UNIVERSIDAD MICHOACANA DE SAN NICOLÁS DE HIDALGO

“ANÁLISIS DE ATRIBUTOS FUNCIONALES FOLIARES, ASIMETRÍA FLUCTUANTE Y PATRONES DE HERBIVORÍA EN ESPECIES DE ENCINOS EN UN MOSAICO DE AGROSISTEMAS DE AGUACATE Y BOSQUES TEMPLADOS”

TESIS

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PRESENTA

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DEDICATORIA

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Resumen general

La fragmentación del bosque templado por las actividades humanas altera las interacciones bióticas como la herbivoría y las características morfológicas, fisiológicas y fenológicas de las plantas. El objetivo de este trabajo fue determinar los efectos del cambio de uso de suelo de bosque a huertas de aguacate sobre la herbivoría, asimetría fluctuante (AF), morfología, calidad y los atributos funcionales en *Quercus castanea* y *Q. obtusata* presentes en bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate. Se seleccionaron 3 sitios con bosque nativo> huertos; 2 con bosque nativo=huertos y 3 con bosque nativo< huertos. Para cada especie y sitio, se seleccionaron 30 individuos. La colecta de hojas fue de 30 hojas al azar para analizar los patrones de herbivoría y de manera selectiva para la AF, morfología, calidad y atributos funcionales. Se usó el programa Image J para calcular la herbivoría, AF y área foliar, y el programa TpsDig y CoordGen6 para la morfología foliar. La calidad de la planta (cobertura del dosel, DAP, área y clorofila foliar), los atributos funcionales (área foliar específica, masa fresca foliar, contenido de agua foliar, peso seco foliar, área foliar y concentración de clorofila) se midieron con diferentes instrumentos como el densiómetro, la balanza analítica y SPAD. La herbivoría, AF, morfología foliar, la calidad de la planta y los atributos funcionales asociados al tamaño (área foliar específica, peso seco foliar, área foliar) fueron mayores en encinos en fragmentos de bosque pequeños y mayor área de huerto. Los atributos relacionados a la cantidad de agua como masa fresca foliar y contenido de agua foliar fueron mayores en el bosque mayor a huertos. Se concluye que los diferentes tamaños de huertos de aguacate modifican los patrones de herbivoría, esto podría deberse a una pérdida de enemigos naturales y aumento de insectos herbívoros que genera la fragmentación. Además de cambios en la calidad de la planta y atributos funcionales, AF y morfología foliar en los encinos debido a los diferentes grados de estrés que están sometidos y a la posible mayor disponibilidad de luz y arrastre de fertilizantes de los huertos hacia el bosque, principalmente en los fragmentos de bosque pequeño.

Palabras clave: cambio de uso de suelos, tamaños de huertos, encinos, disponibilidad de luz, bosque nativo.

General abstract

The fragmentation of the temperate forest by human activities alters biotic interactions such as herbivory and the morphological, physiological and phenological characteristics of plants. The aim of this work was to determine the effects of land use change from forest to avocado orchards on herbivory, fluctuating asymmetry (FA), morphology, quality and functional attributes in *Quercus castanea* and *Q. obtusata* present in adjacent native forests to avocado orchards, under different proportions of vegetation cover between native forest and avocado orchards. 3 sites with native forest > orchards were selected; 2 with native forest=orchards and 3 with native forest<orchards. For each species and site, 30 individuals were selected. The leaf collection was 30 random leaves to analyze the herbivory patterns and selectively for FA, morphology, quality and functional attributes. The Image J program was used to calculate herbivory, FA and leaf area, and the TpsDig and CoordGen6 programs for leaf morphology. Plant quality (canopy cover, DBH, leaf area and chlorophyll), functional attributes (specific leaf area, leaf fresh mass, leaf water content, leaf dry weight, leaf area and chlorophyll concentration) were measured with different instruments such as densiometer, analytical balance and SPAD. Herbivory, FA, leaf morphology, plant quality and size-associated functional attributes (specific leaf area, leaf dry weight, leaf area) were higher in oaks in small forest fragments and larger orchard area. The attributes related to the amount of water such as fresh leaf mass and leaf water content were higher in the forest greater than orchards. It is concluded that the different sizes of avocado orchards modify the herbivory patterns, this could be due to a loss of natural enemies and an increase in herbivorous insects generated by fragmentation. In addition to changes in the quality of the plant and functional attributes, AF and foliar morphology in oaks due to the different degrees of stress that they are subjected to and the possible greater availability of light and dragging of fertilizers from the orchards to the forest, mainly in small forest fragments.

Introducción general

En México más de 100,000 ha de bosque se han transformado debido al cambio de uso de suelos en las últimas dos décadas (FAO, 2015), de las cuales una porción se ha utilizado para la agricultura. Por ejemplo, México es líder en la producción de aguacate a nivel mundial (Anguiano et al. 2006; Secretaría de Economía 2012; Cho et al 2021) y a principios del 2020, la superficie de las zonas aguacateras del país abarcaba 241,140 hectáreas y una producción de 206,466 toneladas (AGRICULTURA-SIAP 2020) de las cuales el estado de Michoacán produjo más del 80%. El derrame económico en la producción por el cultivo de aguacate en México es de más de 2,500 millones de dólares anuales (SAGARPA 2017; SADER-ASERCA-SIMA 2019). Sin embargo, el desarrollo de la franja aguacatera en el Estado de Michoacán ha generado en las últimas décadas una alta tasa de conversión de los bosques templados (BTs) a huertos de aguacate, con aproximadamente 690 ha/año, convirtiendo el paisaje en fragmentos de BTs mezclados con huertas de aguacate (Chávez-León et al 2012, Cho, et al. 2021).

La fragmentación de bosques, transforma grandes áreas conectadas en fragmentos de distintos tamaños y grado de aislamiento, lo que disminuye la biodiversidad debido a la simplificación y homogenización del paisaje y a la formación de fragmentos de bosque entremezclados con matrices de vegetación distinta (Martinson y Fagan 2014; Haddad et al. 2015; Rossetti et al. 2017; Zambrano et al 2019). Además, la fragmentación se caracteriza por traer cambios en los factores abióticos y bióticos (Haddad et al., 2015; Rodríguez-Echeverry, et al. 2018). Por ejemplo, la temperatura, radiación solar y velocidad del viento aumentan mientras que la fertilidad y humedad del suelo disminuyen en comparación con bosques conservados (Silva y Simonetti 2009; Tuff, et al. 2016; Bernaschini, et al. 2019). La fragmentación causa cambios en el ecosistema como alteración en los servicios ecosistémicos del bosque como la captura y almacenaje de carbono, protección de suelos, ciclos hidrológicos, mitigación al cambio climático global (Manzo-Delgado et al. 2014; Reinmann et al. 2020; Seidl et al. 2020, Rawat et al. 2020) y cambios en los ensamblajes de diferentes grupos funcionales como polinizadores y depredadores, además de la herbivoría, afectando la reproducción de plantas y el control biológico de plagas (Winfree et al. 2009; Prieto-Benítez y Méndez 2011; Rossetti et al. 2017; Campbell et al. 2018; Cusser et al. 2019).

En un contexto de fragmentación, los insectos herbívoros pueden verse afectados mediante fuerzas top-down y bottom-up (Hawkins et al. 1997; Pace et al 1999; Schüepp et al. 2014; Pfeifer et al. 2017; Anderson et al. 2019). Por ejemplo, en las interacciones bióticas como la herbivoría, los insectos están regulados por la diversidad de depredadores y los recursos disponibles (Vidal y Murphy, 2018). La fragmentación puede alterar los procesos top-down (impulsados por depredadores) y bottom-up (impulsada por los recursos) (Murphy et al., 2016; Bagchi et al., 2018). De acuerdo con Holt (1996) las especies de niveles tróficos más altos (depredadores), son más afectados por la fragmentación del hábitat debido a sus altos requerimientos de espacio y energía. Por lo tanto, las poblaciones de los herbívoros pueden ser beneficiadas al generarse espacios libres de enemigos naturales aumentando sus poblaciones (procesos top-down) (Barberena-Arias y Aide 2002; Tscharntke et al. 2007; Anderson et al. 2019). A su vez, la fragmentación modifica las características de la planta como la expresión fenotípica tal como la arquitectura (complejidad estructural), defensa de las plantas, calidad nutricional y atributos funcionales (Castagneyrol et al. 2012; Lohbeck et al. 2013; Barbour et al. 2015) como resultado del cambio de la disponibilidad de nutrientes en el suelo y el medio ambiente que definen la interacción con los herbívoros (procesos bottom-up) (Loranger et al., 2012, 2013; Hahn and Maron, 2016).

Los atributos funcionales, definidos como las características fisiológicas, morfológicas y fenológicas que determinan la adecuación de un individuo y el funcionamiento de un ecosistema (Violle et al. 2007; Reich 2014), pueden modificarse por la fragmentación como los rasgos foliares adquisitivos y conservativos que se conocen como “espectro de economía foliar”. Por ejemplo, los rasgos foliares adquisitivos como el área foliar, área foliar específica, contenido de clorofila y contenido de agua en la hoja, se asocian a plantas en condiciones de alta disponibilidad de recurso. Por otro lado, los rasgos conservativos (reducción del área total y el área foliar específica e incremento de la densidad, el grosor y las defensas a base carbono) son causados por la sequía, la tolerancia a la temperatura y para evitar la pérdida de agua en las hojas que ocurre con la fragmentación (Wright and Westoby 2002; Jimenez-Rodríguez et al. 2018). Los rasgos conservativos reducen la abundancia y riqueza de insectos herbívoros debido a la baja calidad de la planta (nutrientes, clorofila, cantidad de agua) (Rautiainen et al. 2005; Maguire et al. 2016).

La calidad de la planta es importante para el consumo foliar de los insectos, en los fragmentos y el borde del bosque templado existe mayor disponibilidad de luz que ocasiona mayor tasa fotosintética y por consecuencia mayor crecimiento de la biomasa y la tasa de crecimiento anual (calidad) por ejemplo en *Quercus* spp. (Reinmann y Hutyra 2017). De acuerdo con la hipótesis del vigor de la planta de Price (1991), las plantas con mayor calidad tendrán una mayor abundancia de insectos herbívoros debido a que presentan una posible mayor cantidad de recursos, calidad nutricional y menor cantidad de metabolitos secundarios. De igual forma, se han encontrado en especies del género *Quercus,* entre ellas *Q. castanea* y *Q. obtusata* un efecto de borde de los fragmentos de bosque con mayor calidad (cobertura del dosel y diámetro a la altura del pecho) asociado a mayor herbivoría (Maldonado-López et al. 2015).

Un factor adicional a la fragmentación, es la aplicación de fertilizantes en los agrosistemas (Anaya y Burgos 2015; Ramankutty et al. 2018). Por ejemplo, a las huertas de aguacate se les aplican dosis de fertilizantes de entre 55 y 180 $kg \cdot ha^{-1} \cdot año^{-1}$ que son las adecuadas para la producción (Lovatt, 2001). El exceso en la aplicación provoca efectos de arrastre y lixiviados de fertilizantes a cuerpos de agua y fragmentos de bosque contaminándolos (Anaya y Burgos 2015).). Las propiedades químicas del suelo se modifican cerca de los agrosistemas (Pellissier et al. 2014; Fried et al. 2018) degradándose y reduciendo la cantidad de nutrientes y materia orgánica, sustituyéndola por la deposición de nutrientes sintéticos como el Nitrógeno (N), Fósforo (P), Potasio (K) y la acidificación (aumento de los protones) en el suelo, producto de la lixiviación (Manning 2012; Ramankutty et al. 2018). Las propiedades químicas del suelo determinan las adaptaciones funcionales de las plantas que afectan la expresión de los atributos funcionales de las hojas (Manning 2012; Jager et al.,2015; Ramankutty et al. 2018). Por ejemplo, algunas especies de plantas se han asociado a suelos de mayor disponibilidad de nutrientes, expresando una alta concentración de nitrógeno, fósforo foliar, área foliar específica (AFE), área foliar total (AFT), contenido de clorofila (CC) y escaso grosor foliar (GF) (Gourlet-Fleury et al. 2011; Jager et al., 2015) lo que cambia la calidad de la planta y con ello la preferencia de los insectos herbívoros en la interacción insecto-planta (Lavorel et al., 2013; Loranger et al., 2012, 2013).

La fragmentación a su vez provoca estrés en las plantas debido a cambios ambientales, que ocasionan inestabilidad en el desarrollo (ID). La ID es la incapacidad de un genotipo para

producir consistentemente el mismo fenotipo en un ambiente particular, produciendo cambios en el fenotipo como la morfología, forma y el tamaño de las hojas (Møller and Swaddle 1997; Zvereva et al., 1997; Freeman et al., 2004; Cuevas-Reyes et al. 2013; Cuevas-Reyes et al. 2018b). Un indicador de ID causado por factores genéticos o ambientales, es la Asimetría Fluctuante (AF), que se describe como la magnitud de los cambios aleatorios entre dos lados de un carácter bilateral de un organismo (Palmer and Strobeck, 1986; Møller and Shykoff, 1999). Los organismos que se desarrollan en ambientes bajos de estrés son capaces de amortiguar la mayoría de los errores aleatorios en su desarrollo, sin embargo, cuando aumenta el estrés ambiental, la capacidad de dichos organismos para recuperarse de las perturbaciones disminuye, lo que se refleja en una mayor AF (Leamy and Klingenberg 2005; Cuevas-Reyes et al. 2013). La AF en plantas resultado del estrés se asocia a disturbios del hábitat (Maldonado-López et al. 2019), fertilidad del suelo (Cuevas-Reyes et al.2018b), y la herbivoría (Cuevas-Reyes et al. 2011a, b, 2018a) entre otros. Algunos autores han descrito una relación positiva entre la herbivoría y AF (Cornelissen and Stiling 2005). De acuerdo con la hipótesis del estrés de las plantas (White 1984), el insecto herbívoro selecciona hojas más asimétricas con mayor calidad nutricional y menores concentraciones de metabolitos secundarios (Cornelissen and Stiling 2005; Cornelissen and Stiling 2011). Por otra parte, la herbivoría genera AF (hipótesis de herbivoría generando estrés) las hojas se vuelven asimétricas por el alto consumo que están sometidas por parte de los insectos herbívoros (Møller and Shykoff 1999; Alves-Silva and Del-Claro 2016). Sin embargo, en otros casos se ha observado un patrón neutro (Telhado et al. 2010).

Las especies del género *Quercus* proveen servicios ambientales como el reciclaje de nutrientes, el balance hídrico y el secuestro de carbono, además de que mantienen un conjunto de interacciones complejas con otros organismos, como los hongos (Rasmussen et al. 2018), insectos (Wolton y Luff 2016), vertebrados (Barragán et al. 2018) y otras plantas (Maclean et al. 2017), por lo que se les puede considerar como especies clave que contribuyen significativamente a mantener la diversidad en las comunidades bióticas (Maldonado-López et al. 2015). A pesar de la importancia del género *Quercus* que se encuentra en el bosque templado, el porcentaje de cobertura vegetal transformado a huertos de aguacate es alto. México es el mayor productor de aguacate a nivel mundial con un 31% y un territorio ocupado del 27% por lo que su estudio es importante para conocer, mantener las interacciones bióticas y el ecosistema.

