo, Ciudad Universitaria, C.P. 58030, Morelia, Michoacán, México.

[2]CONACYT-Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Avenida San Juanito Itzícuaro SN, Nueva Esperanza, 58330 Michoacán, México.

[3]Escuela Nacional de Estudios Superiores Unidad Morelia, UNAM. Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-Hacienda de San José de la Huerta, Morelia, 58190 Michoacán, México.

[4]Laboratorio de Agroecología, Universidad Michoacana de San Nicolás de Hidalgo, Ciudad Universitaria, C.P. 58030, Morelia, Michoacán, México.

[5]Universidade Estadual de Montes Claros, Programa de Pós-Graduação em Ciências Biológicas, Departamento de Biologia Geral, Laboratório de Biologia da Conservação, Montes Claros, Minas Gerais, Brazil. Av. Ruy Braga s/n, Caixa postal 126, CEP 39.401-089

Corresponding author: pcragalla@gmail.com

Abstract

Human activities negatively impact biodiversity. Habitat fragmentation is widely considered as a primary factor leading to species extinction worldwide. Forest fragmentation as well as edge effects negatively affect arthropod communities. We analyzed the effects of forest fragment size and forest edge and interior on the structure and composition of canopy arthropod community in *Quercus deserticola* along a forest fragmentation gradient at the Cuitzeo Basin in Mexico. Six forest fragments where *Q. deserticola* occurs were selected and classified as (i) small (≤ 10 ha); (ii) medium (≥ 25 ha); and (iii) large (≥ 65 ha). In each forest fragment, seven trees were randomly selected: two at the edge of the fragment and five in the interior of the fragments to collect canopy arthropods using fogging techniques. Individuals of *Q. deserticola* in small fragments and interior had higher arthropod abundance and morphospecies richness in comparison with individuals that occurred in medium-size, large fragments and forest edge. We found differences in arthropod abundance among fragment sizes and arthropod orders. The most abundant orders in all fragment sizes (small, medium-size and large) were Hemiptera, Hymenoptera and Coleoptera. Significant differences in arthropod abundance between trophic guilds were detected. Phytophages and predators were the most abundant trophic guilds in all fragment sizes, while parasitoids and detritivores were less abundant. Small fragments had higher abundance of phytophages, predators and parasitoids. Small fragments can be considered keystone resources for maintaining of arthropod community diversity in a fragmented landscape in Mexican temperate forests. Deforestation rates are increasing in Mexican forests with potentially serious implications. Is important to conserve oak forests in Mexico as important reservoirs of arthropod fauna.

Arthropods as excellent bioindicators because they are diverse, abundance and responsive to environmental alterations.

Keywords: Forest fragmentation Edge effect Canopy arthropods Trophic guilds

Introduction

Canopy arthropods of temperate and tropical forests represents an important proportion of the global biodiversity, estimating 6.1 million species of arthropods worldwide (Basset et al. 2007; Hamilton et al. 2013). Particularly, the canopy is associated to a unique and rich community of specialist arthropods species (Tovar-Sánchez et al. 2013; Stork et al. 2015, 2018), grouped in different trophic levels such as phytophages, predators, parasites, parasitoids, pollinators and detritivores (Hamilton et al. 2010; Nakamura et al. 2017). Arthropods guilds have important ecological roles, since they participate in ecosystem services as decomposition, nutrient cycling, energy transfer and soil formation (Yang and Gratton 2014; Maguire et al. 2015; Schowalter et al. 2018). When phytophages arthropods outbreaks occur, the patterns of primary production and biogeochemical cycling are altered (Medvigy et al. 2012; Schowalter 2012). Different factors could be associated with arthropod diversity on tree canopies. Environmental factors such as temperature, humidity, light incidence and wind speed, as well as aspects of the structure and composition of plant communities, including species richness, plant density and quality, have been proposed as drivers of canopy arthropod diversity (Tal et al. 2008; Ulyshen 2011). Additionally, forest fragmentation can alter abiotic and biotic conditions, generating changes in the arthopod diversity (Maldonado-López et al. 2016). Forest fragmentation is a dynamic process in which the forest is progressively reduced to patches with different sizes, and degrees of isolation undergoing to a rapid and abrupt abiotic and biotic changes (Haddad et al. 2015; Fletcher et al. 2018). Usually, a decrease in fragment area causes habitat loss, leading to declining population sizes of several species, inbreeding depression and local extinction, reducing species diversity (Ibanez et al. 2014). Abiotic changes associated to forest fragmentation such as increasing wind speed, light availability and temperature, and decreasing soil moisture and nutrients affect plant quality (i. e. canopy cover, chlorophyll content and plant size and chemical defenses) (Arroyo-Rodríguez et al. 2017; Han et al. 2019; Schmidt et al. 2019), which in turn, different factors associated plant quality can influence canopy arthropod diversity and the preference, abundance and distribution of insect herbivores (Rautiainen et al. 2005; Maldonado-López et al. 2016). For example, some studies have documented that in oaks species, plant quality was higher in individuals that occurred in small fragments and the edge of fragments than in individuals of the large fragments and in the interior of the fragments due to more abruptly changes in the abiotic conditions (Silva and Simonetti 2009; Maldonado-López et al. 2016; Garcia-Jain et al. 2021). In the literature there are two scenarios in fragmented habitats: the first one, where insect abundance increases as a result of the reduction of predators and parasitoids (top-down forces) (Pfeifer et al. 2017; Schüepp et al. 2014), because highly specialized species or groups and higher trophic levels (Holt et al. 1999; Burkle et al. 2013; Martinson and Fagan 2014; Rossetti et al. 2017) seem to be consistently more sensitive to the effects of fragmentation, due to its higher resource, energy and forest area (Holt et al. 1999; Gravel et al. 2011; Murphy et al. 2016). Second, it has been observed that herbivory levels can be reduced as a result of changes in plant nutritional quality and concentration of defensive compounds of plants (bottom-up forces) (Maguire et al., 2016; Maldonado-López et al., 2016) due to changes in environmental conditions mainly in small fragments and forest edges. In this way, plants can impact herbivores directly by influencing their performance and survival and indirectly by mediating the effects of natural enemies (Sobek et al. 2009; van Dam and Heil 2011).

Arthropod species respond in different ways to habitat fragmentation (Cagnolo et al. 2009; Bagchi et al. 2018) as result of the variation in their dispersal abilities, habitat requirements, life histories, and distribution patterns (Tscharntke et al. 2002; Nufio et al. 2011; Heidrich et al. 2020). In this way, arthropod community differs in the composition of the functional groups occupying different trophic niches such as detritivores, phytophages, predators, parasites, parasitoids and pollinators (Hamilton et al. 2010; Nakamura et al. 2017; Maldonado-López et al. 2018). The response of arthropod communities to habitat fragmentation is highly variable because the changes in a particular habitat can increase the resource availability for some species or reduce the resources for others (Barberena-Arias and Aide 2002). For example, Gravel et al. (2011) showed that predators was poorly represented in small forest fragments due to stochastic extinction, and that specialist predators was more affected as result of the presence of the abrupt environmental changes and low resource availability in small forest fragments. Similarly, forest fragmentation can uncouple the insect herbivore assemblages and their natural enemies, reducing levels of predation and parasitism and leading to pest outbreaks of herbivores (Kruess and Tscharntke 1994; Anton et al. 2007). Therefore, fragmentation can increase the resource consumption levels by insects with a broad niche breadth, either in terms of diet or habitat (Layman et al. 2007; Martinson and Fagan 2014). In contrast, resource consumption by predators with a narrow niche breadth decline with increasing fragmentation (Ewers and Didham 2006; Layman et al. 2007). Recent studies suggest that bottom-up and top-down forces interact together by molding and structuring arthropod communities (Castagneyrol et al. 2014, 2017; Vaca-Sánchez et al. 2021).

Habitat fragmentation can reduce arthropod abundance leading to a decline in arthropods communities (Forkner et al. 2008; Sanchez-Bayo and Wyckhuys 2019). For example, Tovar-Sánchez et al. (2003) found that sites with higher levels of fragmentation had low diversity levels of ectophagous canopy arthropods associated to *Q. castanea*, *Q. crassipes*, *Q. crassifolia*, *Q. greggii*, *Q. laeta* and *Q. rugosa*. This fact suggests that a strong disturbance can change habitat quality in small fragments leading to local extinction of host plants and therefore, a reduction in the arthropod community and the amount of leaf area consumed by insects associated to the canopy of the different oak species.

The genus *Quercus* (Fagaceae) is a highly diverse group of woody plants that supports a great diversity of canopy arthropods (Tovar-Sánchez and Oyama 2006; Maldonado-López et al. 2018; Vaca-Sánchez et al. 2021). However, due to their great economic importance, oak forests have had high deforestation rates (11,156 ha per year) between 2007 and 2015 (Mas et al. 2017). The Cuitzeo Basin which harbor 16 oaks species has been highly fragmented due to the expansion of agriculture, urban development and deforestation (Castillo-Santiago et al. 2013). Therefore, the main objective of this study was to evaluate the changes in structure and composition of the canopy arthropod community associated to *Quercus deserticola* along a gradient of forest fragmentation. We addressed the following questions: (i) Are there differences in the diversity and composition of *Q. deserticola* canopy arthropod communities among the different fragments size? (ii) Are there edge effects on the canopy arthropod diversity associated to Q. deserticola across a fragmented landscape? ? (iii) Does the arthropod guild composition vary among the different fragments size, forest edge and forest interior?

Materials and methods

Study system

Quercus deserticola Trel. is a white oak (section *Quercus*), deciduous tree, that grows up to 10 m. The leaves of *Q. deserticola* vary from oblong-oblanceolate to lanceolate, with a slightly shiny and rough dark green upper surface; and a clear underside with abundant trichomes. This species occurs in semitropical and temperate forests of Mexico. It is a mexican endemic oak that inhabits in high, cold and dry regions, in xerophytic areas (at altitudes between 2000 - 2800 m), with a geographical distribution along the Trans-Mexican Volcanic Belt (Arizaga et al. 2009).

Study sites

This study was carried out in the hydrological Basin of Cuitzeo lake from October to December 2017. This basin has an area of 4,026 km^2 and is located in the north of the state of Michoacán, Mexico. The Cuitzeo Basin has experienced high fragmentation of natural vegetation in the last decades. Land cover and large use change analyses indicate that the period 1986-1996 was characterized by high rates of deforestation and forest degradation throughout the basin (Mendoza et al. 2011) due to strong human pressures including urban growth, expansion of the agricultural and the removal of trees for charcoal production (López et al. 2006, Aguilar et al. 2012, Castillo-Santiago et al. 2013). Thus large continuous oak populations have been reduced to a many small fragments of variable size. To select the study sites, we used a database from previous analysis of land covers and land-use changes in the Cuitzeo Basin, remaining oak forest have been characterized into 1241 fragments of different sizes (López et al. 2001; López et al. 2006; Mendoza et al. 2011). Six forest fragments where *Q. deserticola* occurs were selected and classified as (i) small (≤ 10 ha) (El Tigre: 19° 37 'N, 101° 24' W, and La Concepción: 19 42' N, 101° 18' W); (ii) medium (≥ 25 ha) (Capula: 19 ° 42 'N, 101 ° 24' W, and Las Canoas: 19° 51' N, 101° 14' W); and (iii) two large fragments (≥ 65 ha) (Atécuaro: 19° 37' N, 101° 10' W, and El Remolino: 19° 37' N, 101° 20' W).

Canopy arthropod diversity

To analyze canopy arthropod diversity between different fragment sizes, and edge effect, we chose randomly two trees of *Q. deserticola* at the edge and 5 trees in the interior of the fragments. Each canopy tree was fogged using a mix of synergized pyrethrins (30 g/L) and piperonyl butoxide (150 g/L) with a Swingfog SN-50 Thermal Fogger. Fogging was carried out between 6:00 and 7:00 h, for a period of 5 min. The arthropod collection was done 2 h after fogging using 6 funnel-shaped trays (1 m^2 in area) installed under each tree canopy. After 2 h of the first collection, a second collection was performed to capture the remaining arthropods using ropes to shake the canopy (Marques et al. 2006; Tovar-Sánchez et al. 2013; Maldonado-López et al. 2018). The arthropods collected were stored in 70% ethanol and transported to the Agroecology Laboratory of Universidad Michoacana de San Nicolás de Hidalgo, for taxonomic identification. Arthropods were identified to family level and assigned to trophic guilds (Triplehorn et al. 2005; Ubick et al. 2017). Arthropod abundance and species richness were estimated using morphospecies criteria (recognizable taxonomic units) (Triplehorn et al. 2005; Scholtz and Holm 2012; Ubick et al. 2017).

Statistical analysis

We performed rarefaction curves of the arthropod families to indicate whether the number of samples was big enough to capture the majority of arthropod diversity. Canopy arthropod abundance and species richness were compared among different fragment sizes using a generalized linear model (GLM) analysis with a Poisson error distribution and a log link function. Fragment size was used as the independent variable and arthropod abundance and richness as the response variables. Additionally, a two-way GLM analyses were applied to determine the differences in abundance and species richness of arthropods between fragment sizes and forest edge and forest interior, arthropod orders and trophic guilds. We also used a Poisson error distribution and a log link function for all cases (SAS 2000). Non-Metric Multidimensional Scaling (NMDS) was performed to characterize arthropod community structure between fragments with different size, and between forest edges and forest interior. NMDS was performed using Bray-Curtis distance in the software PAST 4.03 (Hammer et al. 2001).

Results

A total of 12,739 arthropods were collected, of these 4,696 were registered in small fragments, 4,039 in medium fragments and 4,004 in large fragments, representing 716 morphospecies (N= 492 in small fragments, N= 460 in medium fragments and N= 422 in large fragments) and grouped in 155 families and 16 orders (See Table1 S1). The rarefaction curves showed that the number of arthropods were adequately sampled, curves reaching an asymptote in all cases for different fragment sizes. Therefore, our diversity estimation was reliable. The rarefaction curves indicate that the number of arthropod families was different between fragment sizes. The rarefaction analysis showed that the richness of arthropod families was significantly higher in small fragments, followed of medium-size and large fragments (Fig. 1).

We found significant differences in arthropod abundance among fragment sizes ($\chi^2 = 70.4$, *d.f.* = 2, $P < 0.0001$) (Fig. 2a) and between morphospecies richness ($\chi^2 = 37.2$, *d.f.* = 2,

$P < 0.0001$) (Fig. 2b). Individuals of *Q. deserticola* growing in small fragments had higher arthropod abundance and morphospecies richness in comparison to individuals that occurred in medium-size and large fragments. The two-way GLM analysis showed significant differences in arthropod abundance among fragment sizes ($\chi^2 = 23.2$, *d.f.* = 2, $P < 0.0001$) and forest edges and forest interior ($\chi^2 = 280.4$, *d.f.* = 1, $P < 0.0001$). Individuals of *Q. deserticola* that occurs in small fragments and forest interior had higher arthropod abundance in comparison with individuals that occurred in medium-size, large fragments and forest edges (Fig. 2c). We found significant differences in morphospecies richness among fragment sizes ($\chi^2 = 17.3$, *d.f.* = 2, $P = 0.002$) and forest edges and forest interior ($\chi^2 = 128.9$, *d.f.* = 1, $P < 0.0001$), which was higher morphospecies richness in small fragments and forest interior than medium-size, large fragments and forest edges (Fig. 2d).