En este estudio analizamos los efectos del cambio de uso de suelo a huertas de aguacate sobre la calidad de la planta, atributos funcionales foliares, la morfología foliar, asimetría fluctuante y su relación con los patrones de herbivoría en *Quercus castanea* y *Q. obtusata* presentes en bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate en el interior y borde de la franja aguacatera del estado de Michoacán, México. Las preguntas específicas fueron: i) ¿El efecto del cambio de uso de suelo a huertas de aguacate tiene consecuencias en la calidad de la planta, patrones de herbivoría, morfología y asimetría fluctuante foliar en *Quercus castanea* y *Q. obtusata* presentes en bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate en el interior y borde? (CAPÍTULO I) ii) ¿Los atributos funcionales foliares cambian entre bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate afectando los niveles de herbivoría? (CAPÍTULO II)

Objetivo general

Determinar los efectos del cambio de uso de suelo a huertas de aguacate, sobre la asimetría fluctuante foliar, calidad de la planta, atributos funcionales foliares y sus consecuencias sobre los patrones de herbivoría, en *Quercus castanea* y *Q. obtusata* presentes en bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate

Objetivos particulares

1) Evaluar los cambios en la calidad de la planta y los atributos funcionales foliares en *Q. castanea* y *Q. obtusata* en los bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate.
2) Determinar los patrones de herbivoría y su relación con la calidad de la planta y los atributos funcionales foliares en *Q. castanea* y *Q. obtusata* en los bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate.
3) Determinar si existen cambios en la morfología foliar en *Q. castanea* y *Q. obtusata* en los bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate.

4) Determinar los patrones de asimetría fluctuante y su relación con los niveles de herbivoría en *Q. castanea* y *Q. obtusata* en los bosques nativos adyacentes a las huertas de aguacate, bajo diferentes proporciones de cobertura vegetal entre bosque nativo y huertas de aguacate.

Hipótesis general

Se espera que el cambio de uso de suelo a huertas de aguacate represente condiciones de estrés ambiental para el desarrollo de los encinos, afectando la calidad de la planta y los atributos funcionales de los encinos, la herbivoría y la AF acorde a la proporción en la cobertura vegetal entre huertos de aguacate y bosques nativos adyacentes.

Hipótesis particulares

1) Se espera una mayor variación en la calidad de la planta y los atributos funcionales foliares de especies de encinos en sitios de mayor proporción de cobertura de huertos y menor cobertura de bosque adyacente, que en sitios de menor cobertura de huertos y mayor cobertura vegetal de bosque.

2) Se esperan mayores niveles de herbivoría y menor relación con la calidad y atributos funcionales foliares en especies de encinos en sitios de mayor proporción de cobertura de huertos y menor cobertura de bosque adyacente (mayor susceptibilidad), en comparación con sitios de menor cobertura de huertos y mayor cobertura de bosque.

3) Se espera que exista variación en la morfología foliar de las dos especies de encinos entre los diferentes sitios de estudio debido a las diferencias en las condiciones ambientales que representan un mosaico de proporciones en la cobertura vegetal entre la matriz de bosque y los huertos de aguacate.

4) Los niveles de herbivoría foliar y los niveles de asimetría fluctuante presentarán una relación positiva en encinos de sitios de mayor proporción de cobertura de huertos y menor cobertura de bosque, en comparación con sitios de mayor cobertura de bosque y menor de huertos de aguacate.

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Changes in land use of temperate forests associated to avocado production in Mexico: Impacts on soil properties, plant traits and insect-plant interactions

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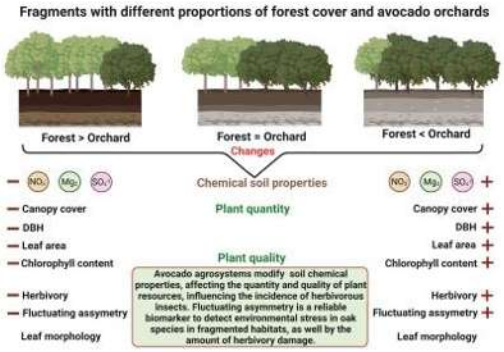
HIGHLIGHTS

- The conversion of forests to agrosystems is one of the main threats to biodiversity.
- We analyzed the soil properties, plant quantity and quality, leaf morphology, herbivory and FA in avocado agrosystems.
- Avocado agrosystems changes soil properties affecting quantity and quality of resources and the incidence of herbivorous.
- Agrosystems homogenize the landscape generating forest fragments interspersed with crops.
- FA is a reliable biomarker to detect environmental stress in oak species in fragmented habitats and by herbivory damage.

GRAPHICAL ABSTRACT



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ABSTRACT

CONTEXT: Temperate forest ecosystems harbor great biodiversity and provide key ecosystem services. However, in Mexico they have been deforested for use in avocado orchards, which represents a major threat to ecosystems functioning and the conservation of biodiversity.

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Avocado orchards
Forest fragmentation
Oaks
Plant quality and quantity
Environmental stress

OBJECTIVE: We evaluated the changes in soil chemical properties in a fragmented landscape of avocado agrosystems and forests in Mexico and the effects on plant quantity and quality (leaf area, canopy cover, DBH and chlorophyll content), leaf morphology, herbivory and fluctuating asymmetry in *Quercus castanea* and *Q. obtusata*.
METHODS: Eight study sites were selected: i) areas with a more proportion of forest and less of avocado orchards, ii) areas with equal proportion of both forest and orchards, iii) areas with more proportion of orchards. In all sites, 15 adult trees at the edge and 15 trees in the interior of each fragment were selected for each oak species. Soil samples were also collected in all study sites to analyze their chemical properties.
RESULTS AND CONCLUSIONS: We found higher concentration of Mg^{2+}, NO_3^- and SO_4^{2-} in soils of sites with more proportion of orchards. Total leaf area, canopy cover and DBH, as well the herbivory and FA levels were higher in these sites and in the edges of fragments for both oak species. Chlorophyll content was higher at forest edges than in the interior of fragments for all sites analyzed. Leaves of both oak species were more elongated and wider in sites with more proportion of orchards, as well in forest edges. Plant traits, herbivory and FA were related to chemical soil properties according to the proportion of forest and orchards, indicating that the mechanisms driving this interaction are scale-dependent and vary among habitat types according to proportion of forest. Herbivory was positively correlated with leaf area, DBH, chlorophyll content and FA for both oak species, indicating that herbivory increase as resource availability and quality increased along mosaic of avocado agrosystems. Our results showed that land use change of forest to avocado orchards, creates fragments with intense edge effects changing chemical soil properties, which in turn affect quantity and quality of resources to insect herbivores, as well as leaf morphology and FA levels of *Q. castanea* and *Q. obtusata* individuals.
SIGNIFICANCE: Our study is the first to denote the importance of the maintenance and conservation of temperate forest ecosystems and their potential functional and ecological benefits to avocado cultivation.

1. Introduction

Temperate forest ecosystems (TFEs) harbor great biodiversity and provide key ecosystem services, such as carbon capture and storage, soil protection, hydrological cycles and mitigation of global climate change (Manzo-Delgado et al., 2014; Reinmann et al., 2020; Seidl et al., 2020). The conversion of TFEs to agrosystems affects >40% of the Earth's surface and is one of the main threats to biodiversity and ecosystem services (Foley et al., 2011; Barral et al., 2015; Yang et al., 2020). Agrosystems simplify and homogenize the landscape, generating forest fragments interspersed with crops, thus affecting the chemical properties of the soil (Bianchi et al., 2006; Haddad et al., 2015), reducing species diversity (Ferreira et al., 2018; Follett et al., 2020), and destabilizing processes such as carbon sequestration, climate regulation, pollination, biological control of pests and diseases and edaphic biota (Tscharntke et al., 2007; Campbell et al., 2018).

The fragmentation of TFEs represents a dynamic process where the forest is progressively reduced into fragments of different sizes and degrees of isolation, where the newly created edges experience abiotic changes (Haddad et al., 2015; González et al., 2020) such as a higher incidence of light and temperature, higher wind speed and lower fertility and soil moisture (Arroyo-Rodríguez et al., 2016; Bernaschini et al., 2019). Thus, edge effects involve physical and biotic alterations associated to fragment boundaries, being dominant drivers of change in ecosystem functioning, species composition and diversity, as well as the biotic interactions such as parasitism, predation, seed dispersal, pollination and herbivory (Ewers et al., 2007; Maldonado-López et al., 2016a, 2016b). Additionally, abrupt transitions between native forests and agrosystems can affect the chemical properties of the soil by depositing synthetic nutrients from agrosystems (e.g., nitrogen, phosphorus and potassium) (Tuff et al., 2016; Uzèda et al., 2016), favoring the degradation and reduction of the amount of organic matter and nutrients available to plants (Manning, 2012; Ramankutty et al., 2018). Therefore, chemical soil properties are associated to soil quality and determine functional adaptations of the plants influencing vegetative growth, seedling establishment and survivorship, and the expression of the leaf functional traits (e.g. leaf nitrogen and phosphorus concentration, leaf area and leaf thickness) (Aponte et al., 2011; Jager et al., 2015; Ganatsios et al., 2021), which in turn affects plant-insect interactions (García-Jain et al., 2021). In this way, the fragmentation process can affect both plant growth patterns, leaf production, buds and reproductive structures (Prada et al., 1995; Maldonado-López et al., 2015; García-Jain et al., 2021), as well the chemical defense against herbivorous insects and nutritional quality of leaves (i.e. nitrogen, water and chlorophyll content) (Castagneyrol et al., 2019; Barbour et al., 2015) as result of changes in abiotic conditions (i.e. increasing of solar radiation and temperature and decreasing of humidity and water availability and soil fertility) that reduce plant nutritional quality and increase chemical defense (Cuevas-Reyes et al., 2013; Maldonado-López et al., 2015). For example, a low water availability associated with high temperatures and UV radiation (Ramakrishna and Ravishankar, 2011), can decrease the absorption and the use of nitrogen and carbon, affecting biosynthetic pathways of primary metabolism, and thus, reducing the nutritional quality of leaves and increasing the chemical defenses (Brunner et al., 2015). In addition, higher light incidence in plants from fragmented forests are associated to both a higher photosynthetic capacity and carbon fixation in the form of carbohydrates, generating a surplus of carbohydrates available for the synthesis of carbon-based defenses such as terpenes, alkaloids and phenolic compounds (Niinemets, 2015; Piasecka et al., 2017). Additionally, leaves, as organs exposed to different environmental factors, can modify their morphology in response to changes in the abiotic conditions generated by forest fragmentation, such as the availability of water, soil nutrients and light intensity (Bruschi et al., 2003; Lambrecht and Dawson, 2007; Cuevas-Reyes et al., 2018b; García-Jain et al., 2021).

Forest fragmentation also affects the structure, composition and distribution of vegetation, reducing species diversity and collapsing antagonistic interactions such as herbivory (Rossetti et al., 2017; Cuevas-Reyes et al., 2018b). In some cases, the diversity of herbivorous insects and consumption levels may increase due to the loss of natural enemies (i.e., predators and parasitoids) (top-down forces) since the top trophic levels have high space and energy requirements, resulting in extreme sensitivity to habitat loss (Tscharntke et al., 2007; Pfeifer et al., 2017; Valdés-Correcher et al., 2019). In contrast, the diversity of herbivorous insects and the levels of herbivory may decrease due to changes in the amount of plant resources (e.g., number of leaves and shoots, plant size, canopy cover) and quality of resources (e.g., nutrient and chlorophyll content) (bottom-up forces) (Kittelson et al., 2015; Maguire et al., 2016; Maldonado-López et al., 2016a, 2016b), influencing the preference, abundance and distribution of herbivorous insects (Maldonado-López et al., 2016a, 2016b; García-Jain et al., 2021). Additionally, spik over of insecticides and fungicides applied in crops adjacent to the forest can decline the diversity of herbivorous insects (Ansari et al., 2012).

In parallel, environmental changes associated with forest fragmentation can increase environmental stress in plants, negatively affecting

their fitness and survival (Maldonado-López et al., 2019; García-Jain et al., 2021) and modifying plant-herbivore interactions (Bagchi et al., 2018). Fluctuating asymmetry (FA) is one of the main biomarkers used to estimate developmental instability resulting from environmental and/or genetic stress because it describes the magnitude of random changes between two sides of a bilateral characteristic of an organism (Cuevas-Reyes et al., 2011b; Maldonado-López et al., 2019). Therefore, the phenotypic changes in the shape and size of the leaves represent morphological adjustments caused by changes in abiotic factors (e.g., temperature, humidity, soil fertility) and biotic factors (e.g., pathogens and herbivorous insects) (Cuevas-Reyes et al., 2013; Aguilar-Peralta et al., 2020). Although there is a debate in the ecological literature about whether leaf FA is a better index to measure environmental stress than the leaf size (Kozlov et al., 2022). Most of studies have shown that leaf FA is a sensitive and reliable indicator to detect environmental stress in plants and animals (Cuevas-Reyes et al., 2011a; Maldonado-López et al., 2019; García-Jain et al., 2021; Maldonado-López et al., 2022).

In Mexico, 40% of the TFE coverage has been lost due to deforestation and the change of land use to agrosystems, causing a high fragmentation of forests (Klooster and Masera, 2000; Esperón-Rodríguez and Barradas, 2015). Mexico is the leader in avocado production worldwide (Cho et al., 2021), with an area >241,140 ha, a conversion rate from TFE to avocado orchards >1715 ha/year $^{-1}$, a production amount >216,466 tons/year and an economic benefit of 2,500,000 dollars per year (González-Estudillo et al., 2017, SAGARPA, 2017, Cho et al., 2021). The current TFE scenario is a mosaic of isolated forest fragments interspersed with avocado orchards that affect the spatial distribution of TFEs, altering environmental conditions, the population size of different species and biodiversity in forest fragments as well as at the regional level (Monterrubio-Rico et al., 2019; Reyes-González et al., 2020). Therefore, we evaluated the changes in the chemical properties of the soil in a fragmented landscape of avocado agrosystems and native forest in Mexico and the effects on plant quantity and quality, leaf morphology, herbivory patterns and FA in *Quercus castanea* and *Q. obtusata*. The following questions were addressed: (i) Are the chemical properties of the soil affected by forest fragmentation by agrosystems in terms of the proportion of coverage of forest and avocado orchards? (ii) Are the quantity and quality of plant resources, as well as the levels of herbivory, affected by the proportion of forest cover and cover of avocado orchards? (iii) Does the fluctuating asymmetry of the leaves increase with greater coverage of orchards and levels of herbivory? We expect that, in areas with more proportion of forest, environmental conditions will be harsher (i.e., low soil fertility). As a consequence, individuals of *Q. castanea* and *Q. obtusata* will present less quantity and quality of resources, also exhibiting a different leaf morphology and lower levels of herbivory and fluctuating asymmetry in these habitats. The opposite being expected for areas with more proportion of orchards.

2. Materials and methods

2.1. Study sites

We determined the dynamics of forest cover change and avocado orchards in the avocado belt of Michoacán using medium- and high-resolution satellite images (Landsat, SPOT, Sentinel, and Rapid Eye with the TM 5, ETM + and OLI sensors) to define the location and extent of the main TFE coverages and avocado orchards (Neinavaz et al., 2020). Based on this information, we selected eight study sites where *Quercus castanea* and *Q. obtusata* were found. All study sites had similar size, ranged from 60 to 80 ha. Finally, in each study site, a buffer area of 1000 m of radius was established. Thus, we classified as follows: Three sites with greater coverage of native forest and less coverage of avocado orchards (Hereinafter it will be called: areas with more proportion of forest): (i) Tancítaro: (forest cover > avocado orchard: (77%/23%): (19° 16′ 34" N; 102° 22′ 33.55" W); (ii) Llanitos Agroecological Ranch: (84%/16%): (19° 26′ 0.52 N; 101° 16′ 38.08 W) and (iii) Acuitzio, La Yácata: (74%/26%): (19° 26′ 41.27" N; 101° 16' 55.08" W); two sites with similar coverage of native forest and avocado orchards (Hereinafter it will be called: areas with equal proportion of both forest and orchards): (i) Uruapan, Rancho el Peral (forest cover = avocado orchard: (51%/49%) (19° 27′ 38.61"N; 102° 1′ 48.3" W) and (ii) Tacámbaro, Rancho el Embrujo: (52%/48%) (19° 15′ 53.77" N; 101° 27' 41.34" W); and three sites with lower coverage of native forest and greater coverage of avocado orchards (Hereinafter it will be called: areas with more proportion of orchards): (i) Uruapan, Huitzicho: (forest cover < avocado orchard): (36%/64%) (19° 27′ 13.3″ N; 102° 0′ 53″ W); (ii) Tacambaro, Rancho las Joyas: (35%/65%) (19° 13′ 4.6″ N; 101° 25′ 4.6″ W) and (iii) Tacámbaro, Caramécuaro: (38%/62%) (19° 15′ 38.3″ N; 101° 23′ 43.7″ W) (Fig. 1).

The management history of all study sites is similar and consisted in the exclusion of the native forest for the wood extraction. Then, all these cleared areas were used for the farming of organic avocado variety Hass (no use of synthetic pesticides). Additionally, all avocado orchards studied have a similar age ranging from 15 to 20 years of establishment after felling (Arima et al., 2022). Thus, both the history of the site and its local management are similar in all the sites studied.

Because the samples (i.e. soil properties, quantity and quality of plant resources, FA and herbivory) at a particular spatial location may not be independent of occurrence at neighboring locations, an evaluation of spatial autocorrelation of study sites using the Moran's I coefficient was performed. This coefficient is ideal to characterize and identify dispersed, clustered or random land cover configurations as a function of spatial location (García-Jain et al., 2021). The Moran's I coefficient values range from −1 to 1, where values close to 0 indicates a random pattern of spatial distribution, while values close to −1 represent highly dispersed patterns and values of 1 signifies highly clustered patterns (Fu et al., 2014). The Moran's I coefficient values were close to 0 for all parameters related to the soil properties (magnesium = 0.072; nitrates = −0.12; phosphorus = 0.08; phosphorus pentoxide = −0.054; potassium = −0.041; sulfates = −0.03), quantity (DBH = −0.22, canopy cover = 0.057; leaf area = −0.054) and quality (chlorophyll content = 0.11) of plant resources, as well as in the fluctuating asymmetry (−0.035) and herbivory percentage (HP = −0.022) of *Q. castanea* and *Q. obtusata* individuals that occur in fragments with different proportions of forest cover and avocado orchards, confirming that all study sites are independent data points in all analyses. We included in the Supplementary Materials (Appendix 1), the scatterplots of values of Moran's coefficient for each response variable analyzed.

2.2. Study species

The plant species selected in our study (*Quercus castanea* Née *and Quercus obtusata* Humb. & Bonpl are deciduous woody trees very abundant in all study sites, and are representative of the Mexican temperate forests (Valencia, 2004; Arizaga et al., 2009).

Quercus castanea Née (Section *Lobatae*). This tree species grows up to 30 m in height with oblanceolate, oblong, lanceolate and obovate leaves that are 2.5 to 15 cm long and 1.3 to 5 cm wide; they are grayish green, somewhat lustrous and rough; the underside is gray to yellowish with little tomentum. The species occurs between 1180 and 2600 masl, and its geographical distribution is from Mexico to Central America (Arizaga et al., 2009; Rzedowski, 2005). A large part of the herbivorous insects that consume *Q. castanea* belong to the families Saturnidae and Noctuidae of the order Lepidoptera (Valencia, 2004; Barrios-Díaz et al., 2017).

Quercus obtusata Humb. & Bonpl (*Quercus* section). This species is an endemic tree in Mexico that grows to heights between 15 and 20 m. It has obovate or elliptical leaves that are 5 to 21 cm long by 2 to 13.5 cm wide and a margin with 4 to 8 teeth on each side; the upper surface is green, lustrous and tomentose at the base; the underside is yellowish green with pubescence. It is distributed at altitudes between 620 and 2580 m (Valencia, 2004; Arizaga et al., 2009). The most abundant

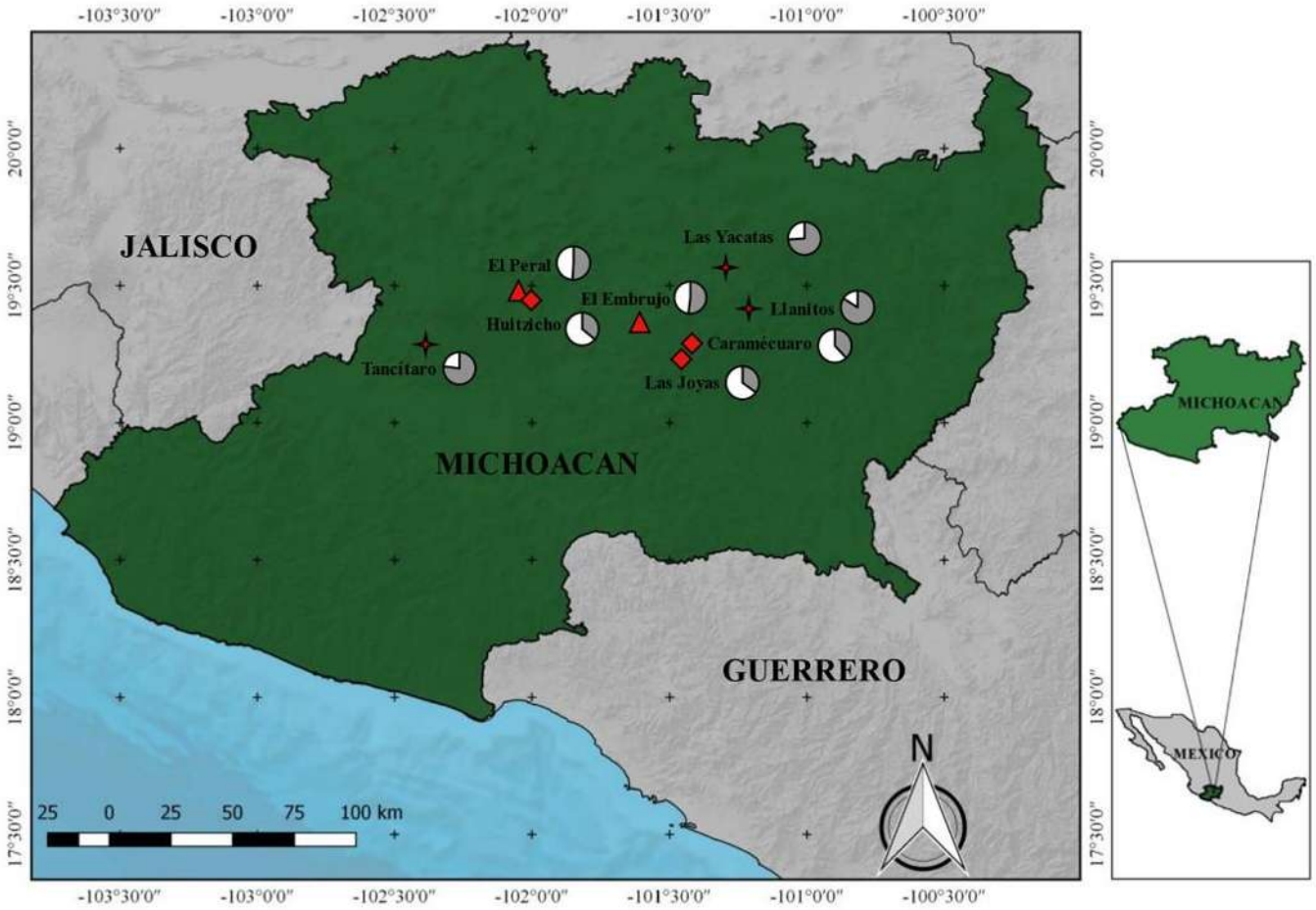

Fig. 1. Map of the distribution of the study sites in the avocado belt in Michoacán state, México. The stars represent sites with higher forest cover than avocado orchards. The the triangles are the sites with similar proportion of forest cover and avocado orchards. The rhombuses represent the sites with less forest cover than avocado orchard. Pie graphs represent the forest (gray) and avocado orchard (white) cover of each study site.

herbivorous insects that consume *Q. obtusata* are *Tortrix viridana* (Lepidoptera: Tortricidae) and *Acraga coa* (Lepidoptera: Dalceridae) (Ortega-Rivera et al., 2019).

2.3. Sampling design

At each study site (eight study sites) and for each oak species (*Q. castanea* and *Q. obtusata*), we selected 15 adult individuals at the edge of the forest fragment adjacent to the avocado orchards and 15 adult trees in the interior area of the forest ($N = 30$ for each species, for each site). To determine the changes in the quantity and quality of plant resources, leaf morphology, herbivory and levels of fluctuating asymmetry, we collected leaves at the end of the rainy season (October–November) after the period of peak herbivore activity (Cuevas-Reyes et al., 2018a). Each tree was marked and georeferenced, and we randomly collected three branches from each stratum of the canopy (i.e., upper, middle and lower) using an extendable cutting pole (Cuevas-Reyes et al., 2011b). To analyze leaf morphology and fluctuating asymmetry, 30 completely expanded leaves without apparent damage by insect herbivores were collected (i.e. 10 leaves per canopy stratum: N = 30 per individual) (Cuevas-Reyes et al., 2011b). In the same trees where the quantity and quality of plant resources as well the fluctuating asymmetry were measured, we randomly collected 30 leaves per tree (10 leaves per crown stratum), to evaluate herbivory levels caused by chewing insects (Cuevas-Reyes et al., 2018a).

2.4. Analysis of the chemical properties of the soil

At each study site, 4 transects of 50 m were made with a separation of 100 m between each of them. In each transect, 5 lysimeters (Irrometer Brand, Riverside, CA, USA) were placed every 10 m at a depth of 30 cm for the extraction of soil solution samples (Cabrera-Corral et al., 2016). The extraction of the soil solutions was performed during the rainy season (September) to obtain a greater leaching of the chemical compounds of the soil. With the soil solution, the quantification of six chemical soil parameters related to plant growth was performed: magnesium (Mg^{2+}), nitrates (NO_3^-), phosphorus (P), phosphorous pentoxide (P_2O_5), potassium (K) and sulfates (SO_4). To quantify magnesium (Mg^{2+}), the reagents HI937520–01 and HI937520–03 (Hanna Instruments, 2016) were used, and we used the Calmagite method. Calmagite (1-[1-hydroxy-4-methyl-2-phenylazo]-2-naphthol-4-sulfonic acid) is a metallochromic indicator that forms a colored complex in alkaline medium with magnesium. The absorbance of the complex was measured at 510–550 nm and was proportional to the concentration of magnesium in the sample (Gindler and Heth, 1971; Attia et al., 2020). For nitrates (NO_3^-), the HI93728–0 kit (Hanna Instruments, 2016) was used based on the cadmium reduction method, where nitrate (NO_3^-) is reduced to nitrites (NO_2^-) using cadmium granules. The solution is treated with copper sulfate (CuSO4), generating granules of azo coloration measured at 543 nm (Logsdon and Cole, 2018). For the case of phosphorus (P) and phosphorus pentoxide (P_2O_5), they were quantified with the reagents HI93717A-0. and HI93717B-0 (Hanna Instruments, 2016), which used the vanadomolybdophosphoric acid method. This

method uses vanadomolybdate $(NH_4)_6$ Mo_7 O_{24}), which precipitates phosphorus, generating molybdate phosphoric acid H_3 [P (Mo_3 Or_{10})$_4$]. The intensity of the staining is proportional to the amount of phosphorus and phosphorus pentoxide present in the sample and was measured at 420 nm (Dushyantha et al., 2019). To quantify potassium (K), we used the reagents HI93750A-0 and HI93750B-0 (Hanna Instruments, 2016), which use the tetraphenylborate turbidimetric method, which uses sodium tetraphenylborate (NaB (C_6H_5) in an acid medium, forming precipitates of potassium tetraphenylborate (KB (C_6H_5)) 4; the absorbance was measured at 420 nm, and the potassium concentration was determined by the turbidity in the sample (Linarez et al., 2020). To determine sulfates (SO_4), the HI93751–0 kit (Hanna Instruments, 2016) was used, which is based on the turbidimetric method of barium chloride crystals. In this method, sulfate ions (SO_4) are precipitated in an acid medium with barium chloride, forming barium sulfate crystals (Ba SO_4). The absorbances of the barium sulfate crystals in suspension were measured at 420 nm to determine the concentration of sulfates in the sample (Rossum and Villarruz, 1961). All these parameters were measured with a multiparametric nutrient photometer (Model HI83325, Hanna Instruments, Woonsocket, RI, USA).

2.5. Quantity and quality of plant resources

To determine the quantity and quality of plant resources, in each marked tree of both plant species studied, we measured the following parameters: (i) diameter at breast height (DBH) as an estimator of plant size (Cuevas-Reyes et al., 2011b); (ii) canopy cover as an indicator of leaf availability (Maldonado-López et al., 2015), using a spherical densimeter consisting of a small wooden box with a convex or concave mirror engraved with 24 squares. The canopy cover was estimated at four different points of the canopy (north, south, east and west in relation to the tree trunk), 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); (iii) leaf area as an indicator of resource availability for insect herbivores; and (iv) the chlorophyll content was quantified using SPAD 502 (Minolta) measurements of 15 leaves, totally expanded and sun exposed for each tree. Chlorophyll content can be used as an indicator of photosynthetic capacity, primary productivity and nutritional status because most of the nitrogen of the plant is found in different types of chlorophyll (Li et al., 2018; García-Jain et al., 2021).