The arthropod abundance was significantly different among fragment sizes ($\chi^2 = 21.1$, *d.f.* = 2, $P < 0.0001$) and between arthropod orders ($\chi^2 = 1979.9$, *d.f.* = 15, $P < 0.0001$). The most abundant orders in all fragment sizes (small, medium-size and large) were Hemiptera, Hymenoptera and Coleoptera respectively. In addition, small fragments had higher arthropod abundance of the orders Araneae and Psocoptera in comparison with medium-size and large fragments. The medium-size fragments showed higher abundance of the Araneae and Acari orders than in the small and large fragments. The order Blattodea was only present in the medium-size fragments. Araneae and Thysanoptera were the most abundant orders in large fragments. Finally, the orders Blattodea, Collembola, Dermaptera, Diptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, Pseudoscorpionida generally represented < 5% of the total of the arthropod abundance registered (Fig. 3).

Trophic guild designated by order and family of the arthropod community (See Table 2 S1). We found significant differences in arthropod abundance between trophic guilds (χ^2 = 16819.4, *d.f.* = 4, *P* < 0.0001). Phytophages and predators were the most abundant trophic guilds in all fragment sizes, while parasitoids and detritivores were less abundant. Parasites were not registered in large fragments. Small fragments had higher abundance of phytophages, predators and parasitoids. Detritivores and parasites were more abundant in medium-size fragments than in small and large fragments (Fig. 4a). We found significant differences in morphospecies richness between trophic guilds (χ^2 = 3312.6, *d.f.* = 4, *P* < 0.0001) (Fig. 4b). Phytophages and parasitoids were more abundant in the edge of the medium-size fragments, while predators were more abundant in the edge of the large fragments (Table 1a). We found in morphospecies richness that detritivores, phytophages and parasitoids were more abundant in the edge of the medium-size fragments, while predators were more abundant in the edge of the large fragments (Table 1b). Phytophages, parasitoids and predators were more abundant in the interior of small fragments (Table 1a). Finally, we found more morphospecies richness of phytophages, parasitoids and predators in the forest interior of small fragments in comparison medium-size and large fragments (Table 1b).

NMDS was adjusted to two dimensions with Bray-Curtis distance. NMDS ordination explained 82% of the variance between sampling points (axis 1 = 68% and axis 2 = 14%). Each point was a two-dimensional representation of the composition of arthropods based on global NMDS. We found that the composition of arthropods varied between forest fragments (ANOSIM *r* = 0.17; n = 42; *P* = 0.02). The results of post-hoc pairwise ANOSIM tests showed that medium-size and large fragments were similar in arthropods composition, but different to small fragments. This fact was corroborated by the observed superimposition between medium-size and large fragments and the separation of the small fragments according to the composition of the arthropod community (Fig. 5a). Finally, NMDS ordination explained 76% of the variance between sampling points (axis 1 = 65% and axis 2 = 11%). We found that the composition of arthropods varied between forest edges and forest interior (ANOSIM $r = 0.35$; n = 42; $P = 0.0003$). The results of post-hoc pairwise ANOSIM tests showed that the forest edges and forests interior were different composition of arthropods (Fig. 5b).

Discussion

Habitat fragmentation is one of the most important threat to global biodiversity (Fahrig 2003; Murphy et al. 2016). In our study, we found an increase in the abundance and richness of canopy arthropods of *Q. deserticola* in small fragments, as well as in the interior of fragments. The orders with the highest abundance in all fragment size were Hemiptera, Hymenoptera and Coleoptera. Phytophages were the most abundant trophic guilds in all fragment sizes followed by predators and parasitoids. Small remnant fragments have been found to be important for both conserving biodiversity and maintaining ecosystem services (Cousins 2006; Mendenhall et al. 2014). These arthropod-mediated ecosystem services such as pollination, decomposition, nutrient cycling, and biological pest control (Isaacs et al. 2009). Small fragments can function as refugia, representing keystone resources, a positive effect for biodiversity (Økland et al. 2006, Maldonado-López et al. 2015; Fahrig et al. 2019). Species richness and density of arthropods in small fragments can be as high as in large fragments (Tscharntke et al. 2002; Rösch et al. 2015). Usually, a series of small or medium-size fragments capture a much greater habitat environment heterogeneity than one large fragment (Tscharntke et al. 2002; Markgraf et al 2020). Species community found in small fragments are not simply a random subset of the species pool found in large fragments, because both fragment quality and community structure change with the site. Habitat heterogeneity makes discontinuous habitat fragments more diverse (Tscharntke et al. 2002; Jachula et al. 2021). For example, Tscharntke et al. (2002) found that the percentage of polyphagous butterfly species and their abundance were higher in small than in large fragments, several small fragments supported more butterfly species than the same area composed of only one or two fragments, due to the heterogeneity of the habitat (Qian and Shimono 2012; Rösch et al. 2015). The trophic theory of island biogeography proposes that area and isolation effects will exclude species that are ecologically specialized in some dimension relative to their generalist counterparts in the same community (Holt 2010; Gravel et al. 2011). Additionally, species that are positioned at higher trophic levels, or have large resource requirements may be especially sensitive to the effects of landscape fragmentation (Kruess and Tscharntke 1994; Holt et al. 1999; Gravel et al. 2011). In addition, abiotic conditions in small fragments change more abruptly than in large fragments, increasing plant quality (i.e., canopy cover, chlorophyll content and plant size), which in turn increases the herbivory levels (Maldonado-López et al 2016; García-Jain et al 2021), support "the plant vigor hypothesis" (Price 1991) that proposes that herbivorous insects preferentially feed on large and more vigorously growing plants, because their higher nutritional quality increases offspring performance. Therefore, we propose that arthropod abundance and species richness increased with habitat fragmentation, due to heterogeneity of the habitat and the increase in the plant quality, representing resources of higher nutritional content and low concentration of chemical defenses for arthropods (García-Jain et al. 2021). Plants under stress conditions increase the concentration of amino acids and decrease the production of secondary metabolites in their tissues, which in turn, increase insect performance and plant susceptibility to phytophages (Torrez-Terzo and Pagliosa 2007; Cornelissen and Stiling 2011) For example, Maldonado-López et al. (2016) found that oak quality (i.e., plant height, diameter at breast height, percentage of leaf canopy cover) and herbivory levels were higher in small fragments, due to abiotic conditions in small fragments change more abruptly than in larger fragments, increasing plant quality which in turn increases the herbivory levels (García-Jain et al. 2021).

Additionally, the composition of the arthropod community between fragment sizes showed that small fragments had a significantly different composition of the arthropod community compared with medium-size and large fragments. Studies have found differences in the abundance and richness of the arthropod community between different fragment sizes (Gibb and Houchuli 2002; Bolger et al. 2008). The theory of patch dynamics (Pickett and Rogers 1997) proposes that the distribution and abundance of species within a fragment are influenced by its heterogeneity, with individual fragments supporting different communities of species and the mosaic of fragments within a landscape influencing the flow of materials, energy, and organisms. For example, Gibb and Hochuli (2002) found that large and small habitat fragments contained different community of spiders, wasps and ants, indicating that predators and parasitoids are affected more strongly than other trophic guilds. On the other hand, Bolger et al. (2008) found that the diversity and density of both native and non-native spiders is enhanced in smaller and older fragments, hypothesize that the pattern observed results from a bottom-up response to increased productivity in small fragments. De la Vega et al. (2012) found that abundance of herbivorous was lower in the forest fragments than in continuous oak forest, due to decrease of resource concentration (Chávez-Pesqueira et al.

2015). Therefore, our results of higher arthropod abundance and species richness in small fragments can be explained by the "crowding effect" that is a relatively positive effect of fragmentation on insect population density (Debinski and Holt 2000; Maldonado-López et al. 2015) that suggests that after forest fragmentation, insect populations may disperse to adjacent fragments, resulting in a local increase in population density (Debinski and Holt 2000; Grez et al. 2004) in small fragments that have a larger edge proportion (Grez et al. 2004; Ewers and Didham 2006). When habitat is removed from a landscape, surviving individuals in the portion of the landscape that is converted to matrix (non-habitat) will move into the remaining habitat fragments (Debinski and Holt 2000; Grez et al. 2004; Prugh et al. 2008). As result of the forest cover decreases, organisms that survive to the immediate process of habitat loss are expected to look for refuge and crowd in the remaining fragments (Ewers and Didham 2006). For example, Maldonado-López et al. (2015) found that plant quality in nine oak species was significantly higher in isolated oaks and small fragments, increasing the abundance and species richness of oak gall wasp species in most fragmented habitats, suggesting "crowding effect". Our results contrast with the predictions of Holt´s (1996) model that a proposes that fragmentation reduces richness of organisms living in smaller fragments due to higher rates of extinction.

Biodiversity lost due to habitat fragmentation are primarily caused by edge effects (Fletcher et al. 2007) due to fragment interior are more stable, both abiotically and biotically (Murcia 1995; Harper et al. 2005). Our results agree with this idea, we found that arthropod abundance and species richness were also higher along fragment interior that in the fragment edges, the NMDS showed differences in the composition of the arthropod community between fragment interior and fragment edges. Another result is the fact that trees of *Q.*

deserticola in the interior of small fragments had higher abundance and species richness of phytophages, predators and parasitoids. Therefore, in our studio we explain our results of greater abundance and species richness of arthropod in the forest interior because it has a more stable microclimate, since the edges of the fragments are hotter and drier. These different conditions near fragments edge often reduce the survival of species typical for the forest interior. Mechanisms that drive edge effects are diverse but include factors such as increased predation levels, as well as differences in wind speed, temperature and radiation levels (Chen et al. 1995; Batary and Baldi 2004). One of the mechanisms of edge effects that directly affect insects is linked to the availability and quality of key resources (Ries and Sisk 2004; Ries et al. 2004). However, insect responses can be neutral or even negative if the edge offers supplementary resources or few attractions, respectively (Ries and Sisk 2008). Alterations in the abiotic parameters at the forest edge leads to a variety of edge effects, including decreases in leaf litter decomposition (Didham et al. 1998), and influxes of exotic species (Vitousek et al. 1997; Cadenasso and Pickett 2001).

Habitat fragmentation are a primary driver of species losses, fragmentation differentially impacts species with different life histories and trophic level (Pfeifer et al. 2017; Caitano et al. 2020). Previous studies showed that species more sensitive to fragmentation were also found to share particular life history traits such as large body size, low dispersal ability and high food and habitat specialization (Tscharntke et al. 2002; Lizée et al. 2011; Nufio et al. 2011). Abundance of different trophic guilds is changing in response to habitat fragmentation (Soliveres et al. 2016; Newbold et al. 2019). For example, Moreno et al (2014) found lower litter decomposition in small fragments, supporting by reductions in diversity of the detritivores in small fragments (Rantalainen et al. 2005). In this way, we found that detritivores decreased with fragmentation, due to in fragmented habitats humans tend to reduce decaying matter. For the case of phytophages, were most abundant in all fragment size. Phytophages are abundance because nearly 75% of the total biodiversity and biomass of extant macro-organism is comprised of plants and their herbivores (Wilson 2001; Agrawal 2011). Also, we found that parasitoids and predators are most abundance in small fragments. Specifically, arthropod communities associated with oak canopies respond to predation by natural enemies as parasites or parasitoids (Tovar-Sánchez et al. 2013; Maldonado-López et al. 2018; Vaca-Sánchez et al. 2021). Interactions between species may act through different trophic levels in bottom-up and top-down directions (Valencia-Cuevas et al. 2015). Therefore, we explain our results based on guilds such as phytophages, predators, detritivores and parasitoids presented higher abundance and species richness in oak canopies (Tovar-Sánchez et al. 2013; Maldonado-López et al. 2018; Vaca-Sánchez et al. 2021). In this way, the high diversity of predators and parasitoids found in our study could be explained by the great abundance of phytophages arthropods. We propose that our results can be explained by a combination of both factors, where bottom-up forces will set the stage for top-down forces act. Particularly, in oak communities, some studies have suggested bottom-up forces as the main regulatory mechanism of the distribution and abundance of herbivorous insects through leaf nutritional quality and phenology (Feeny 1970; Schultz and Baldwin 1982; West 1985; Faeth and Bultman 1986; Rossiter et al. 1988). However, more recent studies suggest that bottom-up and top-down forces interact together by molding and structuring arthropod communities (Forkner and Hunter 2000; Castagneyrol et al. 2014, 2017). For example, a meta-analysis including 172 studies showed that top-down forces were stronger than bottom-up forces to control herbivorous insects, where, chewing, sucking and gall-making herbivores were more affected by top-down than bottom-up forces, and parasitoids and predators had equally strong top-down effects on insect herbivores (Vidal and Murphy 2018).

One conservation strategy for the sustainability of the arthropod community is that small and medium-size fragments should be dispersed enough to cover such a wide range of geographic area as to maximize beta diversity, but large fragments should be close enough to allow dispersal between fragments, to reduce the probability of extinction of species sensitive to fragmentation and to stabilize predator-prey interactions. In conclusion, our study showed significant differences in the composition of the arthropod community associated with the canopy of *Q. deserticola* among fragment sizes. The sites more fragmented had higher levels of arthropod abundance and richness, thus a greater presence of arthropod guilds (phytophages, predators, parasitoids and parasites). Since many arthropod species are associated to *Q. deserticola* and the oak species, it is important to conserve Mexican oaks throughout the fragmented landscapes. Small fragments can be considered keystone resources for maintaining of arthropod community diversity in a fragmented landscape in Mexican temperate forests. Oak and pine trees are the dominant species in most of the temperate forests of Mexico and they provide fundamental ecosystem services. Deforestation rates are increasing in Mexican forests with potentially serious implications. This study suggests that it is important to conserve oak forests in Mexico as important reservoirs of arthropod fauna.

Acknowledgements

García-Jain is a doctoral student from the Programa de Doctorado Institucional en Ciencias Biológicas, Universidad Michoacana de San Nicolás de Hidalgo (UMSNH) and was supported by CONACyT (scholarship no. 305239) and PFCTI/ICTI/2019/A/315. The study was funded by Coordination of Scientific Research (UMSNH), as part of research project

002. This project was supported by CONACYT PDC2016-Project-3053. The authors thank Dr. Gabriel Otero Colina for his help in identifying the families of the order Acari.

References

Agrawal AA, Hastings AP, Johnson MT, Maron JL, Salminen JP (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. Science, 338 (6103), 113-116

Aguilar R, Ghilardi A, Vega E, Skutsch M, Oyama K (2012) Sprouting productivity and allometric relationships of two oak species managed for traditional charcoal making in central Mexico. Biomass and bioenergy, 36, 192-207

Anton C, Zeisset I, Musche M, Durka W, Boomsma JJ, Settele J (2007) Population structure of a large blue butterfly and its specialist parasitoid in a fragmented landscape. Mol. Ecol., 16, 3828–3838

Arizaga S, Martínez-Cruz J, Salcedo-Cabrales M, Bello-González MA, (2009) Manual de la biodiversidad de encinos michoacanos. Secretaría de Medio Ambiente y Recursos Naturales, México. D.F.

Arroyo-Rodríguez V, Saldaña-Vázquez RA, Fahrig L, Santos BA (2017) Does forest fragmentation cause an increase in forest temperatura? Ecol Res 32:81-88 https://doi.org/10.1007/s11284-016-1411-6

Bagchi R, Brown LM, Elphick CS, Wagner DL, Singer MS (2018) Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant–herbivore interactions. Oecologia, 187(2), 521-533

Barberena-Arias MF, and Aide TM (2002) Variation in species and tropic composition of insect communities in Puerto Rico. Biotropica 34:357–367

Basset Y, Corbara B, Barrios H, Cuénoud P, Leponce M, Aberlenc H… et al. (2007) IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest: rationale, study sites and field protocols. Bull Inst R SC N B-E 77:39–69

Batary P, and Baldi A (2004) Evidence of an edge effect on avian nest success. *Conservation Biology*, *18*(2), 389-400

Bolger DT, Beard KH, Suarez AV, Case TJ (2008). Increased abundance of native and non-native spiders with habitat fragmentation. Diversity and Distributions, 14(4), 655-665

Burkle LA, Marlin JC, Knight TM (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339:1611- 1615 https://doi.org/10.1126/science.1232728

Cadenasso ML, and Pickett STA (2001) Effect of edge structure on the flux of species into forest interiors. Conserv. Biol. 15:91–97

Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conservation Biology, 23, 1167–1175

Caitano B, Chaves TP, Dodonov P, Delabie JHC (2020) Edge effects on insects depend on life history traits: a global meta-analysis. Journal of Insect Conservation, 24(2), 233-240

Castagneyrol B, Bonal D, Damien M, Jactel H, Meredieu C, Muiruri EW, Barbaro L (2017) Bottom-up and top-down effects of tree species diversity on leaf insect herbivory. Ecol Evol 7(10):3520–3531 https://doi.org/10.1002/ece3.2950

Castagneyrol B, Regolini M, Jactel H (2014) Tree species composition rather than diversity triggers associational resistance to the pine processionary moth. Basic Appl Ecol 15(6):516–523 https://doi.org/10.1016/j.baae.2014.06.008

Castillo-Santiago MA, Ghilardi A, Oyama K, Hernández-Stefanoni JL, Torres I, Flamenco-Sandoval A, Fernández A, Mas JF (2013) Estimating the spatial distribution of woody biomass suitable for charcoal making from remote sensing and geostatistics in central Mexico. Energy Sustain Dev 17:177–188 https://doi.org/10.1016/j.esd.2012.10.007

Chávez-Pesqueira M, Carmona D, Suárez-Montes P, Núñez-Farfán J, Aguilar R (2015). Synthesizing habitat fragmentation effects on plant–antagonist interactions in a phylogenetic context. Biological Conservation, 192, 304-314

Chen J, Franklin JF, Spies TA. (1995) Growing season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecol. Appl. 5:74–86

Cornelissen T, and Stiling P (2011) Similar responses of insect herbivores to leaf fluctuating asymmetry. Arthropod Plant Int 5:59–69 https://doi.org/10.1007/s11829010-9116-1

Cousins SA (2006) Plant species richness in midfield islets and road verges–the effect of landscape fragmentation. Biological conservation, 127(4), 500-509

De La Vega X, Grez AA, Simonetti JA (2012) Is top-down control by predators driving insect abundance and herbivory rates in fragmented forests?. Austral Ecology, 37(7), 836-844

Debinski DM, and Holt RD (2000) A survey and overview of habitat fragmentation. Conservation Biology 14:342–355

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. Ecol. Monogr. 68:295–323

Ewers RM, and Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological reviews, 81(1), 117-142

Faeth SH, Bultman TL (1986) Interacting effects of increased tannin levels on leaf-mining insects. Entomology 40(3):297–301 https://doi.org/10.1111/j.15707458.1986.tb00515.x

Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, ... Watling JI (2019). Is habitat fragmentation bad for biodiversity?. Biological Conservation, 230, 179-186

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

Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51(4):565–581 https://doi.org/10.2307/1934037

Fletcher JR, Didham RJ, Banks-Leite RK, Barlow C, Ewers J, Rosindell RM, Holt J, Gonzalez RD, Pardini A, Damschen R, Melo EI, Ries FPL, Prevedello L, Tscharntke JA, Laurance T, Lovejoy WF, Haddad NM (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15

Fletcher JR, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined?. Canadian journal of zoology, 85(10), 1017-1030

Forkner RE, Hunter MD (2000) What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81(6):1588–1600 https://doi.org/10.1890/ 0012-9658(2000) 081

Forkner RE, Marquis RJ, Lill JT, Corff JL (2008) Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of *Quercus*. Ecol Entomol 33:276–285

García-Jain SE, Maldonado-López Y, Oyama K, Fagundes M, de Faria ML, Espírito-Santo MM, Cuevas-Reyes P (2021) Effects of forest fragmentation on plant quality, leaf morphology and herbivory of *Quercus deserticola*: is fluctuating asymmetry a good indicator of environmental stress?. Trees, 1-15

Gibb H, and Hochuli DF (2002). Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol. Conserv. 106, 91–100 doi:10.1016/S0006-3207(01)00232-4

Gravel D, Massol F, Canard E, Mouillot D, Mouquet N (2011) Trophic theory of island biogeography. Ecology letters, 14(10), 1010-1016

Grez A, Zaviezo T, Tischendorf L, Fahrig L (2004) A transient, positive effect of habitat fragmentation on insect population densities. Oecologia 141:444–451

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science advances,1(2), e1500052

Hamilton AJ, Basset Y, Benke KK, Grinbacher PS, Miller SE, Samuelson GA, Stork NE, Weiblen GD, Yen JD (2010) Quantifying uncertainty in estimation of tropical arthropod species richness. Am Nat 176:90–95

Hamilton AJ, Novotny WEK, Bassset Y, Benke KK, Grimbacher PS, Samuelson GA, Weiblen GD, Yen JDL, Stork NE, Weiblen GD, Yen JDL (2013) Estimating global arthropod species richness: refining probabilistic models using probability bounds analysis. Oecologia 171:357–365

Hammer O, Harper DAT, Ryan PD (2001) PAST:Paleontological Statistics software package for education and data analysis. Palaeontol Electron 4:9

Han P, Becker C, Sentis A, Rostás M, Desneux N, Lavoir AV (2019) Global change-driven modulation of bottom–up forces and cascading effects on biocontrol services. Current opinion in insect science, 35, 27-33

Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19:768–782

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, ... Müller J (2020) Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. Nature ecology & evolution, 4(9), 1204-1212

Holt RD (1996) Food webs in space: an island biogeographic perspective. Pages 313.323 in G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, London

Holt RD (2010) Toward a trophic theory of island biogeography, in The Theory of Island Biogeography Revisted, eds J. B. Losos and R. E. Ricklefs (Princeton, NJ: Princeton University Press), 143–185 doi:10.1515/9781400831920.143

Holt RD, Lawton JH, Polis GA, Martinez ND (1999) Trophic rank and the species area relationship. Ecology, 80, 1495–1504 https://doi.org/10.1890/00129658(1999)080[1495:TRATSA]2.0.CO;2

Ibanez I, Katz DSW, Peltier D, Wolf SM, Barrie BTC (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess– multiresponse dynamics. J Ecol 102:882–895 https://doi.org/10.1111/13652745. 12223

Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Frontiers in Ecology and the Environment, 7(4), 196-203

Jachuła J, Denisow B, Wrzesień M (2021) Habitat heterogeneity helps to mitigate pollinator nectar sugar deficit and discontinuity in an agricultural landscape. Science of The Total Environment, 782, 146909

Kruess A, and Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581-1584

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology letters, 10(10), 937-944

Lizée MH, Bonardo R, Mauffrey JF, Bertaudière-Montes V, Tatoni T, Deschamps-Cottin M (2011) Relative importance of habitat and landscape scales on butterfly communities of urbanizing areas. C R Biol 334:74–84

López E, Bocco G, Mendoza M, Aguirre JR (2006) Peasant emigration and land use change at the watershed level: A GIS-based approach in Central Mexico. Agricult. Sys. 90:62-78

López E, Bocco G, Mendoza M, Duhau E (2001) Predicting land-cover and land-use change in the urban fringe: A case in Morelia city, Mexico. Landscape and urban planning, 55(4), 271-285

Maguire DY, Buddle CM, Bennett EM (2016) Within and among patch variability in patterns of insect herbivory across a fragmented forest landscape. PLoS ONE 11:e0150843 https://doi.org/10.1371/ journal.pone.0150843

Maguire DY, James PM, Buddle CM, Bennett EM (2015) Landscape connectivity and insect herbivory: A framework for understanding tradeoffs among ecosystem services. Global Ecology and Conservation,4, 73-84

Maldonado-López Y, Cuevas-Reyes P, Oyama K (2016) Diversity of gall wasps (Hymenoptera: Cynipidae) associated with oak trees (Fagaceae: Quercus) in a fragmented landscape in Mexico. Arthropod Plant Int 10:29–39. https://doi.org/10.1007/s11829-015-9404-x

Maldonado-López Y, Vaca-Sánchez MS, González-Rodríguez A, Oyama K, López-Barbosa E, Fagundes M, Cuevas-Reyes P (2018) Hybridization increases canopy arthropod diversity in the *Quercus affinis*× *Quercus laurina* complex. Journal of Insect Conservation, 22(5), 781-793

Maldonado-López Y, Cuevas-Reyes P, Stone GN, Nieves-Aldrey JL, Oyama K (2015) Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees. Ecosphere 6:31 https://doi.org/10.1890/ES1400355.1

Markgraf R, Doyon F, Kneeshaw D (2020) Forest landscape heterogeneity increases shrub diversity at the expense of tree seedling diversity in temperate mixedwood forests. Forests, 11(2), 160

Marques MI, Adis J, dos Santos GB, Battirola LD (2006) Terrestrial arthropods from tree canopies in the Pantanal of Mato Grosso, Brazil. Rev Bras Entomol 50:257–267

Martinson HM, Fagan WF (2014) Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. Ecol Lett 17:1178–1189. https://doi.org/10.1111/ele.12305

Mas JF, Lemoine-Rodríguez R, González R, López-Sánchez J, Piña-Garduño A, Herrera-Flores E (2017) Evaluación de las tasas de deforestación en Michoacán a escala detallada mediante un método híbrido de clasificación de imágenes SPOT. Madera y Bosques 23(2) https://doi.org/10.21829/myb.2017.2321472

Medvigy D, Clark KL, Skowronski NS, Schäfer KVR (2012) Simulated impacts of insect defoliation on forest carbon dynamics. Environ. Res. Lett. 7

Mendenhall CD, Karp DS, Meyer CF, Hadly EA, Daily GC (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. Nature, 509(7499), 213-217

Mendoza ME, López-Granados E, Genelettic D, Pérez-Salicrup DR, Salinas V (2011) Analysing land cover and land use change processes at watershed level: A multitemporal study in the Lake Cuitzeo Watershed, Mexico. App. Geog. 31 237-250

Moreno ML, Fernández MG, Molina SI, Valladares G, Scharf I (2014) The role of small woodland remnants on ground dwelling in-sect conservation in Chaco Serrano, Central Argentina. Journal of Insect Science, 13(1)

Murcia C (1995) Edge effects in fragmented forests: application for conservation. Trends Ecol Evol 10:58–62 https://doi.org/10.1016/S0169-5347(00)88977-6

Murphy SM, Battocletti AH, Tinghitella RM, Wimp GM, Ries L (2016) Complex community and evolutionary responses to habitat fragmentation and habitat edges: what can we learn from insect science? Curr. Opin. Insect Sci. 14, 61–65 doi:10.1016/j.cois.2016.01.007

Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, ... Ashton LA (2017) Forests and their canopies: achievements and horizons in canopy science. Trends in ecology & evolution, 32(6), 438-451 https://doi.org/10.1016/j.tree.2017.02.020

Newbold T, Bentley LF, Hill SL, Edgar MJ, Horton M, Su G, ...Purvis A (2019) Global effects of land use on biodiversity differ among functional groups. Functional Ecology, 34(3), 684-693

Nufio CR, McClenahan JL, Bowers MD (2011) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. J Insect Conserv 15:409–419

Økland RH, Bratli H, Dramstad WE, Edvardsen A, Engan G, Fjellstad W, Heegaard E, Pedersen O, Solstad H (2006) Scale-dependent importance of environment, land use and landscape structure for species richness and composition of SE Norwegian modern agricultural landscapes. Landsc Ecol 21(7):969–987

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Ewers RM (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187-191 https://doi.org/10.1038/nature24457

Pickett ST, and Rogers KH (1997) Patch dynamics: the transformation of landscape structure and function. In Wildlife and landscape ecology (pp. 101-127). Springer, New York, NY

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251 https://doi.org/10.2307/3545270

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008). Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

Qian H, and Shimono A (2012) Effects of geographic distance and climatic dissimilarity on species turnover in alpine meadow communities across a broad spatial extent on the Tibetan Plateau. Plant ecology, 213(8), 1357-1364

Rautiainen M, Stenberg P, Nilson T (2005) Estimating canopy cover in Scots pine stands. Silva Fenn 39:137–142

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Ries L, Sisk TD (2008) Edge effects are predicted by a simple model in a complex landscape. Oecologia 156:75–86

Rösch V, Tscharntke T, Scherber C, Batáry P (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia , 179, 209–222

Rossetti MR, Tscharntke T, Aguilar R, Batáry P (2017) Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecol Lett 20:264–272 https://doi.org/10.1111/ele.12723

Rossiter M, Schultz JC, Baldwin IT (1988) Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. Ecology 69(1):267–277. https://doi.org/10.2307/1943182

Sanchez-Bayo F, and Wyckhuys KAG (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. doi:10.1016/j.biocon.2019.01.020

SAS, 2000. Categorical data analysis using the SAS system. SAS Institute, Cary

Schmidt M, Lischeid G, Nendel C (2019) Microclimate and matter dynamics in transition zones of forest to arable land. Agric for Meteorol 268:1–10 https://doi.org/10.1016/j.agrformet.2019.01.001