2.6. Leaf morphometric and fluctuating asymmetry measurements

To identify the differences in the morphology and size of the leaves of *Q. deserticola* and *Q. obtusata* trees growing in fragments with different proportions of forest and orchards (forest > orchard vs. forest = orchard vs. forest <orchard) and different habitat type (forest edge vs. forest interior), we used geometric morphometric techniques. We first took a digital image of each leaf fully expanded and without apparent damage by herbivorous insects ($N = 30$ per individual) and then, 32 anatomical marks (landmarks) and two additional marks as a reference for the size were placed. All landmarks represent the shape of the leaves and correspond to homologous loci which are unambiguous and repeatable marks in all leaves (Cuevas-Reyes et al., 2018a) (Fig. 2). The TpsDig program was used to record the coordinates (x, y) of the 32 anatomical landmarks in each image of the leaf (Rohlf, 2015). The average of the configuration of all the leaves was considered as a reference to eliminate the effect of the leaf size, and then, we performed a Procrustes superimposition analysis to configure the coordinates of each landmark using the CoordGen6 program. This analysis translates and rotates the landmark settings into a common position and eliminate the size differences (scaling) between them providing the centroid size and shape coordinates (Rohlf and Slice, 1990; Klingenberg, 2013). Therefore, the

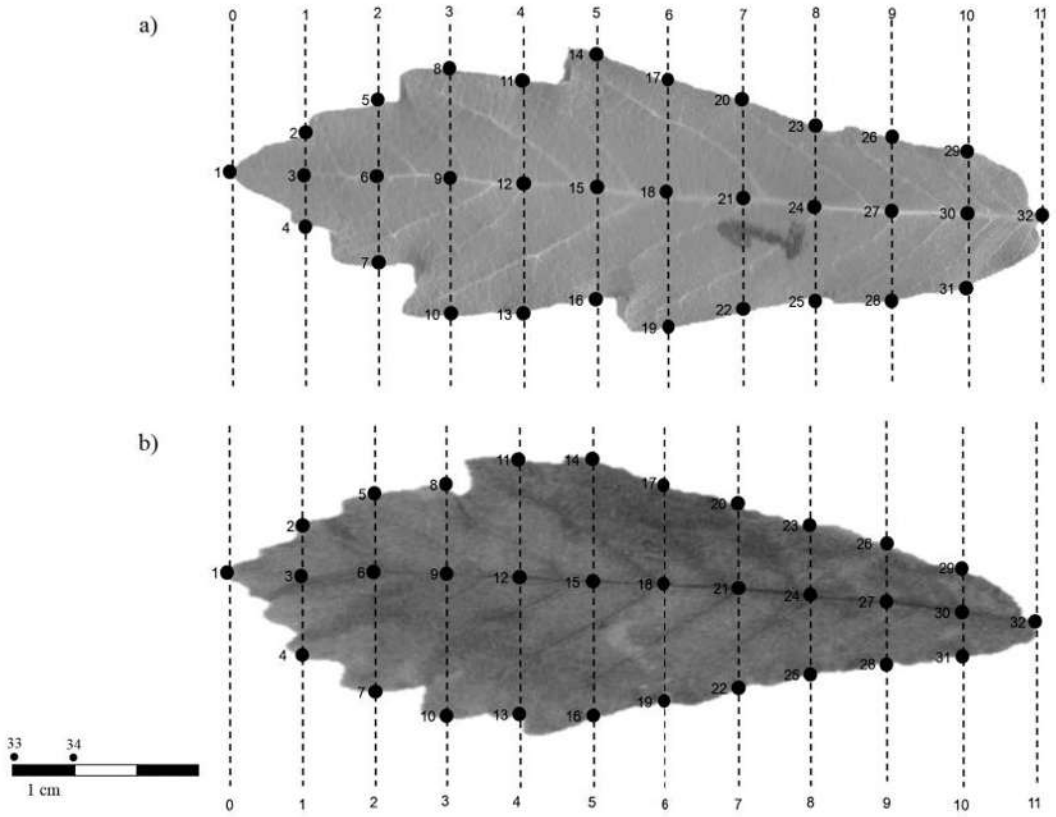

Fig. 2. Morphometric measurements of leaves of (a) *Q. castanea* and (b) *Q. obtusata* showing the 32 morphological landmarks on the leaf margin and two additional landmarks (33 and 34) as a reference ruler of scale.

average of the Procrustes shape coordinates (i.e. the Procrustes mean) represent the leaf shape, which is the result of the minimum sum of the squared distances in relation to the other shapes within the sample; which is denominated shape of reference (Bookstein, 1996). We calculated the variable forms using a principal component analysis to determine the differences in leaf morphology between individuals that occurs in sites with different proportions of forest and orchards (forest > orchards, forest = orchards and forest < orchards) and habitat type (edge vs. interior) for each oak species studied (Cuevas-Reyes et al., 2018a; García-Jain et al., 2021).

The fluctuating asymmetry was estimated in each leaf used to assess the morphology for each *Q. deserticola* and *Q. obtusata* trees that occurs in fragments with different proportion of forest and orchards. In each leaf, the distance from the edge of the leaf to the central rib at the midpoint of the leaf was calculated toward the right side (Ai) and the left side (Bi), in the widest part of the leaf using the ImageJ program (Cuevas-Reyes et al., 2018b). The fluctuating asymmetry was calculated from each digital image as the absolute value of the difference between the distances of the middle vein to the right and left of the leaf margin (| Ai - Bi |), divided by the mean distance ((Ai + Bi)/2) (Cuevas-Reyes et al., 2018a). To control the measurement error in fluctuating asymmetry, a subsample of 10 leaves was selected to be remeasured without reference to previous measurements. In these subsamples, we evaluated the degree of significance of fluctuating asymmetry in relation to the measurement error using a two-way mixed model ANOVA. If the individual x leaf x side interaction is significant, it indicates that the variation in FA is greater than that expected due to measurement errors ($F_{9.25} = 33.1$; $P < 0.0002$).

Palmer and Strobeck (1986) separated three types of asymmetry (i.e., fluctuating asymmetry, directional asymmetry and antisymmetry). Fluctuating asymmetry calculates the variance of the random differences between the two sides of a distributed bilateral trait with a mean value of zero. Directional asymmetry is defined as the differences between the two sides that are distributed around a mean significantly greater or less than zero, and antisymmetry is the absence of symmetry and is characterized by presenting a bimodal or platykurtic distribution of the differences between two sides around a mean of zero (Palmer and Strobeck, 1992). In this way, it was necessary to confirm that our data reflected only fluctuating asymmetry. To accomplish this, Student's *t-test* and the Lilliefors normality test were performed to rule out directional asymmetry, taking into account if the average value of the differences of the right side minus the left side (Ai - Bi) is different from zero (Alves-Silva and Del-Claro, 2016). We found that the average (Ai – Bi) differences did not differ significantly from zero ($t = 4.2$; $P > 0.05$). Therefore, the presence of directional asymmetry in our data was ruled out. In the same way, by means of a Lilliefors normality test, considering the distribution of the differences of (Ai – Bi) (Alves-Silva and Del-Claro, 2016), a normal distribution was obtained ($P > 0.05$), for which antisymmetry was also discarded.

2.7. Herbivory measurements

We obtained a digital image from each leaf randomly collected ($N = 30$ per individual) to estimate the total leaf area and the area removed by herbivorous insects using ImageJ software. The value was calculated for each leaf by (leaf area consumed/total leaf area) * 100 (Cuevas-Reyes et al., 2011a).

2.8. Statistical analysis

We performed a multivariate analysis of variance (MANOVA) to determine the differences in the concentration of chemical properties of the soil (i.e. magnesium, nitrates, phosphorus, phosphorus pentoxide, potassium and sulfates) between sites with different proportions of forest and orchards (forest > orchard vs. forest = orchard vs. forest <orchard) (SAS Institute JMP®, 2022). When significant effects were detected by MANOVA, we applied a one-way ANOVA test for each variable. When needed, we used appropriate transformations of the response variables to satisfy model assumptions, after normality tested.

We built a generalized linear mixed model (GLMM) where the two oak species were pooled together in the model to determine the effects of the sites with different proportions of forest and orchards (forest > orchard vs. forest = orchard vs. forest < orchard), different habitat type (interior vs. edge) and the interaction of forest cover/avocado orchard * habitat type over quantity (i.e., leaf area, diameter at breast height, canopy cover) and quality of resources (i.e., chlorophyll content), herbivory and fluctuating asymmetry. We carried out a separate model for each of the response variables. The sites with different proportions of forest and orchards, the habitat type and oak species were considered as fixed factors (explanatory variables), and the study site was considered a random factor. The residuals were normally distributed in all cases. Spearman correlation analysis was performed to determine the relationship between the following variables: leaf area, diameter at breast height, chlorophyll content, canopy cover, fluctuating asymmetry and herbivory.

To determine whether the different proportions of forest and orchards and the variation in the concentration of soil nutrients had an effect on the quantity and quality of plant resources, herbivory and fluctuating asymmetry, we performed a principal component analysis (PCA) that included both oak species and all significant soil nutrient variables (excepting SO_4), quantity and quality of plant resources, herbivory and fluctuating asymmetry. Through this analysis, we obtained a PCA of the dispersion of points that showed the association of the individuals of the different covers of the forest-avocado orchard with the different nutrients of the soil (Mg^{2+} NO_3^-, P, P_2O_5, K), the quantity and quality of plant resources (i.e. canopy cover, diameter at breast height, leaf area, chlorophyll content), the herbivory and the fluctuating asymmetry (SAS Institute JMP®, 2022; Stokes et al., 2000).

3. Results

3.1. Effects of forest fragmentation (proportion of forest and orchards) on chemical soil properties

In accordance with the MANOVA test for general effects, we found significant differences in soil nutrients between the three forest-orchard covers (Table 1a). These significant differences were found between forest-orchard covers for Mg^{2+}, NO^{-3}, P, P_2O_5 and K (Table 1b). Areas with more proportion of forest exhibited a higher content of K, while areas with equal proportion of both forest and orchards showed higher contents of P and P_2O_5, and finally, areas with more proportion of orchards presented higher contents of Mg^{2+} and NO^{-3} (Fig. 3).

Table 1
Comparison of chemical properties of the soil between the three forest-orchard covers in accordance with the MANOVA test.

(a) MANOVA test for overall effects

Source	Pillai trace	*df*	*F*	*P* <
Intersection	0.995	6	460.64	0.000*
Forest-orchard covers	1.50	12	7.15	0.000*

(b) ANOVA tests between-subject effects

Source	Variable response	*df*	*F*	*P* <
Forest-orchard covers	Mg^{2+} (mg/L)	2	5.39	0.015*
	NO_3^- (mg/L)	2	139.21	0.000*
	P (mg/L)	2	14.70	0.000*
	P_2O_5 (mg/L)	2	4.87	0.020*
	K (mg/L)	2	4.65	0.024*
	SO_4^{2-} (mg/L)	2	1.35	0.283

* Significant values.

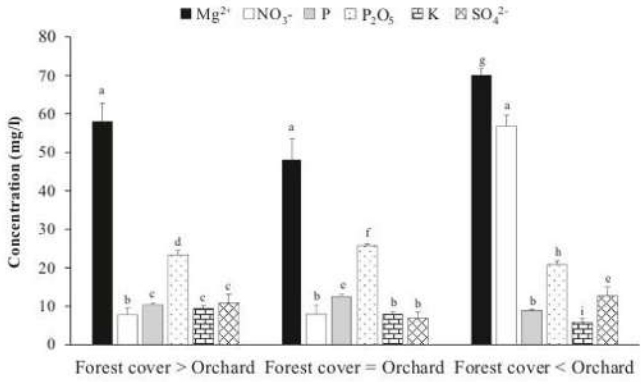

Fig. 3. Comparison of soil nutrient content among sites different proportions of forest cover- avocado orchards. Different letters indicate statistically significant differences according to least mean test ($P < 0.05$).

3.2. Quantity and quality of plant resources, herbivory and fluctuating asymmetry

We found significant differences in leaf area, DBH, canopy cover, fluctuating asymmetry and herbivory between areas with different proportions of forest and orchards for the two oak species (*Q. castanea* and *Q. obtusata*). However, the effect size of the fragmentation and the location were depended on the oak species according to the significant interaction observed between forest-orchard cover × oak species for leaf area, FA and herbivory (Table 2). Additionally, we detected significant differences in leaf area, DBH, chlorophyll content, canopy cover, fluctuating asymmetry and herbivory between individuals from the edge and the interior of the fragments (see Table 2). Individuals of *Q. castanea* had greater leaf area, DBH, canopy cover, herbivory and fluctuating asymmetry in areas with more proportion of orchards (Figs. 4a,b,c,d,f). Leaf area, DBH, chlorophyll content, fluctuating asymmetry and herbivory were greater at the edges than in the interior of the forest fragments (see Figs. 4a,b,c,d,f). We observed the leaf area, DBH, canopy cover, fluctuating asymmetry and herbivory were higher in individuals of *Q. obtusata* from areas with less forest cover (Figs. 4a,b,c,d,f). For both oak study species the quality and quantity of traits had higher values at the edge than in the interior of the fragments, regardless of the type of proportions the forest and orchard (see Figs. 4a,b,c,d,f).

We detected variation in the quantity and quality of plant resources, herbivory percentage and fluctuating asymmetry, as well as in the soil nutrients in areas with different proportion of forest and orchards (Fig. 5). Individuals of both oak species of areas with more proportion of forest, equal proportion of both forest and orchards and more proportion of orchards were separated as follows: the PC1 axis explained 40.2% of the total variance and was associated with the following on the right side: NO^{-3}, Mg^{2+}, FA (fluctuating asymmetry), HP (herbivory percentage), LA (leaf area), C (chlorophyll) and CC (canopy cover) in individuals of areas of more proportion of orchards. On the left side, P and P_2O_5 were related to individuals of areas of equal proportion of both forest and orchards, and K was related to individuals of more proportion of forest. The PC2 axis explained 13.6% of the total variance and was related on the upper side: P and P_2O_5 with individuals of areas of equal proportion of both forest and orchards, and K was associated with individuals of more proportion of forest.

In general, significant positive relationships were observed between herbivory and leaf area, FA, DBH and chlorophyll content for the two oak species studied (Table 3). Thus, herbivory was higher for individuals of both oak species *Q. castanea* and *Q. obtusata*, that had a greater quantity and quality of resources (Table 3).

Table 2
Summary of the results of each generalized mixed model testing the effects of forest-orchard cover, habitat condition (interior vs. edge), oak species and their interactions (forest-orchard cover × interior and edge, forest-orchard cover × oak species, interior and edge × oak species, forest-orchard cover × interior and edge× oak species) on plant quantity and quality, fluctuating asymmetry and herbivory.

Variable response	Explanatory variable	*df*	*F*	*P* <
Leaf area (cm ^{2})	Forest-orchard cover	2	15.7	0.0002*
	Interior and edge	1	5.9	0.01*
	Oak species	2	314.9	0.0001*
	Forest-orchard cover × interior and edge	2	5.9	0.002*
	Forest-orchard cover × oak species	2	4.6	0.01*
	Interior and edge × oak species	1	0.2	0.7
	Forest-orchard cover × interior and edge× oak species	2	1.4	0.2
DBH (cm)	Forest-orchard cover	2	12.7	0.02*
	Interior and edge	1	50.6	0.0001*
	Oak species	2	0.3	0.7
	Forest-orchard cover × interior and edge	2	13.6	0.0001*
	Forest-orchard cover × oak species	2	0.3	0.8
	Interior and edge × oak species	1	5.9	0.001*
	Forest-orchard cover × interior and edge× oak species	2	4.9	0.0001*
Chlorophyll (SPAD units)	Forest-orchard cover	2	0.09	0.9
	Interior and edge	1	44.5	0.0001*
	Oak species	2	50.6	0.0001*
	Forest-orchard cover × interior and edge	2	4.6	0.01*
	Forest-orchard cover × oak species	2	0.19	0.8
	Interior and edge × oak species	1	0.06	0.8
	Forest-orchard cover × interior and edge× oak species	2	2.8	0.06
Canopy cover (%)	Forest-orchard cover	2	8.4	0.0003*
	Interior and edge	1	37.5	0.0001*
	Oak species	2	0.02	0.9
	Forest-orchard cover × interior and edge	2	16.8	0.0001*
	Forest-orchard cover × oak species	2	0.8	0.4
	Interior and edge × oak species	1	0.2	0.6
	Forest-orchard cover × interior and edge× oak species	2	0.08	0.9
Fluctuating asymmetry	Forest-orchard cover	2	45.8	0.0004*
	Interior and edge	1	55.1	0.0001*
	Oak species	2	7.2	0.0080*
	Forest-orchard cover × interior and edge	2	25.7	0.0001*
	Forest-orchard cover × oak species	2	5.0	0.007
	Interior and edge × oak species	1	0.09	0.8
	Forest-orchard cover × interior and edge× oak species	2	4.9	0.007
Herbivory (%)	Forest-orchard cover	2	4.9	0.04*
	Interior and edge	1	81.3	0.0001*
	Oak species	1	9.5	0.002*
	Forest-orchard cover × interior and edge	2	11.3	0.0001*
	Forest-orchard cover × oak species	2	4.8	0.009*
	Interior and edge × oak species	1	0.5	0.5
	Forest-orchard cover × interior and edge× oak species	2	22.0	0.0001*

* Significant values.