Scholtz CH, and Holm E (2012) Insects of Southern Africa. Protea Boekhuis, South Africa

Schowalter TD (2012) Insect responses to major landscape-level disturbance. Annu. Rev. Entomol. 57: 1–20

Schowalter TD, Noriega JA, Tscharntke T (2018) Insect effects on ecosystem services—Introduction. Basic and Applied Ecology 26, 1-7

Schüepp C, Uzman D, Herzog F, Entling MH (2014) Habitat isolation affects plant-herbivore-enemy interactions on cherry trees. Biol Control 71:56–64 https://doi.org/10.1016/j.biocontrol.2014.01.007

Schultz JC, Baldwin IT (1982) Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217(4555):149–151 https://doi.org/10.1126/science.217.4555.149

Silva CA, Simonetti JA (2009) Inquiring into the causes of depressed folivory in a fragmented temperate forest. Acta Oecol 35:458–461 https://doi.org/10.1016/j.actao.2009.01.001

Sobek S, Tscharntke T, Scherber C, Schiele S, Steffan-Dewenter I (2009) Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? Forest Ecology and Management, 258, 609–615

Soliveres S, Van Der Plas F, Manning P, Prati D, Gossner MM, Renner SC, ... Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature, 536(7617), 456-459

Stork NE (2018). How many species of insects and other terrestrial arthropods are there on Earth?. Annual review of entomology, 63, 31-45

Stork NE, McBroom J, Gely C, Hamilton AJ (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. Proceedings of the National Academy of Sciences, 112(24), 7519-7523

Tal O, Freiberg M, Morawetz W (2008) Micro-climatic variability in the canopy of a temperate forest. In: Floren A, Schmidl J (eds) Canopy arthropod research in Europe. Bioform Entomology, Nuremberg, pp 49–59

Torrez-Terzo G, Pagliosa PR (2007) Fluctuating asymmetry as a useful biomarker of Environmental stress: a case of study with *Avicennia schaueriana* Stapf and Leechm. Ex moldenke (Acanthaceae). Insula 33:75–94

Tovar-Sánchez E, Cano-Santana Z, Oyama K (2003) Canopy arthropod communities on Mexican oaks at sites with different disturbance regimes. Biological conservation 115:79-87

Tovar-Sánchez E, Valencia-Cuevas L, Castillo-Mendoza E, Mussali-Galante P, PérezRuíz RV, Mendoza A (2013) Association between individual genetic diversity of two oak host species and canopy arthropod community structure. Eur J Forest Res 132:165–179

Tovar-Sánchez E, and Oyama K. (2006) Community structure of canopy arthropods associated to *Quercus crassifola* X *Quercus crassipes* complex. Oikos 112:370–381 https://doi.org/10.1111/j.0030-1299.2006.14029.x

Triplehorn CA, Johnson NF, Borror DJ (2005) An introduction to the study of insects. Thompson Brooks/Cole, Belmont

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland–cropland landscapes. Ecol. Appl.,12, 354–363

Ubick D, Paquin P, Cushing PE, Roth V (eds) (2017) Spiders of North America: an identification manual. American Arachnological Society. Keene, New Hampshire USA 377pp

Ulyshen MD (2011) Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. For Ecol Manag 261:1479–1489

Vaca-Sánchez MS, Maldonado-López Y, González-Rodríguez A, Oyama K, Fernandes GW, Fagundes M, Cuevas-Reyes P (2021) Canopy arthropod diversity associated with *Quercus laurina*: importance of an oak species diversity gradient on abundance, species richness and guild composition. Journal of Insect Conservation,25(5), 859-874

Valencia-Cuevas L, Mussali-Galante P, Pinero D, Castillo-Mendoza E, Rangel-Altamirano G, Tovar-Sanchez E (2015) Hybridization of *Quercus castanea* (Fagaceae) across a red oak species gradient in Mexico. Plant Syst Evol 301:1085–1097. https://doi.org/10.1007/s00606-014-1151-4

van Dam NM, Heil M (2011) Multitrophic interactions below and above ground: en route to the next level. J Ecol 99:77–88

Vidal MC, and Murphy SM (2018) Bottom-up vs top-down effects on terrestrial insect herbivores: a meta-analysis. Ecol Lett 21(1):138–150 https://doi.org/10.1111/ele.12874

Vitousek PM, D'Antonio CM, Loope LD, Rejminek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1-16

West C (1985) Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. Ecol Entomol 10(1):111–120 https://doi.org/10.1111/j.13652311.1985.tb00540.x

Wilson EO (2001) The Diversity of Life. Toronto, ON: Penguin.

Yang LH, and Gratton C (2014) Insects as drivers of ecosystem processes. Current Opinion in Insect Science, 2, 26-32

Table 1. a) Mean abundances of edge and interior trophic guilds between fragment sizes b) Mean species richness of edge and interior trophic guilds between fragment sizes.

a) Arthropod abundance

		Small fragments	**Medium-size fragments**	**Large fragments**
Edge	Detritivores	5 (± 2.08)	13 (± 5.52)	**17 (± 12.05)**
	Parasites	**0.5 (± 0.5)**	0	0
	Parasitoids	15.8 (± 5.39)	**26.3 (± 8.05)**	6 (± 1.91)
	Phytophages	166.8 (± 39.88)	**215.3 (± 60.38)**	146.3 (± 31.94)
	Predators	26.8 (± 5.36)	26 (± 6.82)	**37.5 (± 13.94)**
Interior	Detritivores	21.3 (± 6.47)	**41 (± 14.64)**	12.7 (± 4.64)
	Parasites	0.4 (± 0.17)	**1.4 (± 0.6)**	0
	Parasitoids	**36.3 (± 3.62)**	22.6 (± 2.15)	26.7 (± 3.90)
	Phytophages	**252.6 (± 28.18)**	181.2 (± 33.99)	232.5 (± 41.18)
	Predators	**73.1 (± 7.79)**	45.5 (± 7.37)	45.8 (± 6.76)

b) Arthropod species richness

		Small fragments	**Medium-size fragments**	**Large fragments**
Edge	Detritivores	3.5 (± 1.32)	**4.3 (± 0.95)**	3 (± 0.41)
	Parasites	**0.3 (± 0.25)**	0	0
	Parasitoids	13 (± 4.92)	**21 (± 6.01)**	5.8 (± 1.70)
	Phytophages	33.5 (± 5.17)	**38.8 (± 3.66)**	32 (± 5.16)
	Predators	14.5 (± 2.75)	14.5 (± 2.40)	**15.8 (± 3.35)**
Interior	Detritivores	**6 (± 0.95)**	5.9 (± 0.81)	4.3 (± 0.58)
	Parasites	0.4 (± 0.16)	**0.8 (± 0.25)**	0
	Parasitoids	**25.6 (± 1.94)**	17.1 (± 1.29)	19.5 (± 2.08)
	Phytophages	**58.9 (± 3.51)**	48.6 (± 3.56)	47 (± 2.94)
	Predators	**30.1 (± 2.02)**	21.2 (± 2.06)	23.1 (± 2.25)

Legend to figures

Figure 1. Rarefaction curves of the arthropod families between different fragment sizes.

Figure 2. Diversity patterns of canopy arthropods associated to *Quercus deserticola* in different fragment sizes. **a)** Differences in total arthropod abundance between fragment sizes. **b)** Differences in total arthropod morphospecies richness. **c)** Comparison in abundance of canopy arthropods among different fragment sizes and forest edges and forest interior. **d)** Species richness of arthropod between forest edges and forest interior. Different letters above bars indicate statistically significant differences ($P < 0.05$).

Figure 3. Differences in abundance of arthropod orders associated to *Q. deserticola* canopy between different fragment sizes

Figure 4. Diversity patterns of arthropod guild composition along fragmented landscape. **a)** Comparison among different fragment sizes in canopy arthropod guild abundance , and **b)** species richness of arthropod guilds. Different letters above bars indicate statistically significant differences ($P < 0.05$).

Figure 5. Ordination plot of arthropod abundance along non-metric multidimensional scaling (NMDS) **a)** in fragments with different size and **b)** forest edges and forest interior

Figure 1

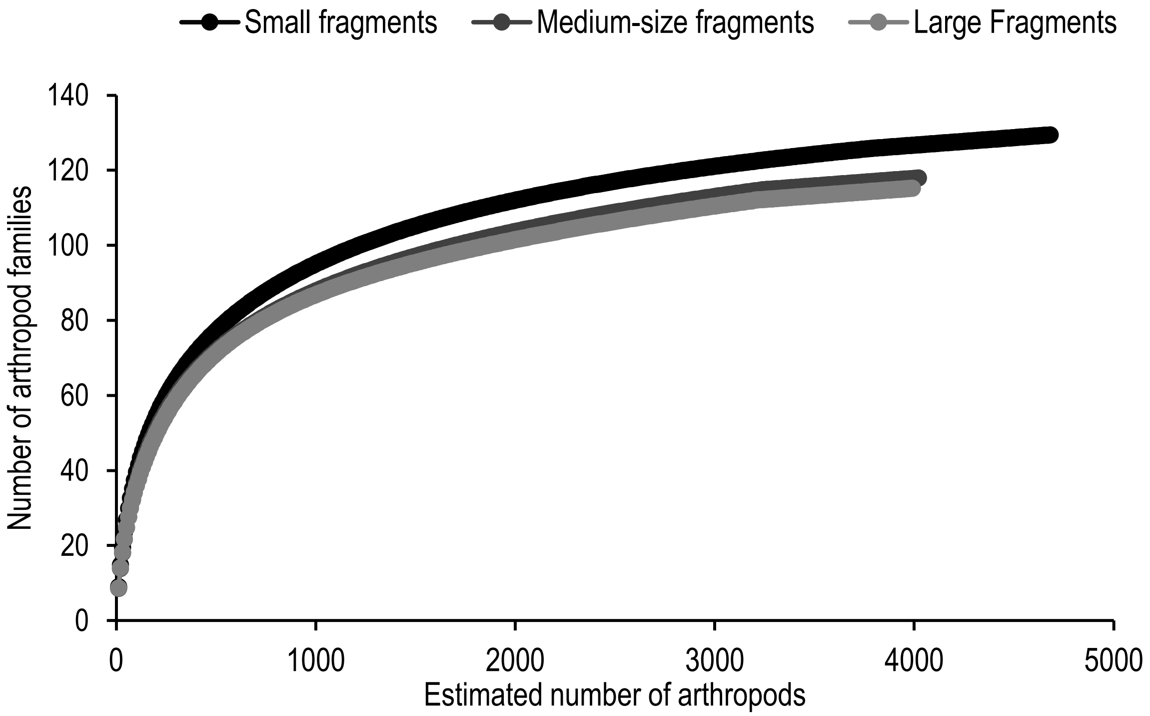

Small fragments
Medium-size fragments
Large Fragments
140
120
100
80
60
40
20
0
Number of arthropod families
0
1000
2000
3000
4000
5000
Estimated number of arthropods

Figure 2

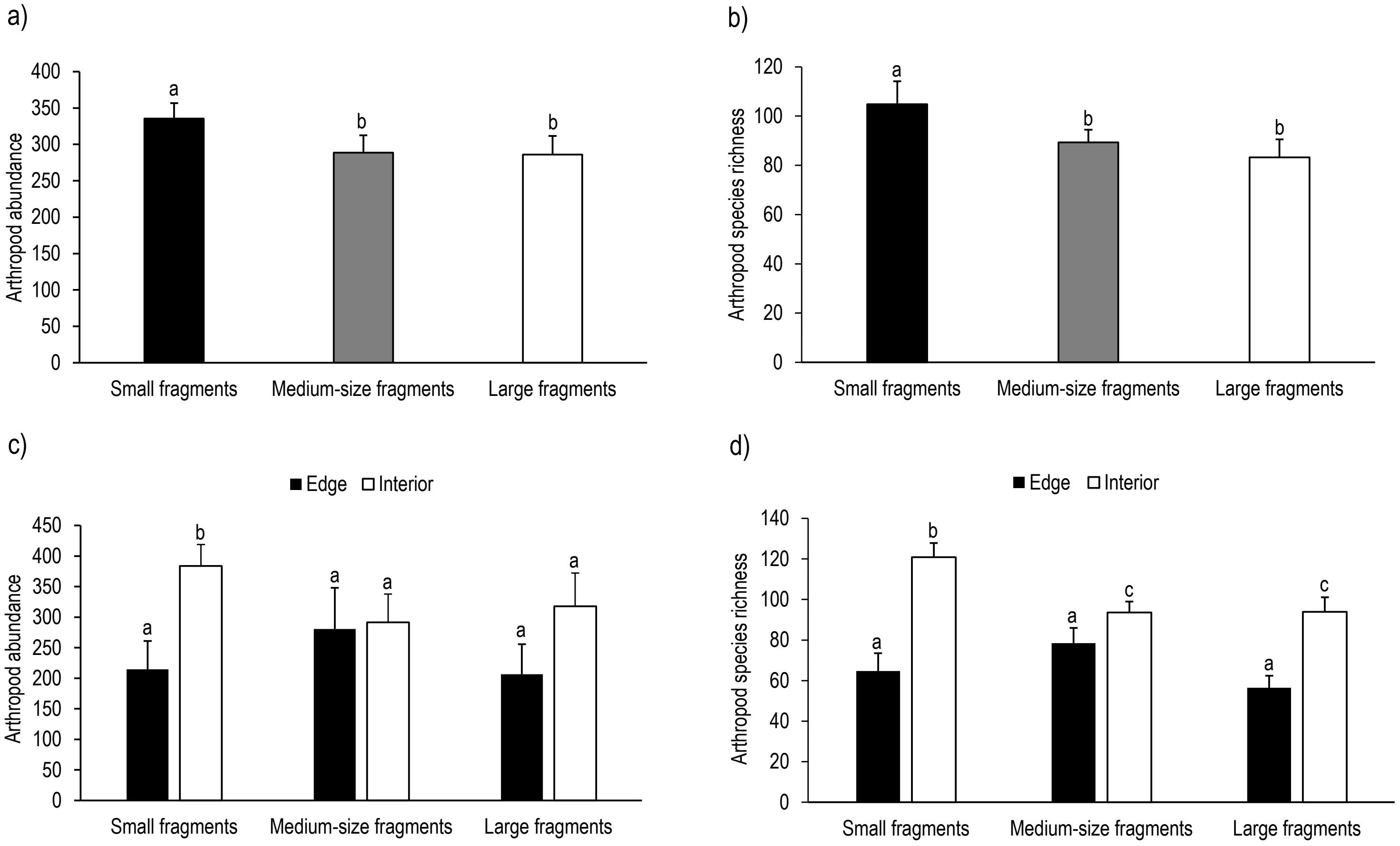
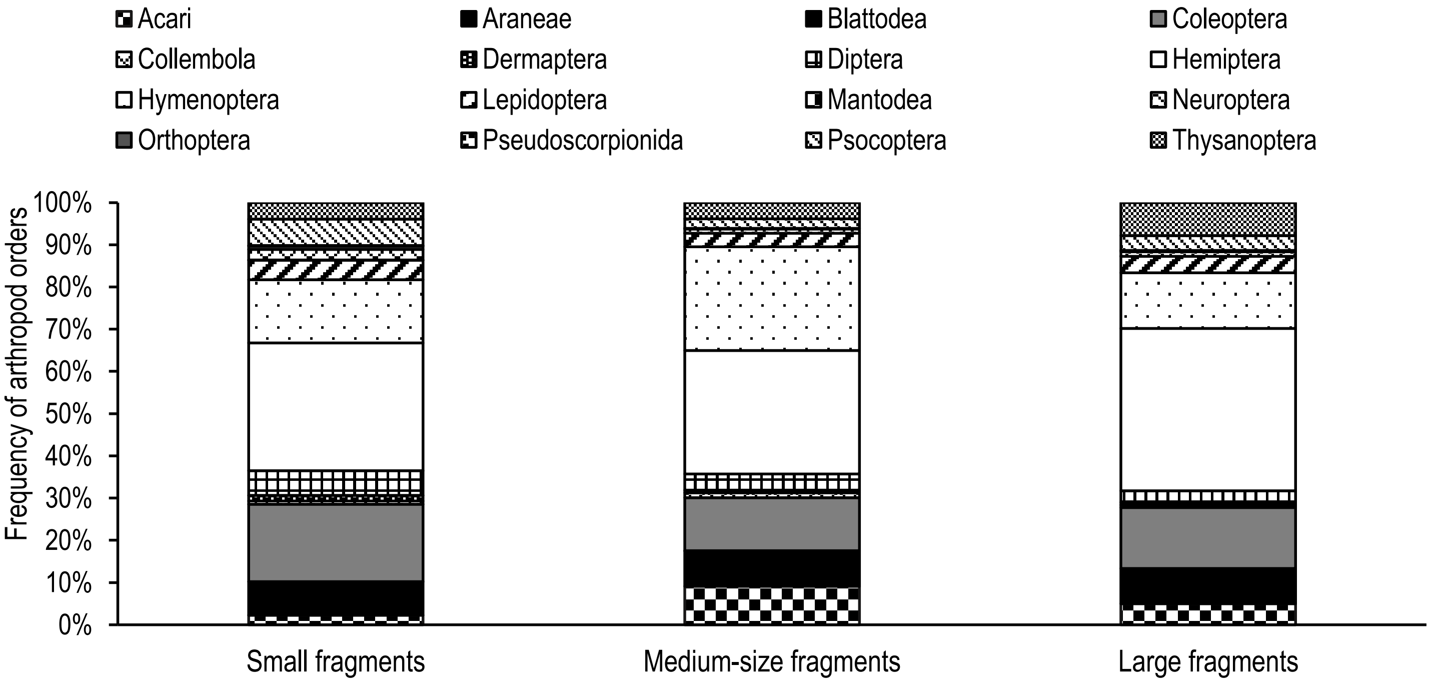

a)
400
350
300
250
200
150
100
50
0
Arthropod abundance
a
b
b
Small fragments
Medium-size fragments
Large fragments
b)
120
100
80
60
40
20
0
Arthropod species richness
a
b
b
Small fragments
Medium-size fragments
Large fragments
c)
■ Edge
□ Interior
450
400
350
300
250
200
150
100
50
0
Arthropod abundance
a
b
a
a
a
a
Small fragments
Medium-size fragments
Large fragments
d)
■ Edge
□ Interior
140
120
100
80
60
40
20
0
Arthropod species richness
a
b
a
c
a
c
Small fragments
Medium-size fragments
Large fragments

Figure 3



Acari
Araneae
Blattodea
Coleoptera
Collembola
Dermaptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Mantodea
Neuroptera
Orthoptera
Pseudoscorpionida
Psocoptera
Thysanoptera
Frequency of arthropod orders
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Small fragments
Medium-size fragments
Large fragments

Figure 4

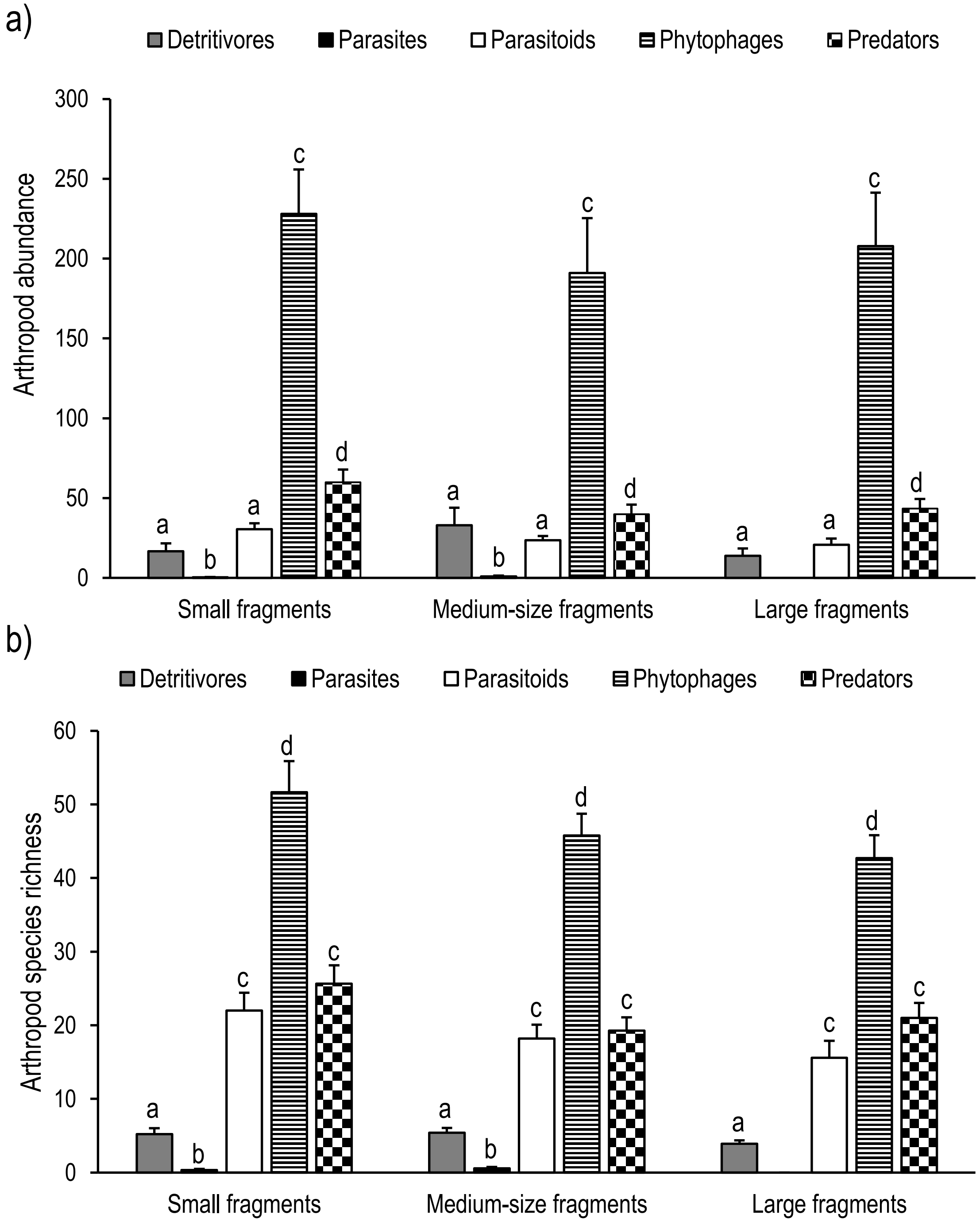
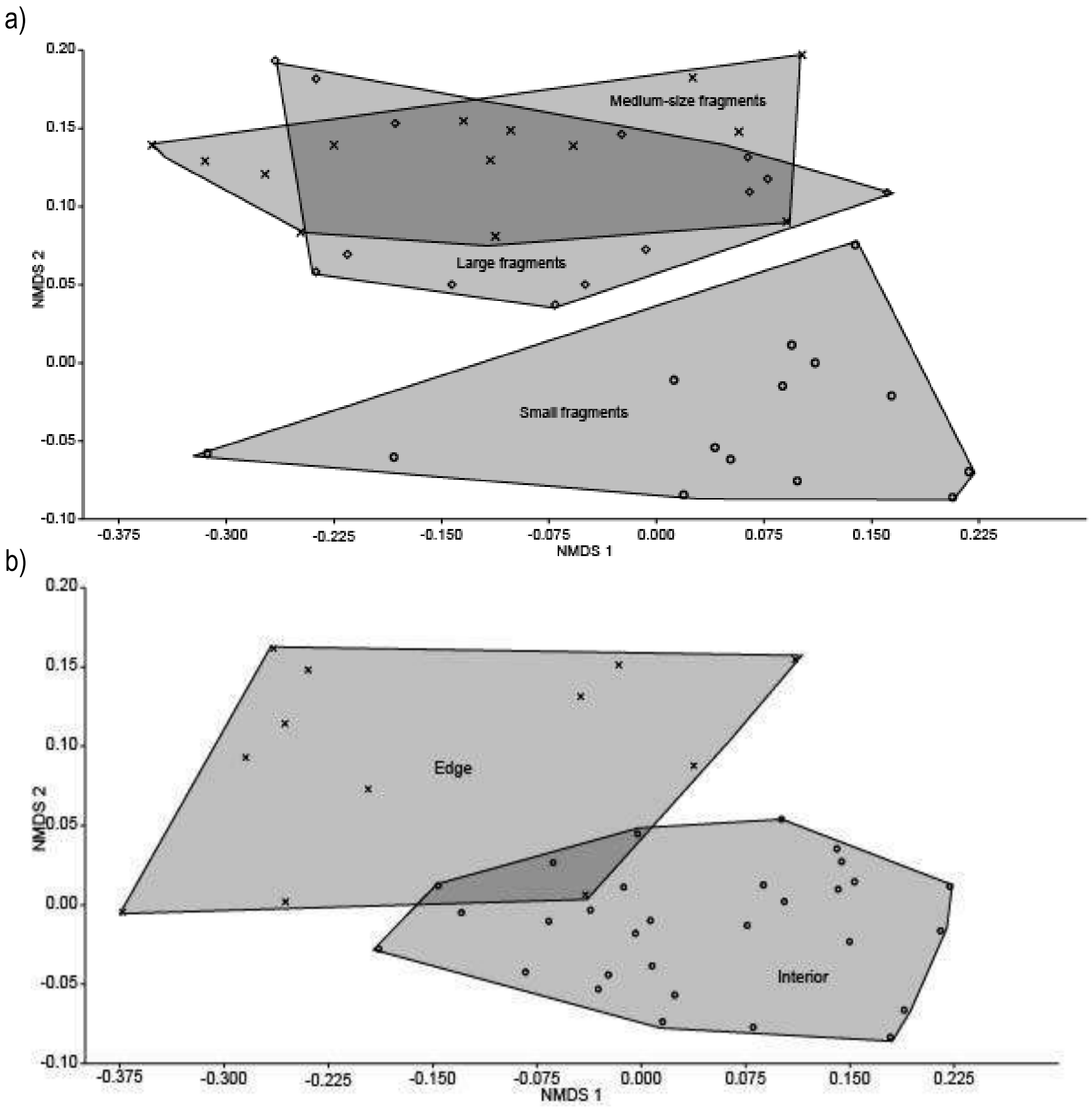

a)
Detritivores
Parasites
Parasitoids
Phytophages
Predators
Arthropod abundance
300
250
200
150
100
50
0
a
b
a
c
d
a
b
a
c
d
a
a
c
d
Small fragments
Medium-size fragments
Large fragments
b)
Detritivores
Parasites
Parasitoids
Phytophages
Predators
Arthropod species richness
60
50
40
30
20
10
0
a
b
c
d
c
a
b
c
d
c
a
c
d
c
Small fragments
Medium-size fragments
Large fragments

Figure 5


a)
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
NMDS 2
Medium-size fragments
Large fragments
Small fragments
-0.375
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
NMDS 1
b)
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
NMDS 2
Edge
Interior
-0.375
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
NMDS 1

SUPPORTING INFORMATION

Forest fragmentation increases canopy arthropod diversity in *Quercus deserticola*

Silvia Ecaterina García-Jain[1], Yurixhi Maldonado-López[2], Ken Oyama[3], Edmundo Carlos López- Barbosa[4], Marcílio Fagundes[5], Maurício Lopes de Faria[5], Mário M. Espítito-Santo[5] and Pablo Cuevas-Reyes[1*]

Table 1. Order, family and their abundance among different fragment sizes

Order	Family	Small fragments	Medium-size fragments	Large fragments	Abundance
Acari	Anystidae	12	9	5	26
	Erythraeidae	29	38	59	126
	Heterobelbidae	8	0	0	8
	Neoliodidae	0	21	0	21
	Nothridae	47	281	111	439
	Phytoseiidae	9	3	11	23
	Scheloribatidae	1	17	14	32
Araneae	Anyphaenidae	138	128	127	393
	Araneidae	117	58	89	264
	Gnaphosidae	2	1	1	4
	Nesticidae	1	0	0	1
	Oonopidae	1	0	0	1
	Oxyopidae	15	1	0	16
	Salticidae	55	99	77	231
	Thomisidae	45	48	38	131
Blattodea	Blaberidae	0	2	0	2
	Blattellidae	0	1	0	1
Coleoptera	Anobiidae	0	0	1	1
	Anthicidae	1	1	0	2
	Anthribidae	0	0	1	1
	Buprestidae	2	2	0	4
	Cantharidae	10	0	0	10
	Carabidae	57	15	36	108
	Cerambycidae	2	0	0	2
	Chrysomelidae	441	172	293	906
	Cleridae	7	1	8	16
	Coccinellidae	79	25	15	119