3.3. Leaf morphology

The foliar morphology of the individuals of *Q. castanea* was different between areas with different proportion of forest and orchards and between the types of habitat (edge and interior of the fragment). The leaves of individuals of areas with more proportion of orchards were

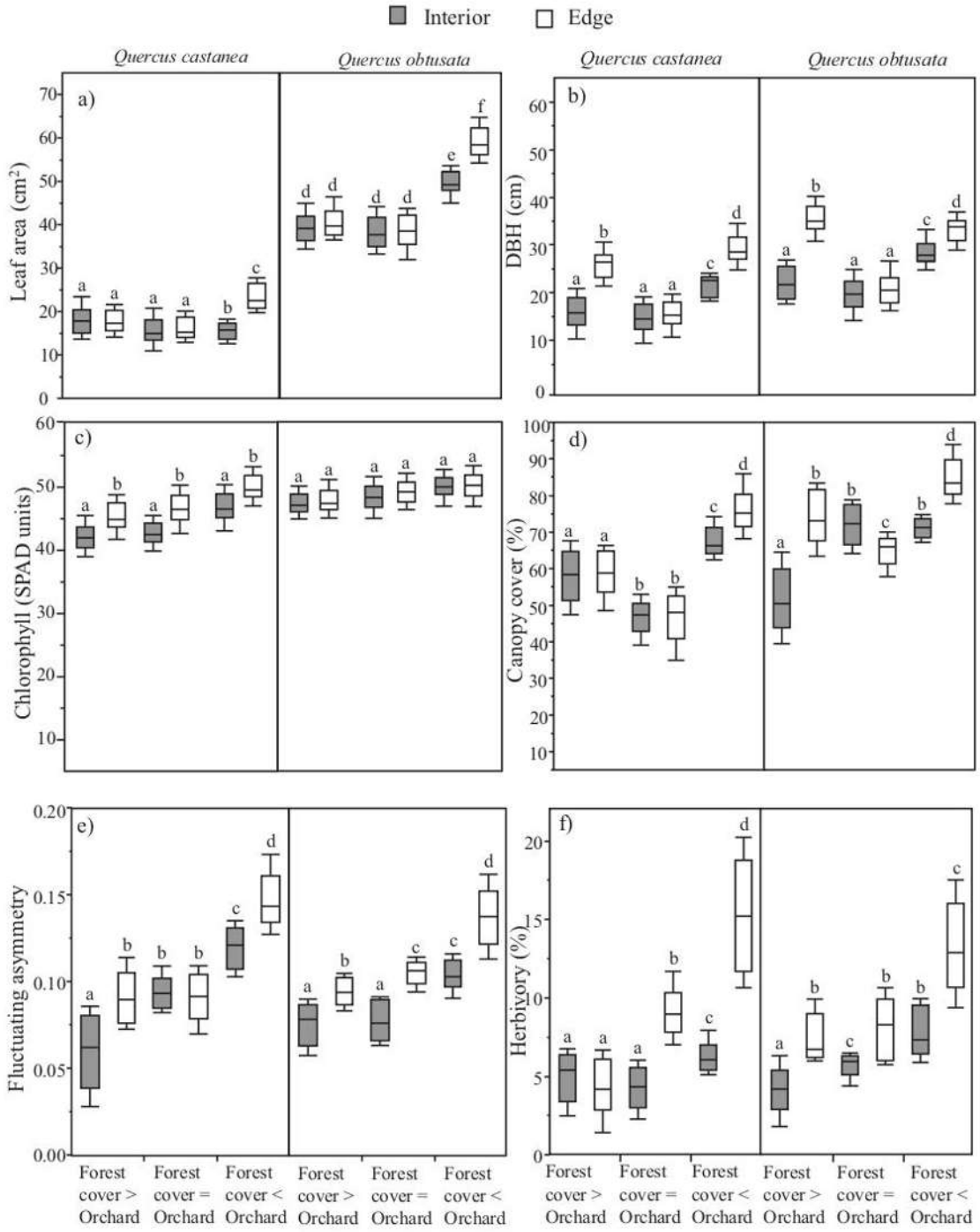

Fig. 4. Quality and quantity of plant resources, fluctuating asymmetry and herbivory of *Q. castanea* and *Q. obtusata* individuals growing in three different proportions of forest and orchards and habitat types (interior and edge of fragments). Different letters indicate statistically significant differences according to LSMeans test ($P < 0.05$).

longer and wider than the leaves of individuals from areas with equal proportion of both forest and orchards and individuals from areas with more proportion of forest (Fig. 6a). The analysis of canonical variants distinguished three groups: forest > orchard, forest = orchard and forest <orchard. CVA1 explained 45.3% of the total variance, and CVA2 explained 19.7% (Axis 1 $\lambda = 0.0.642$ df = 120;$\chi^2 = 784.7$; $P < 0.0001$, Axis 2 $\lambda = 0.8716$ df = 59 $P < 0.0001$) (Fig. 6b). Additionally, we observed that the leaves of the individuals of *Q. castanea* that grew at the edges of the fragments had thinner and longer leaves than those that grew in the interior of the fragments (Fig. 7a). CVA1 explained 54.3% of the total variance, while CVA2 explained 19.4% of the variance ($\lambda = 0.92.4$ df = 60;$\chi^2 = 139.8$; $P < 0.0001$) (Fig. 7b).

The analysis of superimposition of coordinates indicated differences in the leaf morphology of *Q. obtusata* trees between the areas with different proportion of forest and orchards and between the edge and interior of the fragments, with the leaves of the individuals of areas with more proportion of orchards being wider at the base and in the middle part of the leaf and more elongated than the leaves of forest = orchard and forest > orchard individuals (Fig. 6c). We distinguished three different groups according to the analysis of canonical variants: (i)

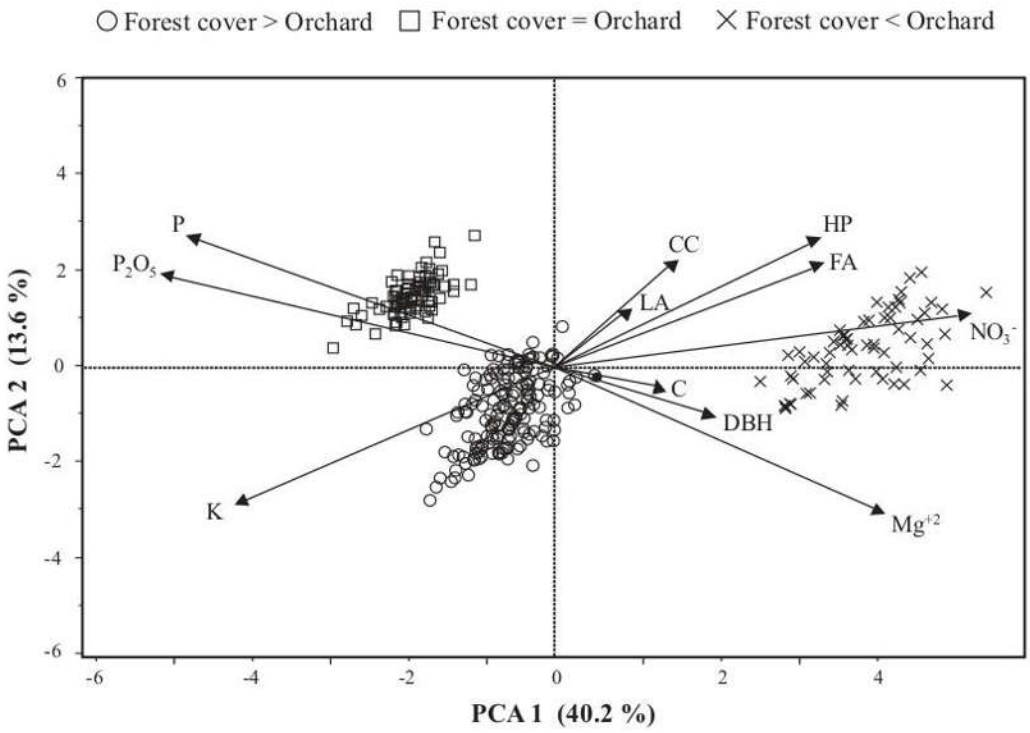

Fig. 5. Results of principal component analyses of plant quality and quantity, fluctuating asymmetry, herbivory percentages and soil nutrients among individuals of three forest-cover orchards for both oak species. CC = canopy cover, C = chlorophyll, DBH = diameter at breast height, LA = leaf area, FA = fluctuating asymmetry, HP = herbivory percentage, Mg^{2+} = magnesium, NO_3^- = nitrates, P = phosphorous, P_2O_5 = pentoxide of phosphorous, K = potassium, SO_4^{2-} = sulfates.

Table 3
Spearman's correlation coefficients of plant quality and quantity, herbivory and fluctuating asymmetry of both oak species studied (* $P < 0.05$).

	Leaf area	FA	Canopy cover	DBH	Chlorophyll content	Herbivory
Leaf area	–					
FA	0.49*	–				
Canopy cover	0.05	0.21*	–			
DBH	0.22*	0.19*	0.31*	–		
Chlorophyll content	−0.29*	0.25*	0.23*	0.27*	–	
Herbivory	0.22*	0.46*	0.22*	0.05	0.31*	–

forest> orchard, (ii) forest = orchard and (iii) forest <orchard. CVA1 explained 55.3% of the total variance, and CVA2 explained 19.1% (Axis 1 $\lambda = 0.696$, df = 120,$\chi^2 = 575.2$, $P < 0.0001$; Axis 2 $\lambda = 0.874$, df = 120,$\chi^2 = 213.3$, $P < 0.0001$) (Fig. 6). Finally, we detected that the leaves of the individuals of *Q. obtusata* that were present at the edges of the fragments had wider and longer leaves than those in the interior of the fragments (Fig. 7c). CVA1 explained 59.4% of the total variance, while CVA2 explained 21.4% of the variance ($\lambda = 0.914$ df = 60;$\chi^2 = 148.5$; $P < 0.0001$) (Fig. 7d).

4. Discussion

4.1. Effects of forest fragmentation (forest cover-avocado orchards) on soil properties

In our study, we detected effects of the conversion of native temperate forests to avocado orchards on the chemical properties of the soil, and we found a higher concentration of magnesium, nitrates and sulfates in fragments with more proportion of avocado orchards. Our results are in agreement with the idea that in forest soils there is a greater leaching of basic ions, nitrates and other chemical compounds in comparison to areas where land use has changed from forest to cropland (Kizilkaya and Dengiz, 2010). A higher concentration of magnesium, nitrates and sulfates in fragments with lower forest cover in relation to avocado orchards could be attributed to the agricultural management of avocado orchards, a result of artificial fertilization based on nitrates generating soil acidification (Blondeel et al., 2019). In addition, the results of the PCA of the properties of the soil between the areas with different proportion of forest and orchards indicated a strong relationship with the concentrations of nitrates and magnesium in the areas with more proportion of orchards. It has been reported that an increase and a saturation of nitrogen in the soil by artificial fertilizers accelerates the nitrogen cycle rates due to the transfer of ammonium to nitrate as a well the abundance of anaerobic microorganisms involved in the transformation of nitrates (Bravo-Espinoza et al., 2012), generating leaching toward forest remnants (Mao et al., 2017), which leads to a deficit of calcium and phosphorus in plants (Zhu et al., 2015). This fact can generate changes in the allocation of growth resources in plants expressed in higher growth rates, height, DBH and leaf production (Blondeel et al., 2019). However, it has been documented that the conversion of forests to agrosystems increases the erosion and degradation of soils, decreasing soil fertility as a result of changes in their physic-chemical properties (Borrelli et al., 2017; Wang et al., 2019).

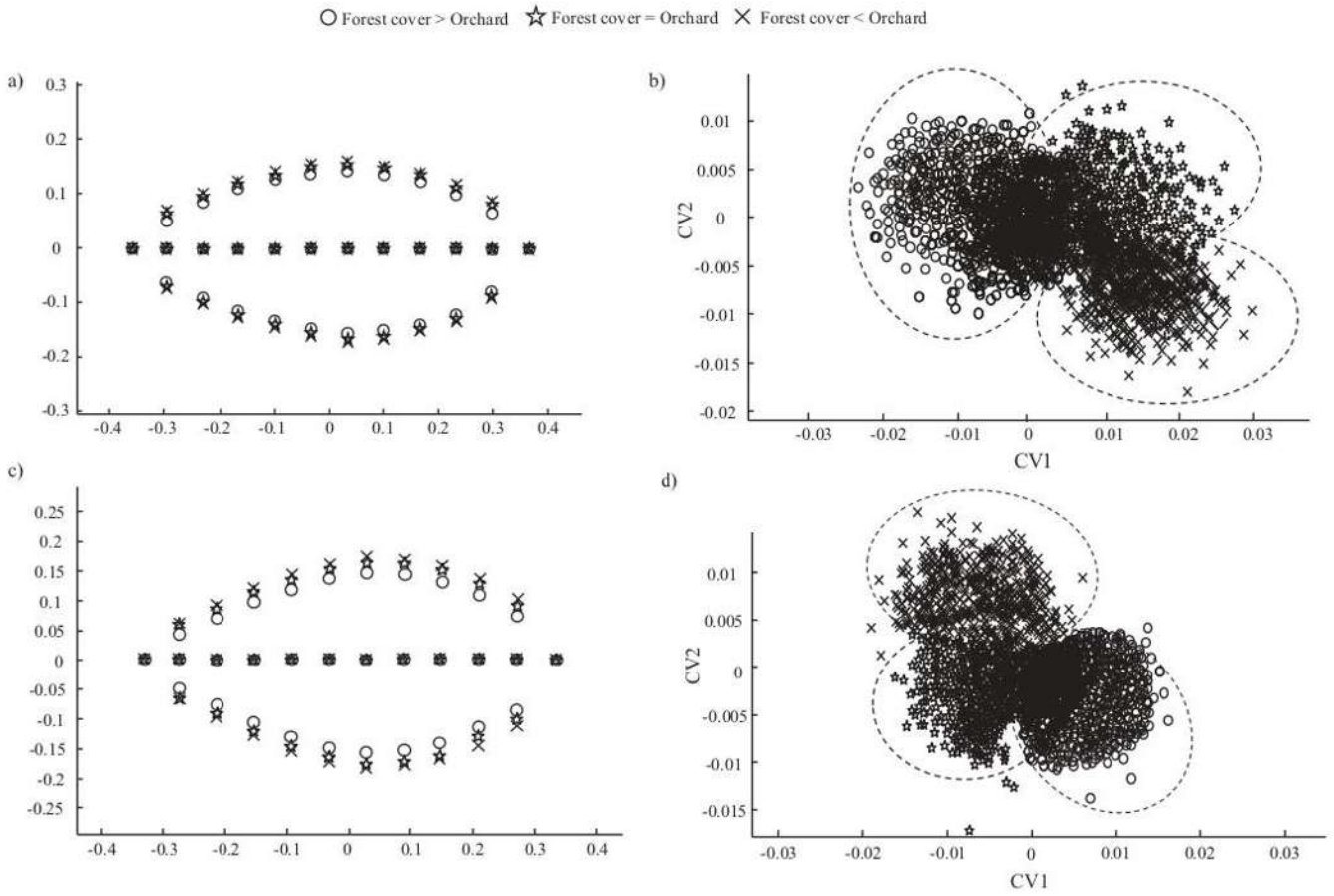

Fig. 6. Leaf morphological variation in *Q. castanea* and *Q. obtusata* among the three different proportions of forest cover orchards and habitat types. For *Q. castanea*: a) Morphological differences and the shape showing the average of the coordinates of the configuration of the leaves. b) Differences in leaf shape morphology among the three different proportions of forest cover-orchard and habitat types according to canonical variate analysis (CVA). For *Q. obtusata*: c) Morphological differences the shape showing the average of the coordinates of the configuration of the leaves. d) Differences in leaf shape morphology among the three different proportions of forest cover-orchard and habitat types according to canonical variate analysis (CVA).

4.2. Effects of soil properties on the quantity and quality of plant resources

We detected changes in attributes associated with the quantity and quality of plant resources in the oak species studied. *Quercus castanea* and *Q. obtusata* individuals had greater canopy coverage, leaf area and DBH at sites with less forest coverage and greater coverage of avocado orchards. These results suggest a greater availability of resources for growth in both oak species at areas with more proportion of orchards, which may be attributable to the fact that higher concentrations of magnesium, nitrates and sulfates were detected in patches with more proportion of orchards (van der Putten et al., 2016). The increase in these chemical compounds in the soil could be related to the agricultural management of the avocado orchard as a result of nitrogen fertilization, which promotes edaphic microbial activity, increasing the availability of nutrients in the soil, which can be used by oaks (Baxendale et al., 2014; Blondeel et al., 2019). For example, it has been reported that the deposition of nitrogen in temperate forests generates an increase in their primary productivity (Tylianakis et al., 2008). These ecosystems naturally have low nitrogen availability in the soil, which is a limiting factor for plant growth in these regions (Tamm, 1991; Schlesinger, 2009). However, in recent decades, there has been a significant increase in nitrogen deposits in these biomes, mainly due to artificial deposition resulting from the intensification of agriculture (Meunier et al., 2016). This could explain the presence of individuals of *Q. castanea* and *Q. obtusata* having greater canopy cover, DBH and leaf area in areas with more proportion of orchards. Regarding the relationships between the quantity and quality of the plant and the properties of the soil, the PCA showed a positive relationship between nitrates and magnesium and the leaf area, chlorophyll content and canopy cover in areas with more proportion of orchards in both study species (*Q. castaena* and *Q. obtusata*). This result indicates that individuals of *Q. castanea* and *Q. obtusata* growing areas with more proportion of orchards would have a greater nutrients availability, expressed in trees with greater canopy cover, leaves with greater area and DBH (Smith et al., 2016). This fact can be supported by proposed by the resource allocation hypothesis (HAS) (Coley et al., 1985), which predicts a faster growth and greater production of larger leaves in sites with a greater availability of resources, such as an increase in nitrogen availability. Therefore, these sites represent potential islands of great availability of soil nutrients that affect the growth of oaks and are ultimately more vigorous (Baxendale et al., 2014). An alternative explanation could be attributed to the intrinsic effects of forest fragmentation such as edge effects, because the solar incidence is higher in areas with more proportion of orchards, increasing photosynthetic activity and carbohydrate fixation and resulting in a higher growth rate (i.e., canopy cover and leaf production) in individuals of *Q. castanea* and *Q. obtusata* (Lohbeck et al., 2015; Reinmann and Hutyra, 2017; Killi et al., 2018; Ghorbanzadeh et al., 2020; García-Jain et al., 2021). This result agrees with that found by Maldonado-López et al. (2015), who reported that canopy coverage and DBH were greater at the edges of the fragments within a community of oaks.

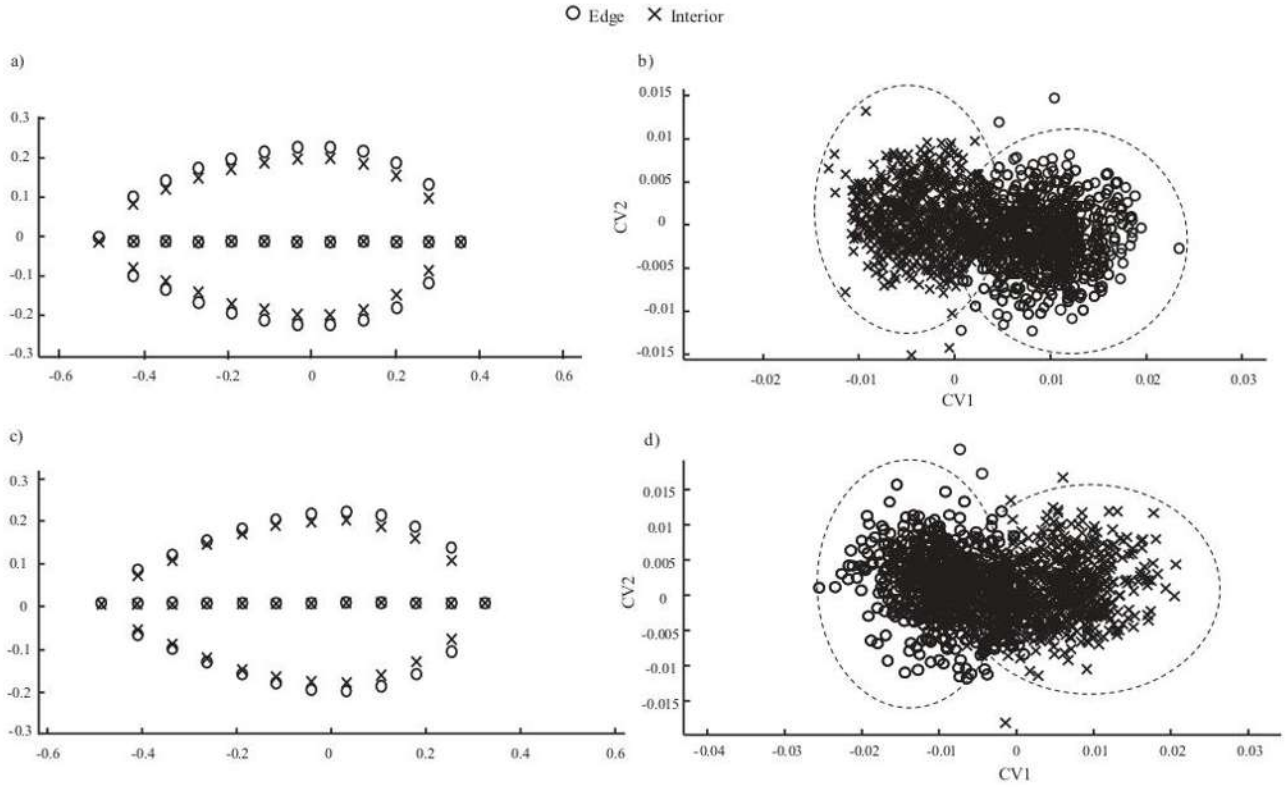

Fig. 7. Leaf morphological variation in *Q. castanea* and *Q. obtusata* differences among the forest interiors and edges. For *Q. castanea*: a) Morphological difference and the shape showing the average of the coordinates of the configuration of the leaves. b) Differences in leaf shape morphology among the three different proportions of forest cover-orchard and habitat types according to canonical variate analysis (CVA). For *Q. obtusata*: c) Morphological difference the shape showing the average of the coordinates of the configuration of the leaves. d) Differences in leaf shape morphology among the three different proportions of forest cover-orchard and habitat types according to canonical variate analysis (CVA).

4.3. Effects of the quantity and quality of plant resources on herbivory and fluctuating asymmetry

Among study sites with different proportion of forest and orchards, we found that individuals of both study species (*Q. castanea* and *Q. obtusata*) showed higher levels of fluctuating foliar asymmetry in the areas with more proportion of orchards, as well as higher FA levels at the edges of fragments than in the interior. It has been reported that FA in plants positively responds to habitat disturbances (Maldonado-López et al., 2019), soil fertility (Cuevas-Reyes et al., 2018b), and herbivory events (Cuevas-Reyes et al., 2011a, 2011b, Cuevas-Reyes et al., 2018a, 2018b), with the latter two (soil fertility and herbivory) being higher in forests than in orchards. These functional adjustments in growth by *Q. castanea* and *Q. obtusata* in the areas with more proportion of orchards can be expressed by an imbalance in the morphology and symmetry of the leaves (Freeman et al., 2004; Cuevas-Reyes et al., 2013; Cuevas-Reyes et al., 2018b).

On the other hand, it is known that forest fragmentation can modify the composition, abundance and distribution of insect herbivores (Kaartinen and Roslin, 2011; Kittelson et al., 2015; Maguire et al., 2016). In our study, we found higher levels of herbivory in areas with more proportion of orchards. This result could be associated with the fact that the individuals of *Q. castanea* and *Q. obtusata* present in these sites showed a strong association between the quantity and quality of plant resources (e.g., leaf area, chlorophyll content, DBH, canopy cover) with the percentages of herbivory. This pattern could be attributed to a greater availability of resources to herbivores, where herbivory could be modulated by a greater amount in the availability of host plant resources (bottom-up forces) (e.g., habitat connectivity, appearance of the host plant) and the quality of the host plant resource (palatability, nutritional quality, chemical defense) (Maron and Crone, 2006; Canelo et al., 2018; Ruiz-Carbayo et al., 2020). For example, it has been found that small forest fragments have more harsh full environmental conditions than in continuous forest, having a decrease in soil and air moisture and an increase in light and temperature (Christianini and Oliveira, 2013; Rossetti et al., 2017). These new environmental conditions generated by the land cover change, modify the patterns of acquisition of resources by plants for growth, having a rapid growth and thus, can represent to insect herbivores high quality resources (e.g. lower physical and chemical defense) (Coley et al., 1985; Rossetti et al., 2017), which could explain the increase in herbivory levels in the sites with less forest cover and more avocado orchard coverage.

At the landscape level, herbivory can be influenced by the isolation of the fragments, the size of these fragments, and the composition of the forest remnants (Tscharntke et al., 2012; Maguire et al., 2016). It has been found that the most connected and larger forest remnants often host a more diverse and abundant herbivore community but tend to have lower levels of herbivory as a result of the control by their natural enemies (top-down forces) (Valdés-Correcher et al., 2019). Under this scenario, in areas with more proportion of orchards, higher levels of herbivory were found, which could be explained by an increase in herbivorous insects associated with the loss of their natural enemies (i.e., predators and parasitoids) (top-down forces) because the higher trophic levels have high space and energy requirements, which makes them very sensitive to habitat loss (Tscharntke et al., 2007; Pfeifer et al., 2017; Valdés-Correcher et al., 2019). However, future studies are necessary to corroborate the potential cascading effects in biotic interactions as result of forest conversion to avocado orchards. Finally, we found higher herbivory levels at the edge rather than in the interior of the three cover types (forest/avocado orchard). De Carvalho Guimarães

et al. (2014) conducted a meta-analysis that showed that the edges of the fragments represented open spaces for the colonization of several plant species, creating new niches and resulting in an increase in the richness of generalist herbivorous insects since they are sites of recovery after a disturbance (Benítez-Malvido and Lemus-Albor, 2005). Contrary, the community of predators and parasitoids are reduced because are highly sensitive to biotic and abiotic changes (e.g. specific food requirements) associated to forest fragmentation, decreasing the pressures from natural enemies to herbivorous insects in these sites (top–down effects) (Pfeifer et al., 2017). In addition, individuals of *Q. obtusata* and *Q. castanea* had a positive relationship between herbivory and FA levels. Some studies have found an association between FA and herbivory (Cuevas-Reyes et al., 2018b; Aguilar-Peralta et al., 2020); since FA is an indicator of imbalance during development, it can potentially indicate compensatory changes between plant nutritional quality and chemical defense against herbivores (Cornelissen and Stiling, 2011; Castagneyrol et al., 2019).

Finally, although belonging to the same genus, we detected that the effect of fragmentation and location varied between the oak species studied. This fact can be explained by the intrinsic differences in physiological, genetic and ecological traits among these oak species, which in turn can influence the responses to habitat fragmentation (Maldonado-López et al., 2015, 2016a, 2016b; Pérez-López et al., 2016; Forner et al., 2020).

4.4. Leaf morphology

In both oak species analyzed, we found that leaf shape was wider and longer in individuals growing in areas with more proportion of orchards compared to individuals of areas with equal proportion of both forest and orchards or areas with more proportion of forest. Plants respond to biotic and abiotic changes generated by habitat fragmentation through morphological, physiological and chemical adjustments (Schöb et al., 2013; Cuevas-Reyes et al., 2018a). These adjustments can be expressed as variations in the shape and size of the leaves (García-Jain et al., 2021), depending on the phenotypic plasticity of the individuals to adapt to the environmental stress caused by forest fragmentation (Agrawal, 2001; Viscosi, 2015). Our results indicate that the foliar morphological differences of *Q. castanea* and *Q. obtusata* between the areas with different proportion of forest and avocado orchards may be the result of changes in environmental variables, where the areas with more proportion of orchards have greater solar incidence and increase in temperature as a result of the fragmentation of the forest matrix (Martínez-Munguía et al., 2015), affecting the morphological variation of the oaks. Previous studies have documented the importance of geographical and environmental factors as regulators of the stability of leaf development, inducing morphological changes in the leaves (Bruschi et al., 2003; Díaz and Cabido, 2001). In addition, it has been reported that in sites with a high availability of nutrients (i.e., incidence of light and nitrogen), plants have much faster growth and longer leaves, which is explained by the resource availability hypothesis (Coley et al., 1985). Particularly for oaks, a correlation between morphological changes and environmental factors such as temperature and precipitation has been documented (Aguilar-Romero et al., 2016, García-Jain et al., 2021), which could explain the morphological differences found in *Q. castanea* and *Q. obtusata* between the areas with different proportion of forest and avocado orchards.

5. Conclusions

We concluded that the conversion of temperate forest ecosystems to avocado orchards have important consequences mainly on the chemical properties of the soils, increasing the amount of nitrates and other chemical compounds, which in turn influence the quantity and quality of resources increasing the leaf area, DBH, canopy cover of *Q. castanea* and *Q. obtusata*, and affecting the biotic interactions increasing the herbivory levels in fragments with more proportion of orchards. We highlight that we detected changes in leaf morphology and higher FA levels in *Q. castanea* and *Q. obtusata* individuals in areas with more proportion of orchards suggesting phenotypic responses to the variation of the local environmental conditions as a result of the conversion of temperate forests to avocado orchards. Our findings confirm that the fluctuating asymmetry is a reliable biomarker to detect environmental stress in *Q. castanea* and *Q. obtusata* in fragmented habitats, as well by the amount of herbivory damage. Our study is the first to denote the importance of the maintenance and conservation of temperate forest ecosystems and their potential functional and ecological benefits on cropping systems, in particular avocado cultivation.

Data availability

Data will be made available upon request.

Declaration of Competing Interest

The authors mentioned above declare that they have no conflicts of interest associated with this manuscript. The work represents original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.agsy.2022.103556.

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Functional leaf traits variability and herbivory patterns in two oak species along a mosaic of avocado agrosystems in Mexico: Importance of native forest cover and abiotic factors

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Abstract

In Mexico, change land-use to avocado orchards affect abiotic conditions and ecological processes. As consequence, it can also affect leaf functional traits expression and plant-insect interactions. We evaluated the changes in chemical soil properties and the effects of local climate variables on leaf functional traits and herbivory in *Quercus castanea* and *Q. obtusata* that occur in fragments with different proportion of forest cover and avocado orchard: forest cover > orchards, forest cover = orchards and forest cover < orchards. In each forest condition, at least 17 individuals of each oak species were selected to analyze leaf functional traits and herbivory. Soil samples were collected to analyze chemical properties. Soils of areas with more proportion of forest had higher concentration of NH^{+4}, K and K_2O, whereas soils with more proportion of orchards displayed higher concentrations of Mg^{+2}, NO_3 and SO_4^{-2}. Leaf thickness, fresh mass and water content were higher in areas with more proportion of forest and were influenced by NO_3^-, Mg^{2+}, SO_4^{-2} and climatic variables as mean annual temperature, wettest quarter temperature and mean annual precipitation. Leaf dry weight, specific leaf area, leaf area and chlorophyll content, as well herbivory were higher in areas with more proportion of orchards and were affected by PO_4^{-2}, P_2O_5, P, K_2O, K, NH^{+4}, and by precipitation of the driest quarter. We highlight the responses and the links of plant functional traits associated to soil properties and local climatic variables and their possible consequences of biotic interactions along the fragmentation mosaic with different covers of avocado orchards and temperate forests.