	Corylophidae	0	1	0	1
	Curculionidae	149	65	130	344
	Erotylidae	5	3	2	10
	Languriidae	1	2	0	3
	Latridiidae	11	38	22	71
	Meloidae	9	0	10	19
	Melyridae	0	2	6	8
	Mordellidae	2	3	2	7
	Nitidulidae	3	1	0	4
	Passalidae	1	0	0	1
	Phalacridae	10	150	22	182
	Salpingidae	8	4	9	21
	Scirtidae	1	0	1	2
	Silvanidae	0	1	1	2
	Staphylinidae	33	6	9	48
	Tenebrionidae	27	15	11	53
	Trogossitidae	2	0	0	2
Collembola	Entomobryidae	18	0	12	30
	Hypogastruridae	6	0	0	6
	Isotomidae	13	47	13	73
Dermaptera	Forficulidae	60	26	24	110
Diptera	Agromyzidae	3	0	0	3
	Asilidae	0	1	0	1
	Cecidomyiidae	8	14	1	23
	Ceratopogonidae	6	14	0	20
	Chamaemyiidae	39	18	17	74
	Chironomidae	1	12	5	18
	Chloropidae	34	31	51	116
	Curtonotidae	1	9	0	10
	Dolichopodidae	9	22	2	33
	Drosophilidae	3	3	0	6
	Empididae	0	0	2	2
	Fanniidae	4	4	0	8
	Heleomyzidae	0	1	0	1
	Muscidae	78	5	2	85
	Phoridae	5	6	0	11
	Psychodidae	3	0	0	3
	Scatopsidae	3	0	1	4
	Sciaridae	67	10	27	104
	Stratiomyidae	1	0	0	1
	Syrphidae	0	1	1	2
	Tachinidae	4	0	0	4
	Therevidae	0	1	0	1

	Tipulidae	1	0	0	1
	Ulidiidae	4	3	2	9
Hemiptera	Achilidae	0	0	2	2
	Anthocoridae	29	15	16	60
	Aphididae	136	102	155	393
	Aradidae	1	1	2	4
	Cicadellidae	326	472	713	1511
	Coreidae	2	1	2	5
	Delphacidae	13	6	10	29
	Fulgoridae	26	21	21	68
	Issidae	1	1	2	4
	Largidae	2	0	7	9
	Lygaeidae	72	16	102	190
	Membracidae	33	38	18	89
	Mesoveliidae	0	3	16	19
	Microphysidae	4	0	0	4
	Miridae	633	290	223	1146
	Pachygronthidae	0	6	0	6
	Pentatomidae	14	7	15	36
	Phylloxeridae	70	73	31	174
	Psyllidae	9	26	12	47
	Pyrrhocoridae	1	1	1	3
	Reduviidae	7	11	6	24
	Rhopalidae	3	1	1	5
	Rhyparochromidae	0	2	6	8
	Scutelleridae	15	22	20	57
	Tingidae	25	65	158	248
Hymenoptera	Aphelinidae	10	10	24	44
	Bethylidae	25	29	23	77
	Braconidae	48	24	29	101
	Ceraphronidae	15	4	0	19
	Chalcididae	0	2	1	3
	Cynipidae	6	2	4	12
	Diapriidae	1	1	1	3
	Dryinidae	3	1	0	4
	Encyrtidae	39	52	42	133
	Eulophidae	135	114	78	327
	Eupelmidae	19	14	11	44
	Eurytomidae	4	3	6	13
	Figitidae	2	3	1	6
	Formicidae	277	662	233	1172
	Ichneumonidae	25	9	11	45
	Megaspilidae	0	1	1	2

	Mymaridae	3	1	3	7
	Ormyridae	12	6	11	29
	Perilampidae	3	0	2	5
	Platygastridae	49	19	16	84
	Pteromalidae	9	23	7	39
	Scelionidae	16	11	19	46
	Tetracampidae	0	0	2	2
	Torymidae	3	4	3	10
	Vespidae	1	0	0	1
Lepidoptera	Arctiidae	11	6	13	30
	Crambidae	1	0	0	1
	Gelechiidae	53	40	31	124
	Geometridae	101	41	64	206
	Gracilariidae	3	2	2	7
	Heliodinidae	3	0	1	4
	Hepialidae	0	7	11	18
	Noctuidae	3	9	5	17
	Nymphalidae	0	0	1	1
	Pterophoridae	8	2	9	19
	Pyralidae	21	11	7	39
	Saturniidae	4	0	1	5
	Tineidae	8	5	2	15
	Tortricidae	0	4	8	12
Mantodea	Mantidae	2	1	1	4
Neuroptera	Chrysopidae	17	5	14	36
	Coniopterygidae	2	17	4	23
	Hemerobiidae	96	18	24	138
	Mantispidae	1	0	1	2
Orthoptera	Gryllidae	35	7	9	51
	Romaleidae	4	0	1	5
	Tettigoniidae	0	0	1	1
Pseudoscorpionida	Pseudogarypidae	8	1	3	12
Psocoptera	Ectopsocidae	33	23	14	70
	Lachesillidae	8	5	6	19
	Liposcelididae	0	2	2	4
	Peripsocidae	13	5	6	24
	Philotarsidae	4	1	0	5
	Psocidae	234	54	111	399
Thysanoptera	Aeolothripidae	6	0	1	7
	Merothripidae	1	0	0	1
	Phlaeothripidae	131	97	284	512
	Thripidae	46	59	29	134

Table 2. Trophic guild designated by order and family of the arthropod community

Trophic guild	**Order**	**Family**
Detritivores	Acari	Heterobelbidae, Neoliodidae, Nothridae, Scheloribatidae
	Blattodea	Blattellidae
	Coleoptera	Latridiidae, Nitidulidae, Tenebrionidae
	Collembola	Entomobryidae, Hypogastruridae, Isotomidae
	Diptera	Chironomidae, Curtonotidae, Fanniidae, Muscidae, Phoridae, Psychodidae, Scatopsidae, Ulidiidae
	Psocoptera	Liposcelididae
Parasites	Diptera	Ceratopogonidae
Parasitoids	Diptera	Tachinidae
	Hymenoptera	Aphelinidae, Bethylidae, Braconidae, Ceraphronidae, Chalcididae, Diapriidae, Dryinidae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Figitidae, Ichneumonidae, Megaspilidae, Mymaridae, Ormyridae, Perilampidae, Platygastridae, Pteromalidae, Scelionidae, Tetracampidae, Torymidae, Vespidae
Phytophages	Blattodea	Blaberidae
	Coleoptera	Anobiidae, Anthribidae, Buprestidae, Cantharidae, Cerambycidae, Chrysomelidae, Corylophidae, Curculionidae, Erotylidae, Languriidae, Mordellidae, Passalidae, Phalacridae, Scirtidae, Silvanidae, Trogossitidae
	Dermaptera	Forficulidae
	Diptera	Agromyzidae, Cecidomyiidae, Chloropidae, Drosophilidae, Heleomyzidae, Sciaridae, Stratiomyidae, Tipulidae
	Hemiptera	Achilidae, Aphididae, Aradidae, Cicadellidae, Coreidae, Delphacidae, Fulgoridae, Issidae, Largidae, Lygaeidae, Membracidae, Miridae, Pentatomidae, Phylloxeridae, Psyllidae, Pyrrhocoridae, Rhopalidae, Rhyparochromidae, Scutelleridae, Tingidae
	Hymenoptera	Cynipidae
	Lepidoptera	Arctiidae, Crambidae, Gelechiidae, Geometridae, Gracilariidae, Heliodinidae, Hepialidae, Noctuidae, Nymphalidae, Pterophoridae, Pyralidae, Saturniidae, Tineidae, Tortricidae
	Orthoptera	Gryllidae, Romaleidae, Tettigoniidae
	Psocoptera	Ectopsocidae, Lachesillidae, Peripsocidae, Philotarsidae, Psocidae
	Thysanoptera	Merothripidae, Phlaeothripidae, Thripidae
Predators	Acari	Anystidae, Erythraeidae, Phytoseiidae
	Araneae	Anyphaenidae, Araneidae, Gnaphosidae, Nesticidae, Oonopidae, Oxyopidae, Salticidae, Thomisidae
	Coleoptera	Anthicidae, Carabidae, Cleridae, Coccinellidae, Meloidae, Melyridae, Salpingidae, Staphylinidae
	Diptera	Asilidae, Chamaemyiidae, Dolichopodidae, Empididae, Syrphidae, Therevidae

	Hemiptera	Anthocoridae, Mesoveliidae, Microphysidae, Pachygronthidae, Reduviidae
	Mantodea	Mantidae
	Neuroptera	Chrysopidae, Coniopterygidae, Hemerobiidae, Mantispidae
	Pseudoscorpionida	Pseudogarypidae
	Thysanoptera	Aeolothripidae

DISCUSIÓN GENERAL

Los resultados de esta tesis mostraron que la fragmentación de bosque provoca cambios en los rasgos de *Q. deserticola* siendo las hojas más grandes y alargadas, aumentando la cantidad de recursos, calidad de la planta, herbivoría y AF en individuos de *Q. deserticola* que crecen en los fragmentos pequeños. Las plantas en los fragmentos pequeños y en los bordes están sujetas a mayores niveles de estrés debido a los cambios abruptos en las condiciones abióticas (Murcia 1995). Nuestros resultados indicaron que las hojas de *Q. deserticola* fueron más grandes y alargadas en los fragmentos pequeños y los bordes. Este resultado puede ser explicado por la hipótesis de la “concentración de recursos” (Coley et al. 1985), que predice que las plantas crecen más rápido y producen hojas más grandes en sitios con mayor disponibilidad de recursos (incidencia de luz y N). Por lo tanto, el aumento de la intensidad de luz en fragmentos pequeños y borde se puede asociar con altas tasas de fotosíntesis, crecimiento más rápido y hojas más grandes (Lohbeck et al. 2015).

Otro resultado importante es que los niveles de herbivoría fueron más altos en individuos de *Q. deserticola* de fragmentos pequeños y de los bordes, donde la cantidad de recursos y la calidad de la planta fue mayor (i.e., contenido de clorofila, DAP, cobertura del dosel). Este resultado puede ser explicado debido a que las condiciones abióticas en los fragmentos pequeños y bordes cambian más abruptamente aumentando la calidad de la planta que a su vez aumenta los niveles de herbivoría (Silva y Simonetti 2009). De acuerdo con la hipótesis “vigor de la planta” (Price 1991) que propone que los herbívoros se alimentan preferentemente de plantas grandes y vigorosas. Por lo tanto, las plantas en los fragmentos pequeños y bordes son más vigorosas, representando recursos de mayor contenido nutricional y baja concentración de defensas químicas.

Los resultados demostraron que los niveles de AF y herbivoría fueron mayores en los fragmentos pequeños y los bordes, así como una relación positiva entre la AF y la herbivoría. Se pueden explicar de dos maneras estos resultados: 1) La herbivoría causa directamente estrés en la planta hospedera, resultando en niveles más altos de AF (Gómez et al. 2003; Santos et al. 2013; Maldonado-López et al. 2019). Se ha demostrado que el daño por herbivoría puede provocar alteraciones en la inestabilidad del desarrollo, es decir, la capacidad de un genotipo para desarrollar el mismo fenotipo independientemente de las condiciones ambientales, las hojas dañadas por insectos muestran pequeñas desviaciones de la simetría perfecta, lo que indica altos niveles de estrés expresado en niveles más altos de asimetría fluctuante en comparación con las hojas sin daño (Alves-Silva y Del-Claro 2016). 2) Plantas con mayor AF podrían ser más susceptible a la herbivoría como resultados de diferencias químicas o nutricionales entre hojas simétricas y hojas asimétricas (Lempa et al. 2000; Ribeiro et al. 2013).

En nuestro estudio encontramos que tanto la abundancia y riqueza de artrópodos del dosel asociados a *Q. deserticola*, se incrementó en los fragmentos pequeños y en los interiores de los fragmentos. Estos resultados se explican debido a que los fragmentos pequeños pueden funcionar como refugios, representando recursos clave, un efecto positivo para la biodiversidad (Økland et al. 2006, Maldonado-López et al. 2015; Fahrig et al. 2019). La biodiversidad aumenta particularmente cuando se consideran organismos como plantas y artrópodos que requieren áreas pequeñas y son sensibles al microhábitat (Tscharntke et al. 2002; Markgraf et al 2020). Además, las condiciones abióticas en los fragmentos pequeños cambian más abruptamente que en los fragmentos grandes, aumentando la calidad de la planta (es decir, la cobertura del dosel, el contenido de clorofila y el tamaño de la planta), lo que a su vez aumenta los niveles de herbivoría (Maldonado-López et al 2016; García-Jain et al 2021). Por tanto, proponemos que la abundancia de artrópodos y la riqueza de especies aumentaron con la fragmentación del hábitat, debido a la heterogeneidad del hábitat y al aumento de la calidad de la planta, representando recursos de mayor contenido nutricional y baja concentración de defensas químicas para los artrópodos. Además, el interior de los fragmentos pequeños presento la mayor abundancia y riqueza de artrópodos, así como la mayor abundancia y riqueza de los fitófagos, depredadores y parasitoides respecto a los fragmentos medianos y grandes. Sugerimos que es debido a que el interior no presenta cambios abruptos en las condiciones ambientales, por lo tanto, las interacciones bióticas no son afectadas y aún están en equilibrio en los interiores. Estas diferencias en las condiciones cerca del borde de los fragmentos a menudo reducen la supervivencia de especies típicas del interior del bosque.

Además, la composición de la comunidad de artrópodos entre los distintos tamaños de fragmentos mostró que los fragmentos pequeños tenían una composición significativamente diferente de la comunidad de artrópodos en comparación con los fragmentos de tamaño mediano y grande. Los órdenes con mayor abundancia en los fragmentos pequeños fueron Coleoptera, Diptera, Lepidoptera y Psocoptera en comparación a la composición de la comunidad de artrópodos de los fragmentos medianos y grandes. Los estudios han encontrado diferencias en la composición de la comunidad de artrópodos entre diferentes tamaños de fragmentos (Gibb y Houchuli 2002; Bolger et al. 2008). Por ejemplo, Gibb y Hochuli (2002) encontraron que los fragmentos de hábitat grandes y pequeños contenían diferente composición de los órdenes Hymenoptera y Araneae , lo que indica que los depredadores y parasitoides se ven afectados con más fuerza que otros gremios tróficos. Por lo tanto, nuestros resultados de mayor abundancia y riqueza de especies de artrópodos en pequeños fragmentos se explican por el “crowding effect” que es un efecto relativamente positivo de la fragmentación sobre la densidad de población de insectos (Debinski y Holt 2000; Maldonado-López et al. 2015). Después de la fragmentación, las poblaciones de insectos pueden dispersarse a fragmentos adyacentes, lo que resulta en un aumento local de la densidad de población (Debinski y Holt 2000; Grez et al.2004).