Keywords: Avocado orchards; soil chemical properties; local climate variables; leaf functional traits; herbivory; *Quercus*

Declarations

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Introduction

In the last decades, the conversion of the natural ecosystems to croplands and the intensification of agriculture were the main factors of biodiversity decline, as a consequence of habitat loss and fragmentation (Tscharntke et al. 2012; Maxwell et al. 2016). Fragmentation is a highly pervasive process, which causes alterations in the microclimatic conditions (e.g., temperature, humidity, light incidence, wind speed) (Lindenmayer et al. 2012; Tuff et al. 2016; Arroyo-Rodríguez et al. 2017; Scanes 2018), habitat connectivity and ecosystem services such as pollination, carbon sequestration and climate regulation, biological control pest and disease control, edaphic biota and soil fertility (Bianchi et al. 2006; Haddad et al. 2015). Additionally, the soil chemical properties change in forest fragments nearby the agrosystems (Tuff et al. 2016; Uzêda et al. 2016), exhibiting lower amount of organic matter and nutrients, and higher levels of synthetic nutrients (N-P-K) and acidification (Manning 2012; Ramankutty et al. 2018). The chemical properties of the soil determine the functional adaptations of the plants, affecting the expression of the leaf functional traits (Jager et al. 2015). For example, plant species with fast-growing leaves have been associated to nutrient-rich soils, where they exhibit a high concentration of leaf nitrogen and phosphorus, high specific leaf area (SLA) and low dry matter content (LDMC) and leaf thickness (Gourlet-Fleury et al. 2011; Jager et al. 2015).

Habitat fragmentation also affect plant phenotypic expression such as architecture (i.e., structural complexity), chemical and physical defenses, nutritional quality and functional traits (Castagneyrol et al. 2012; Lohbeck et al. 2013; Barbour et al. 2015). Specifically, leaf functional traits are defined as measurable characteristics that influence plant performance or fitness, presumably reflecting the evolutionary responses to changes

90 in the environmental conditions. Therefore, the use of functional approaches to quantify the
91 effects of forest fragmentation on phenotypic expression of the plants has increased in the
92 recent years (Violle et al. 2007; Ramirez-Valiente et al. 2017). Some studies demonstrated
93 that the variations on leaf functional traits across environmental gradients are explained
94 within the framework of the worldwide leaf economics spectrum (WLES; Wright et al.
95 2004; Donovan et al. 2011; Aguilar-Peralta et al. 2021), according to which there is a trade-
96 off between the fast acquisition rate and efficient conservation of resources by plants. In
97 habitats with high resource availability, acquisitive strategies (i.e., short-lived leaves with
98 low construction cost) are expected, while conservative strategies (i.e., long-lived leaves
99 with high construction cost) would be selected in environments with low resource
100 availability (Garnier and Navas 2012; Halm and Maron 2016) (Fig. 1).

101 Variations in leaf traits can potentially affect the incidence and preference of insect
102 herbivores (i.e., bottom-up effects) (Loranger et al. 2012, 2013; Lavorel et al. 2013). In
103 fragmented habitats, plants will exhibit conservative strategies, such as thick leaves with
104 low SLA, which usually decrease herbivory levels (Castagneyrol et al. 2019; Ruiz-Carbayo et
105 al. 2020). However, a recent meta-analysis involving 89 independent studies (Rosetti et al.
106 2017) indicated that, despite insect herbivore diversity decreases as the habitat
107 fragmentation increases, herbivory levels did not change significantly, suggesting that
108 generalist herbivore species that remain in fragmented habitats can maintain high herbivory
109 levels in plant communities. However, bottom-up mechanisms related to plant functional
110 traits affecting herbivory in fragmented forests need further investigation.

111 Temperate forests currently occupy 16.3% of Mexico surface (Arasa-Gisbert et al.
112 2018) and suffer a high loss of cover area (27%), with an annual deforestation rate of

190,000 ha/year (Galicia 2016; Guerra-de la Cruz and Galicia 2017). In these ecosystems, one of the main causes of land cover change is the establishment of avocado orchards (*Persea americana* Mill) (Barsimantov and Antezana 2012). Mexico is the largest producer of avocado worldwide with the 31% of global production, and has the largest cultivated area in the world (27%) (FAOSTAT 2019). The genus *Quercus* is a very diverse group of tree species distributed in temperate forests, subtropical and tropical regions of the northern hemisphere (Cavender-Bares 2016). Mexico is an important center of oak diversification and endemism (Hipp et al. 2018) with about 170 species (32-40 % of the diversity in the world), of which 100 are endemic (Valencia 2004; Hipp et al. 2020).

The aim of this study was to evaluate the variation in leaf functional traits and herbivory levels in *Quercus castanea* and *Q. obtusata* across a gradient of forest cover/avocado orchard proportion, with contrasting soil fertility and climatic conditions. Specifically, we addressed the following questions: i) Does leaf traits and herbivory levels of *Q. castanea* and *Q. obtusata* differ in function of the proportion of native forest to avocado orchard cover? ii) How leaf functional traits and herbivory are affected by soil chemical properties and climatic conditions along the gradient of forest cover? As illustrated in Fig. 1, we expect that, in areas with higher proportion of forest cover, environmental conditions will be harsher (i.e., low soil fertility and drier climatic conditions). As a consequence, individuals of *Q. castanea* and *Q. obtusata* will present acquisitive leaf traits and higher herbivory levels in these habitats, the opposite being expected for areas with a lower proportion of forest cover in relation to avocado orchards.

Material and methods

136 *Study area*

137 This study was conducted in the "avocado belt" in the center-west of the Michoacán state,
138 Mexico, characterized by a landscape of pine-oak forest fragments mixed with avocado
139 orchards (Barsimantov and Antezana 2012). First, we determined the forest and avocado
140 orchard cover in the avocado belt using medium and high-resolution satellite images
141 (Landsat, SPOT. Sentinel, and Rapid Eye with the TM 5, ETM + and OLI sensors) and
142 supervised classification to determine the location and extent of the main temperate forest
143 coverages and avocado orchards (Neinavaz et al. 2020). From this information, eight
144 fragments with different proportion of forest and avocado orchards cover (Hass variety)
145 were selected and where *Quercus castanea* and *Q. obtusata* occurs, and then, were
146 classified as follows: (i) sites with more proportion of forest; (ii) sites with equal proportion
147 of both forest and orchards and (ii) sites with more proportion of orchards (see Table 1). In
148 each study site, a buffer area of 1000 m of radius was established. All study sites have a
149 similar history of management, which consisted in clear-cutting the native temperate forest
150 for organic avocado farming without use of synthetic pesticides. Additionally, all the
151 avocado orchards studied have a similar age ranging between 15 and 20 years after felling
152 (Arima et al. 2022).

153

154 *Study system*

155 *Quercus castanea* Neé is a red oak which belongs to the section Lobatae (Nixon 1993). It is
156 a tree with height ranging between 5 and 15m, and a trunk diameter between 30 and 60 cm.
157 The leaves are obovate oblanceolate with underside veins conspicuously elevated and
158 reticulate, margins with 2 to 5 short teeth, 8-12 secondary veins on each side of the mid-

159 vein, gray-greenish coloration, and fasciculate, sessile trichomes (Arizaga et al. 2009). It
160 occurs in altitudes between 1300 and 2800 masl in the Central Plateau of México and the
161 Trans-Mexican volcanic belt (Valencia 2004). A large part of the herbivorous insects that
162 consume *Q. castanea* belonging to the families Saturnidae and Noctuidae (Lepidoptera)
163 (Valencia 2004; Barrios-Díaz et al. 2017).

164 *Quercus obtusata* Humb. & Bonpl. is a white oak belonging to the section Quercus
165 (Nixon 1993). It is a tree with height ranging between 10 and 30 m, and a trunk diameter
166 from 50 to 60 cm. The leaves are obovate, long obovate or elliptical with thickened margins
167 and slightly curled. The leaf adaxial surface is lustrous and tomentose near the base; the
168 abaxial surface is pubescent with glandular hairs (Arizaga et al. 2009). It occurs in altitudes
169 between 1430 and 2900 masl in the Central Plateau of México and Trans-Mexican volcanic
170 belt (Valencia 2004). The main herbivorous insects that attack *Q. obtusata* are *Tortrix*
171 *viridana* (Lepidoptera: Tortricidae) and *Acraga coa* (Lepidoptera: Dalceridae) (Ortega-
172 Rivera et al. 2019). Oak species present different types of physical (e.g., leaf thickness,
173 trichomes and pubescence) and chemical (mainly phenolic compounds such as phenols,
174 hydrolyzable and condensed tannins) defenses against herbivore attack (Visakorpi et al.
175 2019).

176

177 *Soil properties analyses*

178 Based on data from a previous study where analyzed the chemical soil properties in eight
179 sites with different proportion of forest and avocado orchards cover (Pérez-Solache et al.
180 2022), we selected a subset of data that include nine soil chemical parameters related to
181 plant growth: magnesium (Mg^{2+}), ammonium (NH^{+4}), nitrates (NO_3^-), phosphorus (P),

182 phosphorus pentoxide (P_2O_5), phosphates (PO_4^{-2}), potassium (K), potassium oxide (K_2O)
183 and sulfates (SO_4^{2-}). Chemical soil analyses are described in detail in the Supplementary
184 Information.
185
186 *Leaf functional trait analyses*
187 In each study site, at least 17 adult trees per oak species (*Q. castanea* and *Q. obtusata*) were
188 marked. To analyze leaf functional traits, we collected three branches per individual and
189 selected 10 fully expanded leaves without apparent damage by herbivore insects from each
190 canopy strata (upper, middle and lower; N= 30 leaves per individual. After this, all leaves
191 were cut from each branch and weighed to obtain the leaf fresh weight, fresh matter and
192 water content (Cornellissen et al. 2003). Finally, all leaves were dried using an oven with
193 air circulation at 60 °C for 72 hours.
194 As an indicator of plant water use, we measured (i) leaf water content (LWC: leaf
195 fresh mass leaf dry mass / total leaf area); (ii) for light acquisition, we measured
196 chlorophyll content (CC) in three leaves per individual using a portable chlorophyll meter
197 SPAD 502 (Minolta), and specific leaf area (SLA) was estimated dividing leaf area/dry
198 mass; and (iii) for nutrient use and conservation, leaf area (LA) was obtained using the
199 ImageJ program (Rasband 2006) from digitalized images; leaf thickness (LT) was obtained
200 using a micrometer Mitutoyo (Kawasaki, Japan); leaf fresh matter (LFM) was calculated by
201 dividing leaf fresh weight / the leaf area; and leaf dry weight (LDW) was measured
202 weighing the leaves with an analytical balance. A description of the functional role of each
203 trait analyzed was included in the Supplementary Information, Table S1.

205 *Herbivory measurements*

206 We evaluated herbivory damage in the same trees where the leaf functional traits were
207 measured. We first removed three branches from the each of the canopy strata (upper,
208 middle and lower) and then, 10 leaves totally expanded were randomly collected from each
209 stratum (N= 30 leaves per tree) (Cuevas-Reyes et al. 2018). All collected leaves were
210 digitized to estimate the total area of the leaf and the area removed using the software
211 ImageJ 1.51j87 (https://imagej.nih.gov/ij/). We calculated the percentage of removed leaf
212 area (PRLA) for each leaf by (leaf area consumed/total leaf area) * 100 (Cuevas-Reyes et
213 al. 2018).

214

215 *Climatic variables*

216 We also assessed climatic variables that potentially have influence on the variability of
217 functional leaf traits. We obtained 19 bioclimatic variables available in WorldClim
218 (http://worldclim.org/version2) (Fick and Hijmans 2017) for each study site, and then, we
219 carried a paired correlation analysis for each climatic variable to eliminate redundant
220 variables (the criterion was eliminated one variable from each pair with $r > 0.80$ retaining
221 the more general climatic variable). The selected variables were mean annual temperature
222 (MAT), mean annual precipitation (MAP), mean temperature of the wettest quarter (WQT),
223 mean precipitation of the wettest quarter (PWQ) and mean precipitation of the driest
224 quarter (PDQ). Climatic variables of each study site are described in detail in the
225 Supplementary Information (Table S2).

226

227 *Statistical analyses*

We performed a spatial autocorrelation analysis using the Moran's I coefficient, which is effective for characterizing and identifying random, dispersed or clustered land cover configurations as a function of spatial location (Kowe et al. 2019). The Moran's I values range from -1 to 1, where values close to 0 indicates a random spatial distribution, while values close to -1 or 1 represents high negative or positive spatial autocorrelation of the data (Fu et al. 2014; García-Jaín et al. 2021). We found Moran's I coefficient values close to 0 for all parameters related to the soil properties (magnesium = 0.067; ammonium = -0.02; nitrates = -0.04, phosphorus = 0.08, phosphorus pentoxide = -0.05, phosphates = 0.07, potassium = -0.03, potassium oxide = 0.06, sulfates = 0.03), leaf functional traits (LWC = -0.19, LFM = -0.11, CC = 0.11; SLA = -0.09, LA = 0.16; LT = -0.08, LDW = 0.11) and the percentage of removed leaf area (PRLA = -0. 18) in *Q. castanea* and *Q. obtusata*, confirming that all study sites are independent data points in all analyses.

Because the data did not show a normal distribution, the comparison of chemical properties of soil among the three forest/orchard coverage classes were analyzed using Kruskal-Wallis non-parametric tests and multiple comparisons (Dunn´s Method). Leaf functional traits were compared among coverage classes through one-way analyses of variance (ANOVA, one model for each trait), using average values of individual trees. The Pearson's correlation coefficient was use to verify the effect of each leaf functional trait on the percentage leaf damage. Finally, we performed an analysis of principal components analysis (PCA) to explore the association between leaf functional traits, herbivory levels and soil nutrients in the three forest/orchard coverage classes. A similar analysis was conducted for the association between leaf traits, herbivory levels and climatic variables.

Data analyses were conducted using the JMP software (version 13; SAS Institute Inc., Cary, NC, USA).

Results

Chemical properties of soil

We found significant differences for all soil nutrients among the different forest/orchard coverage classes in accordance with the Kruskal–Wallis tests (Table 2a). Soils from sites with forest cover > orchard presented higher concentrations of NH^{+4}, K and K_2O, while soils from forest = orchard cover showed higher concentrations of P, P_2O_5, PO_4^{-2}. Finally, soils from sites with forest cover < orchard displayed higher concentrations of Mg^{+2}, NO^{-3} and SO_4^{-2} (Table 2b).