La abundancia de los gremios tróficos es distinta en respuesta a la fragmentación del hábitat (Soliveres et al. 2016; Newbold et al. 2019). Por ejemplo, Moreno et al (2014) encontraron una menor descomposición de la hojarasca en pequeños fragmentos, respaldada por reducciones en la diversidad de los detritívoros en pequeños fragmentos (Rantalainen et al. 2005). Encontramos que los detritívoros disminuyeron con la fragmentación, debido a que en hábitats fragmentados los humanos tienden a reducir la materia en descomposición. Para el caso de los fitófagos, encontramos que es el gremio trófico más abundante en todos los tamaños de fragmentos. Además, encontramos que los parasitoides y depredadores son más abundantes en pequeños fragmentos. Específicamente, las comunidades de artrópodos asociadas con el dosel de los encinos responden a la depredación de enemigos naturales como parásitos o parasitoides (Tovar-Sánchez et al. 2013; Maldonado-López et al. 2018; Vaca-Sánchez et al. 2021). Por lo tanto, explicamos nuestros resultados con base a que los gremios como fitófagos, depredadores, detritívoros y parasitoides se presentan con mayor abundancia y riqueza de especies en el dosel de los encinos (Tovar-Sánchez et al.2013; Maldonado-López et al.2018; Vaca-Sánchez et al. 2021). De esta forma, la gran diversidad de depredadores y parasitoides encontrados en nuestro estudio podría explicarse por la gran abundancia de fitófagos. Es decir, existe una relación denso-dependiente entre los insectos fitófagos y sus enemigos naturales.

Podemos concluir que la fragmentación del bosque afecta la morfología de las hojas, cantidad de recursos, la calidad de la planta, los niveles de AF y herbivoría. Encontramos que la morfología de las hojas, cantidad de recursos y la calidad de la planta, los niveles de AF y herbivoría se incrementan en los fragmentos pequeños y los bordes de los fragmentos. Las medidas del manejo forestal orientadas a la conservación deben considerar fragmentos de bosque pequeños para la conservación de especies de encinos para garantizar la persistencia a largo plazo de los bosques de encinos ya que son hábitats de los cuales dependen muchas especies. Dado que muchas especies de artrópodos están asociadas a *Q. deserticola* y a especies de encinos, es importante conservar los encinos mexicanos a lo largo de los paisajes fragmentados. Los pequeños fragmentos pueden considerarse recursos clave para el mantenimiento de la diversidad de la comunidad de artrópodos en un paisaje fragmentado en los bosques templados mexicanos. Nuestro estudio sugiere que es importante conservar los bosques de encino en México como importantes reservorios de fauna de artrópodos. Considerando que los hábitats fragmentados son cada vez más comunes en el mundo y los efectos que tienen sobre la biodiversidad, la evidencia de nuestro estudio sobre la gran cantidad de especies de artrópodos encontrados en los fragmentos pequeños podría ser útil para apoyar y dirigir esfuerzos de conservación en los hábitats más fragmentados, para mantener y conservar los servicios ecosistémicos que brindan los bosques.

REFERENCIAS GENERALES

Aguilar-Peralta JS, Gonzalez-Rodriguez A, Maldonado-Lopez Y, Fagundes M, Faria ML, Avila-Cabadilla LD, Alvarez-Anorve MY, Cuevas-Reyes P (2020) Contrasting patterns of morphology, fluctuating asymmetry and leaf herbivory in three plant species of different successional stages of a tropical dry forest. Trees 34:1075–1086 https://doi.org/10.1007/s00468-020-01982-z

Albarrán-Lara AL, Mendoza-Cuenca L, Valencia-Avalos S, González-Rodríguez A, Oyama K, (2010) Leaf fluctuating asymmetry increases with hybridization and introgression between *Quercus magnoliifolia* and *Quercus resinosa* (Fagaceae) throght an altitudinal gradient in Mexico. Int: J. Plant. Sci. 171, 310-322

Alves-Silva E, Del-Claro K (2016) Herbivory causes increases in leaf spinescence and fluctuating asymmetry as a mechanism of delayed induced resistance in a tropical savanna tree. Plant Ecol Evol 149:73–80 https://doi.org/10.5091/plecevo.2016.1093

Arroyo-Rodriguez V, Saldana-Vazquez RA, Fahrig L, Santos BA (2017) Does forest fragmentation cause an increase in forest temperatura? Ecol Res 32:81–88 https://doi.org/10.1007/s11284-016-1411-6

Askew RR, Melika G, Pujade-Villar J, Schönrogge K, Stone GN, Nieves-Aldrey JL (2013) Catalogue of parasitoids and inquilines in cynipid oak galls in the West Palaearctic. Zootaxa 3643:1– 133

Bagchi R, Brown LM, Elphick CS, Wagner DL, Singer MS (2018) Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant–herbivore interactions. Oecologia, 187(2), 521-533

Barberena-Arias MF and Aide TM (2002) Variation in species and tropic composition of insect communities in Puerto Rico. Biotropica 34:357–367

Basset Y, Corbara B, Barrios H, Cuénoud P, Leponce M, Aberlenc H… et al. (2007) IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest: rationale, study sites and field protocols. Bull Inst R SC N B-E 77:39–69

Bello M, and Labat J (1987) Los encinos (*Quercus*) del estado de Michoacán, México. Cuadernos de estudios michoacanos 1. CEMCA-INIFAR-SARH. México

Bocco G, López-Granados E, Mendoza ME (2012) La investigación ambiental en la cuenca del Lago de Cuitzeo: Una revisión de la bibliografía publicada. Contribuciones para el desarrollo sostenible de la cuenca del lago de Cuitzeo, Michoacán, 317-345

Bocco G, Mendoza M, Masera OR (2001) La dinámica del cambio del uso del suelo en Michoacán: Una propuesta metodológica para el estudio de los procesos de deforestación. Investigaciones geográficas, (44), 18-36

Bolger DT, Beard KH, Suarez AV, Case TJ (2008). Increased abundance of native and non-native spiders with habitat fragmentation. Diversity and Distributions, 14(4), 655-665

Bucher R, Herrmann JD, Schüepp C, Herzog F, Entling MH (2010) Arthropod colonization of trees in fragmented landscapes depends on species traits. The Open Ecol. J. 3: 111-117

Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conservation Biology, 23, 1167–1175

Castagneyrol B, Bonal D, Damien M, Jactel H, Meredieu C, Muiruri EW, Barbaro L (2017) Bottom-up and top-down effects of tree species diversity on leaf insect herbivory. Ecol Evol 7(10):3520–3531 https://doi.org/10.1002/ece3.2950

Castagneyrol B, Regolini M, Jactel H (2014) Tree species composition rather than diversity triggers associational resistance to the pine processionary moth. Basic Appl Ecol 15(6):516–523 https://doi.org/10.1016/j.baae.2014.06.008

Castillo-Santiago MA, Ghilardi A, Oyama K, Hernández-Stefanoni JL, Torres I, Flamenco-Sandoval A, Fernández A, Mas JF (2013) Estimating the spatial distribution of woody biomass suitable for charcoal making from remote sensing and geostatistics in central Mexico. Energy Sustain Dev 17:177–188 https://doi.org/10.1016/j.esd.2012.10.007

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899 https://doi.org/10.1126/science.230.4728.895

Cornelissen T, Stiling P (2011) Similar responses of insect herbivores to leaf fluctuating asymmetry. Arthropod Plant Int 5:59–69 https://doi.org/10.1007/s11829-010-9116-1

Cuevas-Reyes P, Canche-Delgado A, Maldonado-Lopez Y, Fernandes GW, Oyama K, Gonzalez-Rodriguez A (2018) Patterns of herbivory and leaf morphology in two Mexican hybrid oak complexes: Importance of fluctuating asymmetry as indicator of environmental stress in hybrid plants. Ecol Indic 90:164–170 https://doi.org/10.1016/j.ecolind.2018.03.009

Cuevas-Reyes P, Oyama K, Gonzalez-Rodriguez A, Fernandes GW, Mendoza-Cuenca L (2011) Contrasting herbivory patterns and leaf fluctuating asymmetry in *Heliocarpus pallidus* between different habitat types within a Mexican tropical dry forest. Journal of Tropical Ecology 27(4) 383-391

Debinski DM, and Holt RD (2000) A survey and overview of habitat fragmentation. Conservation Biology 14:342–355

Delgado JD, Arroyo NL, Arevalo JR, Fernandez-Palacios JM (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landsc Urban Plan 81:328–340 https://doi.org/10.1016/j.landurbplan.2007.01.005

Endara MJ, and Coley PD (2010) The resource availability hypothesis revisited: a meta-analysis. Func. Ecol. 25:389–398 https://doi.org/10.1111/j.1365-2435.2010.01803.x

Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, ... Watling JI (2019). Is habitat fragmentation bad for biodiversity?. Biological Conservation, 230, 179-186

Fletcher JR, Didham RJ, Banks-Leite RK, Barlow C, Ewers J, Rosindell RM, Holt J, Gonzalez RD, Pardini A, Damschen R, Melo EI, Ries FPL, Prevedello L, Tscharntke JA, Laurance T, Lovejoy WF, Haddad NM (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15

Freeman DC, Brown ML, Duda JJ, Graraham JH, Emlen JM, Krzysik AJ, Balbache H, Kovacicf DA, Zak JC (2005) Leaf fluctuating asymmetry, soil disturbance and plant stress: a multiple year comparison using two herbs, *Ipomoea pandurata* and *Cnidoscolus stimulosus*. Ecol Ind 5:85–95

García-Jain SE, Maldonado-López Y, Oyama K, Fagundes M, de Faria ML, Espírito-Santo MM, Cuevas-Reyes P (2021) Effects of forest fragmentation on plant quality, leaf morphology and herbivory of *Quercus deserticola*: is fluctuating asymmetry a good indicator of environmental stress?. Trees, 1-15

Gibb H, and Hochuli DF (2002). Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol. Conserv. 106, 91–100 doi: 10.1016/S0006-3207(01)00232-4

Gibbs JP, and Stanton EJ (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. Ecol. Appl. 11:79-85

Gomez JM, Garcia D, Zamora R (2003) Impact of vertebrate acorn and seedling predators on a Mediterranean *Quercus pyrenaica* forest. For Ecol Manag 180:125–134

Grez A, Zaviezo T, Tischendorf L, Fahrig L (2004) A transient, positive effect of habitat fragmentation on insect population densities. Oecologia 141:444–451

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science advances,1(2), e1500052.

Hamilton AJ, Basset Y, Benke KK, Grinbacher PS, Miller SE, Samuelson GA, Stork NE, Weiblen GD, Yen JD (2010) Quantifying uncertainty in estimation of tropical arthropod species richness. Am Nat 176:90–95

Hamilton AJ, Novotny WEK, Bassset Y, Benke KK, Grimbacher PS, Samuelson GA, Weiblen GD, Yen JDL, Stork NE, Weiblen GD, Yen JDL (2013) Estimating global arthropod species richness: refining probabilistic models using probability bounds analysis. Oecologia 171:357–365

Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005). Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19:768–782

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, ... Müller J (2020) Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. Nature ecology & evolution, 4(9), 1204-1212

Holt RD (1996) Food webs in space: an island biogeographic perspective. Pages 313–323 in G. A. Polis and K. Winemiller, editors. Food webs: contemporary perspectives. Chapman and Hall, New York, New York, USA

Jaeger JAG, Soukup T, Madrinan LF, Schwick C, Kienast F (2011) Landscape fragmentation in Europe. Joint EEA-FOEN report No2/2011. EEA Publications, Copenhagen

Kappelle M (2006) Ecology and Conservation of Neotropical Montane Oak Forests.

Ecological Studies 185. Springer, Berlin, Germany

Laurance WF, Camargo JLC, Luizao RCC, Laurance SG, Pimmd SL, Bruna EM, Stouffer FC, Williamson GB, Benitez-Malvido J, Vasconcelos GL, Van Houtan KS, Zartman CE, Boyle SA, Didhamm RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest fragments: a 32-year investigation. Biological conservation 144(1), 56-67

LeBrun EG, Plowes RM, Gilbert LE (2012) Imported fire ants near the edge of their range: disturbance and moisture determine prevalence and impact of an invasive social insect. Journal of Animal Ecology, 81(4), 884-895

Lempa K, Martel J, Koricheva J (2000) Covariation of fluctuating asymmetry, herbivory and chemistry during birch leaf expansion. Oecologia 122:354–360. https://doi.org/10.1007/s004420050041

Levey DJ, Caughlin TT, Brudvig LA, Haddad NM, Damschen EI, Tewksbury JJ, Evans DM (2016) Disentangling fragmentation effects on herbivory in understory plants of longleaf pine savanna. Ecology 97:2248–2258 https://doi.org/10.1002/ecy.1466

Lewington R, and Streeter D (1993) La historia natural de los robles. Dorling-Kindersley, España

Lindenmayer DB, and Fischer J (2006) Habitat fragmentation and landscape change: An Ecological and Conservation Synthesis Washington (DC): Island Press 317 pp

Lohbeck M, Lebrija-Trejos E, Martinez-Ramos M, Meave JA, Poorter L, Bongers F (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. PLoS ONE 10:e0123741. https://doi.org/10.1371/journal.pone.0123741

López E, Bocco G, Mendoza M, Aguirre JR (2006) Peasant emigration and land use change at the watershed level: A GIS-based approach in Central Mexico. Agricult. Sys. 90:62-78

Lustig A, Stouffer DB, Doscher C, Worner SP (2017) Landscape metrics as a framework to measure the effect of landscape structure on the spread of invasive insect species. Landscape Ecology, 32(12), 2311-2325

Maguire DY, Buddle CM, Bennett EM (2016) Within and among patch variability in patterns of insect herbivory across a fragmented forest landscape. PLoS ONE 11:e0150843 https://doi.org/10.1371/ journal.pone.0150843

Maguire DY, James PM, Buddle CM, Bennett EM (2015). Landscape connectivity and insect herbivory: A framework for understanding tradeoffs among ecosystem services. Global Ecology and Conservation, 4, 73-84

Maldonado-López Y, Cuevas-Reyes P, Oyama K (2016) Diversity of gall wasps (Hymenoptera: Cynipidae) associated with oak trees (Fagaceae: Quercus) in a fragmented landscape in Mexico. Arthropod Plant Int 10:29–39 https://doi.org/10.1007/s11829-015-9404-x

Maldonado-López Y, Cuevas-Reyes P, Stone GN, Nieves-Aldrey JL, Oyama K (2015) Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees. Ecosphere 6:31 https://doi.org/10.1890/ES1400355.1

Maldonado-López Y, Vaca-Sanchez MS, Canché-Delgado A, Garcia-Jain SE, Gonzalez-Rodriguez A, Cornelissen T, Cuevas-Reyes P (2019) Leaf herbivory and fluctuating asymmetry as indicators of mangrove stress. Wetlands Ecol Manag 27:571–580 https://doi.org/10.1007/s11273-019-09678-z

Maldonado-López Y, Vaca-Sánchez MS, González-Rodríguez A, Oyama K, López-Barbosa E, Fagundes M, Cuevas-Reyes P (2018) Hybridization increases canopy arthropod diversity in the *Quercus affinis*× *Quercus laurina* complex. Journal of Insect Conservation, 22(5), 781-793

Markgraf R, Doyon F, Kneeshaw D (2020) Forest landscape heterogeneity increases shrub diversity at the expense of tree seedling diversity in temperate mixedwood forests. Forests, 11(2), 160

Mas JF, Lemoine-Rodríguez R, González R, López-Sánchez J, Piña-Garduño A, Herrera-Flores E (2017) Evaluación de las tasas de deforestación en Michoacán a escala detallada mediante un método híbrido de clasificación de imágenes SPOT. Madera y Bosques 23(2) https://doi.org/10.21829/myb.2017.2321472

Masera OR, Ordóñez MJ, Dirzo R (1997) Carbon emissions from Mexican forests: current situation and long-term scenarios. Climatic change, 35(3), 265-295

Medvigy D, Clark KL, Skowronski NS, Schäfer KVR (2012) Simulated impacts of insect defoliation on forest carbon dynamics. Environ. Res. Lett. 7

Mendoza ME, López-Granados E, Genelettic D, Pérez-Salicrup DR, Salinas V (2011) Analysing land cover and land use change processes at watershed level: A multitemporal study in the Lake Cuitzeo Watershed, Mexico. App. Geog. 31 237-250

Møller AP, and Swaddle JP (1997) In: Asymmetry, Developmental Stability and Evolution. Oxford University Press, Oxford pp.285

Mooney KA, Halitschke R, Kessler A, Agrawal AA (2010) Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science 237:1642–1644 https://doi.org/10.1126/science.1184814

Moreno ML, Fernández MG, Molina SI, Valladares G, Scharf I (2014) The role of small woodland remnants on ground dwelling in-sect conservation in Chaco Serrano, Central Argentina. Journal of Insect Science, 13(1)

Murcia C (1995) Edge effects in fragmented forests: application for conservation. Trends Ecol Evol 10:58–62 https://doi.org/10.1016/S0169-5347(00)88977-6

Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, Ashton LA (2017) Forests and their canopies: achievements and horizons in canopy science. Trends in ecology & evolution, 32(6), 438-451 https://doi.org/10.1016/j.tree.2017.02.020

Newbold T, Bentley LF, Hill SL, Edgar MJ, Horton M, Su G, ...Purvis A (2019) Global effects of land use on biodiversity differ among functional groups. Functional Ecology, 34(3), 684-693

Nixon KC (1993) The genus *Quercus* in Mexico. En: Ramamoorthy T.P. Bye R. Lot A. y Fa J. (Eds.). Biological Diversity of Mexico: Origins and Distribution. Pp 397-420. Oxford University Press, New York

Nixon KC (2006) Global and neotropical distribution and diversity of oak (genus *Quercus*) and oak forest. In: Ecology and conservation of neotropical montane oak forest, pp 3–13 https://doi.org/10.1007/3-540-28909-7_1

Nufio CR, McClenahan JL, Bowers MD (2011) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. J Insect Conserv 15:409–419

Økland RH, Bratli H, Dramstad WE, Edvardsen A, Engan G, Fjellstad W, Heegaard E, Pedersen O, Solstad H (2006) Scale-dependent importance of environment, land use and landscape structure for species richness and composition of SE Norwegian modern agricultural landscapes. Landsc Ecol 21(7):969–987

Ortego J, Bonal JR, Muñoz A (2010) Genetic Consequences of habitat fragmentation in longlived tree species: The Case of the Mediterranean holm oak (*Quercus ilex*, L.). J. Hered.101: 717-726

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Ewers RM (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187-191 https://doi.org/10.1038/nature24457

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251 https://doi.org/10.2307/3545270

Rautiainen M, Stenberg P, Nilson T (2005) Estimating canopy cover in Scots pine stands. Silva Fenn 39:137–142

Ribeiro VA, Silva RN, Sousa-Souto L, Neves FD (2013) Fluctuating asymmetry of and herbivory on *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae) in pasture and secondary tropical dry forest. Acta Bot Brasilica 27:21–25. https://doi.org/10.1590/S0102-33062013000100003

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Ries L, Murphy SM, Wimp GM, Fletcher RJ (2017) Closing persistent gaps in knowledge about edge ecology. Curr Landsc Ecol Rep 2:30–41

Rossetti MR, Tscharntke T, Aguilar R, Batáry P (2017) Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecol Lett 20:264–272 https://doi.org/10.1111/ele.12723

Rozendaal DMA, Hurtado VH, Poorter L (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Func Ecol 20:207–216

Santos JC, Alves-Silva E, Cornelissen TG, Fernades GW (2013) The effect of fluctuating asymmetry and leaf nutrients on gall abundance and survivorship. Basic Appl Ecol 14:489–495 https://doi.org/10.1016/j.baae.2013.06.005

Schowalter TD (2012) Insect responses to major landscape-level disturbance. Annu. Rev. Entomol. 57: 1–20

Schowalter TD, Noriega JA, Tscharntke T (2018) Insect effects on ecosystem services—Introduction. Basic and Applied Ecology 26, 1-7

Schüepp C, Uzman D, Herzog F, Entling MH (2014) Habitat isolation affects plant-herbivore-enemy interactions on cherry trees. Biol Control 71:56–64 https://doi.org/10.1016/j.biocontrol.2014.01.007

Silva CA, Simonetti JA (2009) Inquiring into the causes of depressed folivory in a fragmented temperate forest. Acta Oecol 35:458–461 https://doi.org/10.1016/j.actao.2009.01.001

Soliveres S, Van Der Plas F, Manning P, Prati D, Gossner MM, Renner SC, ... Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature, 536(7617), 456-459

Stone GN, Schönrogge K, Atkinson RJ, Bellido D, Pujade-Villar J (2002) The population biology of oak gall wasps (Hymenoptera:Cynipidae). Annual Review of Entomology 47:633–668

Stork NE (2018). How many species of insects and other terrestrial arthropods are there on Earth?. Annual review of entomology, 63, 31-45

Stork NE, McBroom J, Gely C, Hamilton AJ (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. Proceedings of the National Academy of Sciences, 112(24), 7519-7523

Torrez-Terzo G, Pagliosa PR (2007) Fluctuating asymmetry as a useful biomarker of Environmental stress: a case of study with *Avicennia schaueriana* Stapf and Leechm. Ex moldenke (Acanthaceae). Insula 33:75–94

Tovar-Sanchez E, Oyama K (2006) Community structure of canopy arthropods associated to *Quercus crassifola* × *Quercus crassipes* complex. Oikos 112:370–381 https://doi.org/10.1111/j.0030-1299.2006.14029.x

Tovar-Sánchez E, Valencia-Cuevas L, Castillo-Mendoza E, Mussali-Galante P, Pérez-Ruíz RV, Mendoza A (2013) Association between individual genetic diversity of two oak host species and canopy arthropod community structure. Eur J Forest Res 132:165–179

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland–cropland landscapes. Ecol. Appl.,12, 354–363

Vaca-Sánchez MS, Maldonado-López Y, González-Rodríguez A, Oyama K, Fernandes GW, Fagundes M, Cuevas-Reyes P (2021) Canopy arthropod diversity associated with

Quercus laurina: importance of an oak species diversity gradient on abundance, species richness and guild composition. Journal of Insect Conservation,25(5), 859-874

Valencia-Ávalos S, and Nixón CK (2004) Biodiversidad de Oaxaca. Ed. Redacta. México DF, pp. 219-220

Wirth R, Meyer ST, Leal IR, Tabarelli M (2008) Plant herbivore interactions at the forest edge. Progress in botany. Springer, New York, pp 423–448

Yang LH, and Gratton C (2014) Insects as drivers of ecosystem processes. Current Opinion in Insect Science, 2, 26-32

APPENDIX. Order and family of the arthropod community associated with the canopy of *Quercus deserticola*

Acari (Ácaros)

1

2

3

4

1. Anystidae **2.** Nothridae **3.** Neoliodidae **4.** Erythraeidae

Araneae (Arañas)

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

1-4. Anyphaenidae **5-12.** Araneidae **13.** Gnaphosidae **14.** Nesticidae **15.** Oxyopidae **16-19.** Salticidae **20-22.** Thomisidae

Blattodea (Cucarachas)

1

1. Blattellidae

Coleoptera (Escarabajos)

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

1. Anobiidae **2.** Anthicidae **3.** Buprestidae **4.** Cantharidae **5-8.** Carabidae **9.** Cerambycidae **10-19.** Chrysomelidae **20-22.** Cleridae 2**3-28.** Coccinellidae **29-36.** Curculionidae **37.** Erotylidae **38.** Languriidae **39.** Latridiidae **40.** Meloidae **41-42.** Mordellidae **43.** Nitidulidae **44.** Passalidae **45-46.** Phalacridae **47-48.** Salpingidae **49.** Scirtidae **50.** Silvanidae **51-53.** Staphylinidae **54.** Tenebrionidae **55.** Trogossitidae

Collembola (Colémbolos)

1

2

3

4

1. Entomobryidae **2.** Hypogastruridae **3-4.** Isotomidae

Dermaptera (Tijerillas)

1

2

1-2. Forficulidae

Diptera (Moscas y Mosquitos)

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

1. Agromyzidae **2.** Asilidae **3.** Cecidomyiidae **4.** Ceratopogonidae **5-6.** Chamaemyiidae **7.** Chironomidae **8-9.** Chloropidae **10-11.** Dolichopodidae **12.** Drosophilidae **13.** Empididae **14.** Fanniidae **15.** Muscidae **16.** Sciaridae **17.** Syrphidae **18.** Therevidae **19.** Ulidiidae

Hemiptera (Chinches, Chicharras, Pulgones entre otros)

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

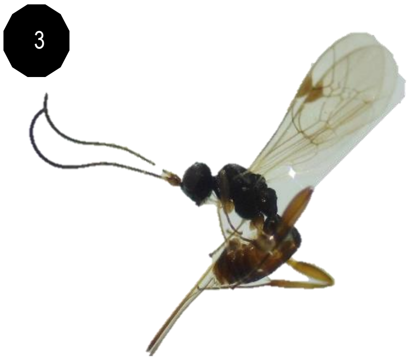
1. Achilidae **2-3.** Anthocoridae **4.** Aphididae **5.** Aradidae **6-9.** Cicadellidae **10-11.** Coreidae **12-13.** Delphacidae **14-15.** Issidae **16-17.** Lygaeidae **18-21.** Membracidae **22.** Mesoveliidae **23.** Microphysidae **24-25.** Miridae **26.** Pachygronthidae **27-29.** Pentatomidae **30-31.** Psyllidae **32.** Pyrrhocoridae **33.** Rhopalidae **34-35.** Scutelleridae **36-37.** Tingidae

Hymenoptera (Abejas, Avispas y Hormigas)

1

2

3



4

5

6

7

8

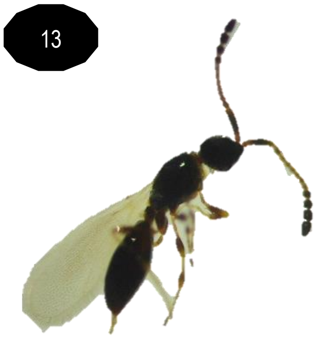
9

10

11

12

13



14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

58

59

1-2. Bethylidae **3-6.** Braconidae **7-8.** Ceraphronidae **9.** Chalcididae **10-12.** Cynipidae **13.** Diapriidae **14-18.** Encyrtidae **19-24.** Eulophidae **25-28.** Eupelmidae **29-30.** Eurytomidae **31-32.** Figitidae **33-35.** Formicidae **36-42.** Ichneumonidae **43-44.** Megaspilidae **45.** Mymaridae **46-47.** Ormyridae **48-50.** Platygastridae **51-53.** Pteromalidae **54-56.** Scelionidae **57-59.** Torymidae

Lepidoptera (Mariposas y Polillas)

1

2

3

4

5

6

7

8

9

10

11

12

13

14

1-2. Arctiidae **3.** Crambidae **4.** Gelechiidae **5.** Geometridae **6.** Gracilariidae **7.** Hepialidae **8.** Noctuidae **9.** Pterophoridae **10.** Pyralidae **11-12.** Saturniidae **13.** Tineidae **14.** Tortricidae

Mantodea (Mantis)

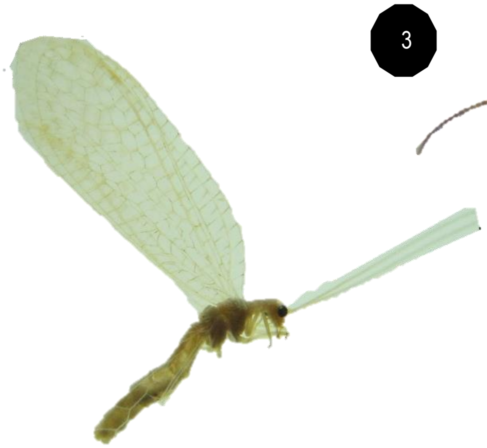
1

1. Mantidae

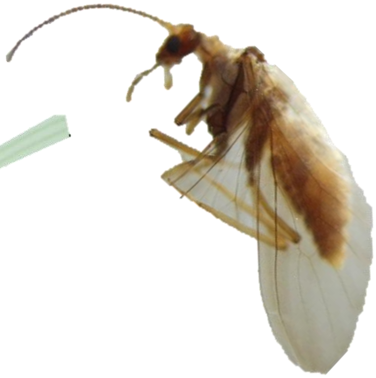
Neuroptera (Crisopas y Hormigas León entre otros)

1

2



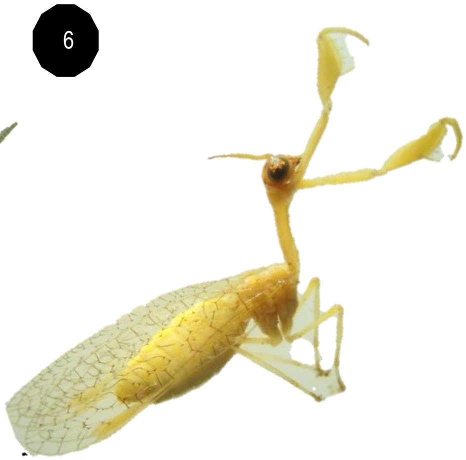
3



4

5

6



1-2. Chrysopidae **3.** Coniopterygidae **4-5.** Hemerobiidae **6.** Mantispidae

Orthoptera (Saltamontes, Grillos y Chapulines)

1

2

3

1. Gryllidae **2.** Romaleidae **3.** Tettigoniidae

Pseudoscorpionida (Pseudoscorpionides)

1

2

1-2. Pseudogarypidae

Psocoptera (Psócidos o Piojos de los libros)

1

2

3

4

5

6

7

8

1. Ectopsocidae **2.** Lachesillidae **3.** Liposcelididae **4.** Peripsocidae **5.** Philotarsidae **6-8.** Psocidae

Thysanoptera (Trips)

1

2

3

4

5

6

1-2. Aeolothripidae **3-5.** Phlaeothripidae **6.** Thripidae