Variation in leaf functional traits and herbivory

Significant differences were found in all functional leaf traits analyzed and in the percentage of removed leaf area (PRLA) among the three forest/orchard coverage classes for both oak species (Table 2). Leaf thickness (Fig. 3a), leaf fresh mass (Fig. 3c) and leaf water content (Fig. 3d) were higher in sites with more proportion of forest, decreasing as the avocado cover increased. On the other hand, we obtained higher values of leaf dry weight (Fig. 3b) and specific leaf area (Fig. 3f) for both oak species in sites with more proportion of orchards, followed by sites with more proportion of forest and sites with equal proportion of both forest and orchards. Particularly for *Q. castanea*, leaf area, chlorophyll content and percentage of removed leaf area were higher in sites with more proportion of orchards, followed by sites with proportion of forest and sites with equal

273 proportion of both forest and orchards (Fig. 2). A similar pattern was observed for *Q.*
274 *obtusata*, for which leaf area was higher in sites with more proportion of orchards, followed
275 by sites with equal proportion of both forest and orchards and sites with more proportion of
276 forest (Fig. 3). For this species, chlorophyll content and the percentage of removed leaf area
277 were higher in sites with more proportion of orchards, sites with more proportion of forest
278 and sites equal proportion of both forest and orchards respectively (Fig. 2).
279 The results of PCAs indicated that leaf functional traits and the PRLA displayed a
280 clear pattern of separation of individuals between the sites with more proportion of
281 orchards and those with sites with more proportion of forest and sites with equal proportion
282 of both forest and orchards for *Q. castanea* (Supplementary Information, Fig. S1a) and *Q.*
283 *obtusata* (Supplementary Information, Fig. S1b). In *Q. castanea* and *Q. obtusata*,
284 individuals from with more proportion of orchards were positioned on the right side of
285 PCA biplots and related to SLA, LA, LDW, CC with PRLA. For both oak species,
286 individuals from sites with more proportion of forest and sites with equal proportion of
287 both forest and orchards were mostly situated on the left side of PCA biplots, being
288 associated with LFM, LWC and LT (Supplementary Information, Fig. S1a,b).
289
290 *Correlations between leaf functional traits and herbivory*
291 We found that in *Q. castanea*, HP was positively correlated with LDW, LA and CC, and
292 negatively with LT. Additionally, LT showed positive correlations with LFM and LWC,
293 and a negative relationship with CC (Table 3). Also, LFM was positively correlated with
294 LWC, and negatively with LA and SLA. In *Q. obtusata*, HP showed positive correlations

295 with LDW, LA, SLA and CC, and a negative relationship with LWC. The LDW was
296 positively correlated with LA, SLA and CC (Table 3).
297 We found that, for *Q. castanea*, PRLA was positively correlated with LDW, LA and
298 CC, and negatively correlated with LT. For *Q. obtusata*, PRLA showed positive
299 correlations with LDW, LA, SLA and CC, and a negative relationship with LWC (Table 3).
300 The PCA analyses that included leaf functional traits, the PRLA and soil nutrients also
301 exhibited the similar pattern of separation of individuals from sites with forest cover >
302 orchard and forest orchard and sites with forest cover < orchard for *Q. castanea* and *Q.*
303 *obtusata* (See Supplementary Information, Fig. S2ab). Thus, the individuals of both species
304 from the sites with more proportion of forest and equal proportion of both forest and
305 orchards were positioned on the right side of PCA biplots and was associated to PO_4^{-2},
306 P_2O_5, P, K_2O, K, NH^{-4}, and with LT, LFM and LWC. Individuals from sites with more
307 proportion of orchards were located at the left side of the biplots of both species, and
308 related to NO^{-3}, Mg^{2+}, SO_4^{-2} with LA, CC, SLA, LDW and PRLA (Supplementary
309 Information, Fig. S2ab).
310 Finally, the PCA analyses that included leaf functional traits, the PRLA and climatic
311 variables displayed a similar pattern of separation of individuals in *Q. castanea* (Fig. 4a)
312 and *Q. obtusata* (Fig. 4b). Individuals growing in sites with more proportion of orchards
313 were separated from those in sites with more proportion of forest and equal proportion of
314 both forest and orchards. Individuals from sites with more proportion of orchards was
315 positioned on the right side and associated to MAT, WQT, PWQ and MAP with LDW, CC,
316 LA, SLA and PRLA. At the left side of PCA biplots, individuals of *Q. castanea* and *Q.*
317 *obtusata* from the other sites were associated to PDQ with LT, LFM and LWC (Fig. 4ab).

318 **Discussion**

319 Despite the functional leaf traits have been proposed as reliable predictors of above-ground
320 biomass, litter decomposition and plant performance through the identification of
321 morphological, physiological and phenological changes along environmental gradients
322 (Violle et al. 2014; Silva et al. 2021), few studies have applied approaches based in the
323 links between plant functional traits and soil properties in crops and agroecosystems
324 (Martin and Isaac 2015; Faucon et al. 2017; Issac et al. 2017). The conversion of forests
325 into croplands usually has a high impact on soils, increasing erosion and degradation,
326 decreasing fertility and changing the biological and physicochemical properties of the soil
327 (Borrelli et al. 2017; Wang et al. 2019). In the present study, soils from sites with more
328 proportion of orchards displayed higher concentrations of Mg^{+2}, NO^{-3} and SO_4^{-2}. In our
329 study, we detected significant effects of the conversion of forests to avocado orchards on
330 the chemical properties of soil in forest fragments with different proportion of forest cover-
331 avocado orchards. The increase of these chemical compounds of the soil could be related to
332 the agriculture management of the avocado orchard, as result of fertilization based on rapid
333 reaction ammonia generated acidification (increased the cumulative proton inputs) of the
334 soil (Schrijver et al. 2011; Blondeel et al. 2018). The soil acidification induced by the
335 saturation of nitrogen input on soil can accelerate nitrogen cycling rates, mainly driven by
336 transferring ammonium to nitrate and subsequent leaching (Mao et al. 2017), decreasing the
337 absorption of calcium and phosphorus in plants (Zhu et al. 2015). Additionally, a higher
338 concentration of nitrates in the soil in these forest fragments can be explained by a high
339 abundance of anaerobic microorganisms involved in the nitrate transformation as a result of
340 soil disturbance (Bravo-Espinoza et al. 2012).

341 Because the changes in soil chemical properties can lead to nutrient imbalances in
342 plants (Tao and Hunter 2012), such as a reduction in phosphorus availability, it is possible
343 to expect changes in functional traits that affect the resource allocation for plant growth
344 (Blondeel et al. 2018). For example, leaf functional traits involved in nutrient acquisition
345 such as specific leaf area, total leaf area and carbon: nitrogen ratio can affect resource
346 acquisition and carbon storage (Wood et al. 2015; Faucon et al. 2015). In our study,
347 changes in soil chemical properties may be related with the leaf functional traits variation
348 expressed by *Q. castanea* and *Q. obtusata* in forest fragments with different proportion of
349 forest cover-avocado orchards.
350 Leaf functional traits are consistently different along the forest cover gradient.
351 Three leaf traits exhibited higher values for both oak species at sites with greater forest
352 cover: LT, LFM and LWC, the former a conservative trait, while the latter two are
353 acquisitive traits in relation to water availability. On the other hand, LDW (conservative),
354 SLA, LA and CC (acquisitive) were higher in the fragments with less forest and higher
355 avocado cover for both oak species. The individuals in these fragments were related to
356 MAT and WQT in the PCA analysis, therefore we expected that higher temperatures would
357 leading to an expression of leaf conservative traits towards drought tolerance in *Q. castanea*
358 and *Q. obtusata*, as predicted by the leaf economics spectrum (Ramirez-Valiente et al.
359 2017; Lohbeck et al. 2013). For *Q. castanea*, a recent study conducted in same region
360 indicated that leaves of this species are thinner where precipitation is more seasonal, and
361 more sclerophyllous in cooler and less seasonal areas, contrary to the reported to
362 Mediterranean oak species (Lara-de la Cruz et al. 2020). The authors related this non-
363 conformity of the leaf traits in *Q. castanea* to the leaf economic spectrum to a longer leaf

364 lifespan in mesic areas, thus selecting for more individuals with more sclerophyllous
365 leaves. Thus, further studies also considering leaf phenology are necessary to unravel the
366 interplay between soil properties and climate as environmental filters for oak functional
367 traits in the studied system.

368 The higher herbivory levels recorded in *Q. castanea* and *Q. obtusata* in fragments
369 with less forest cover partially conforms to the framework that we proposed in the present
370 study (see Fig. 1). In these areas, the oak species were less sclerophyllous, with lower leaf
371 thickness and higher SLA, which are acquisitive leaf traits that confer lower plant
372 resistance to herbivory (Hahn and Maron 2016, Lobregat et al. 2018). Contrary, the lower
373 levels of herbivory in *Q. castanea* and *Q. obtusata* observed in fragments with higher forest
374 cover and lower avocado orchard could be related to a resource conservation strategy,
375 where plants allocate more resources to defense against herbivores (e.g., higher leaf
376 thickness and chemical defense production) (Stevens et al. 2016).

377 Another possible explanation is related to abrupt changes in the insect herbivore
378 assemblages with the increase of habitat fragmentation and loss forest cover (i.e., bottom-
379 up forces) (Rossetti et al. 2017), where specialized insect herbivore species are replaced by
380 generalist species, increasing the insect herbivore incidence and leaf consumption levels
381 (e.g., Pyrallidae, Lymantridae, Geometridae, Arctiidae). Inconsistent patterns have been
382 documented on insect herbivore diversity along forest fragmentation gradients. In some
383 cases, species richness of insect herbivores increases as forest fragmentation increase
384 (Schüepp et al. 2014; Pfeifer et al. 2017). However, in other cases, forest fragmentation
385 decreases the insect herbivore diversity (Harvey and MacDougall 2015; Maldonado-López
386 et al. 2016), but not herbivory levels (Rossetti et al. 2017). It is possible that generalist

387 species of insect herbivores that remain in fragmented habitats can maintain high herbivory
388 levels in plant communities despite the loss of specialist herbivore species as a result of
389 forest fragmentation (Fontúrbel and Murúa 2014; Rossetti et al. 2017 Bagchi et al. 2018)
390
391 **Conclusions**
392 Our study is one of the first in evaluate the directly effects of varying land cover of
393 temperate forests and agrosystems of avocado orchards on soil chemical properties and
394 local climatic variables, and their possible indirect effects on the leaf functional traits and
395 herbivory in *Q. castanea* and *Q. obtusata*. This is a very important approach for landscape
396 management. We emphasize the consequences of the change of land use from forests to
397 avocado orchards on functional traits of the oak species and their potential implications on
398 the individual performance of the oaks and their antagonistic interactions.
399
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684
685

686 **Table 1.**

687

688

Study sites	Latitude	Longitude	Forest-orchard ratio (%)
			689
Tancítaro	19° 16' 34" N	102° 22' 33.55" W	(77-23)
			690
Llanitos	19° 26' 0.52" N	101° 16' 38.08" W	(84-16)
			691
La Yacata	19° 26' 41.27" N	101° 16' 55.08" W	(74-26)
			692
El Peral	19° 27' 38.61" N	102° 1' 48.3" W	(51-49)
			693
El embrujo	19° 15' 53.77" N	101° 27' 41.34" W	(52-48)
			694
Huitzicho	19° 27' 13.3" N	102° 0' 53" W	(36-64)
			695
Las joyas	19° 13' 4.6" N	101° 25' 4.6" W	(35-65)
			696
Caramecuaro	19° 15' 38.3" N	101° 23' 43.7" W	(38-62)

697 **Table 2** a) Kruskal Wallis test for the comparison of soil nutrients between the different

698 forest/orchard coverages (Forest cover > Orchard, Forest = Orchard and Forest cover <

699 Orchard); b) All pairwise multiple comparisons (Dunn´s Method) of soil parameters

700 between the different forest/orchard coverages. Different letters indicate statistically

701 significant differences (P <0.05).

a) Kruskal-Wallis test

Soil nutrients	H	d.f.	$P <$
NH^{+1}	79.5	2	0.001
Mg^{+2}	101.5	2	0.001
NO_3^{-1}	75.9	2	0.001
P	114.6	2	0.001
P_2O_5	114.6	2	0.001
PO_4^{-2}	104.6	2	0.001
K	111.4	2	0.001
K_2O	142.1	2	0.001
SO_4^{-2}	86.1	2	0.001

b) Mean ± standard error

Soil nutrients	Treatments		
	Forest cover>Orchard	Forest cover=Orchard	Forest cover<Orchard
NH^{+4} (mg/l)	0.7 (±0.02)^a	0.5 (±0)^b	0.5 (±0.01)^b
Mg^{+2} (mg/l)	48.0 (±0.6)^a	48.1 (±0)^b	70.1 (±1.2)^c
NO_3^{-1} (mg/l)	7.9 (±0.3)^a	8.0 (±0)^a	57.1 (±0.7)^b
P (mg/l)	10.3 (±0.003)^a	12.5 (±0)^b	8.9 (±0.07)^b
P_2O_5 (mg/l)	23.4 (±0.01)^a	25.8 (±0)^b	20.7 (±0.3)^c
PO_4^{-2} (mg/l)	31.2 (±0.01)^a	33.8 (±0)^b	26.9 (±0.3)^c
K (mg/l)	9.4 (±0.02)^a	7.9 (±1.4^{-16})^b	5.8 (±0.2)^c
K_2O (mg/l)	11.8 (±0.05)^a	9.5 (±5.8^{-16})^b	6.8 (±0.3)^c
SO_4^{-2} (mg/l)	10.9 (±0.40)^a	6.9 (±4.4^{-16})^b	12.4(±0.7)^c

Table 2 ANOVA test results of the comparison of leaf traits and percentage of removed leaf area among the different forest/orchard coverages (Forest cover > Orchard, Forest = Orchard and Forest cover < Orchard) for *Q. castanea* and *Q. obtusata*.

	Quercus castanea			***Quercus obtusata***		
Response variable	d.f.	*F*	*P*<	d.f.	*F*	*P*<
Leaf thickness (mm)	2	29.8	0.0001	2	9.6	0.0001
Leaf dry weight (g)	2	15.6	0.0001	2	3.9	0.02
Leaf fresh mass (g^2cm^2)	2	8.8	0.0001	2	3.8	0.02
Leaf water content (g cm^2)	2	7.2	0.0001	2	19.9	0.0001
Leaf area (cm^2)	2	23.0	0.0001	2	36.6	0.0001
Specific leaf area ($cm^{-2} \cdot g^{-1}$)	2	4.2	0.01	2	12.5	0.0001
Chlorophyll (SPAD units)	2	7.5	0.0008	2	15.9	0.0001
Herbivory (%)	2	33.6	0.0001	2	50.6	0.0001

703 **Table 3** Pearson correlation coefficients obtained between the different foliar functional

704 attributes and the herbivory percentages for *Quercus castanea* (below the diagonal) and *Q.*

705 *obtusata* (above the diagonal) between the different forest/orchard coverages.

706

Leaf traits									
	LT	LDW	LFM	LWC	LA	SLA	CC	PRLA (%)	***Q. obtusata***
LT (mm)		0.13	0.22*	0.16	-0.13	-0.15	0.09	-0.11	
LDW (g)	-0.10		-0.09	-0.08	0.29*	0.67*	0.24*	0.19*	
LFM (g^2cm^2)	0.38*	0.13		0.57*	-0.08	-0.05	0.06	-0.02	
LWC (g cm^2)	0.23*	0.11	0.61*		-0.15	-0.10	-0.24*	-0.29*	
LA (cm^2)	-0.16	0.67*	-0.28*	-0.33*		0.67*	0.26*	0.51*	
SLA ($cm^{-2} \cdot g^{-1}$)	-0.08	-0.10	-0.45*	-0.45*	0.62*		0.09	0.31*	
CC (SPAD units)	-0.27*	0.06	0.04	-0.04	0.02	0.07		0.44*	
PRLA (%)	-0.26*	0.31*	-0.09	0.03	0.19*	-0.03	0.30*		
Q. castanea									

LT= Leaf thickness, LDW= Leaf dry weight, LFM= Leaf fresh matter, LWC= Leaf water content, LA= Leaf area, SLA= Specific leaf area, CC= Content of chlorophyll, PRLA= Percentage of removed leaf area $*P < 0.05$

Legends to figures

Fig. 1 The leaf economic spectrum (LES) conceptual framework and the expected variations in leaf functional traits along the gradient of forest cover/avocado orchard proportion. Leaf traits change from acquisitive to conservative as the proportion of forest cover decreases with fragmentation, with a concomitant decrease in herbivory levels.

Fig. 2 Geographical distribution of the study sites in the avocado belt in Michoacán state, México. The asterisks represent sites with higher forest cover than avocado orchards. The squares are the sites with similar proportion of forest cover and avocado orchards. Triangles represent the sites with less forest cover than avocado orchard. Pie graphs represent the forest (black) and avocado orchard (white) cover of each study site.

Fig. 3. Differences in the leaf functional traits and the herbivory percentage of *Q. castanea* and *Q. obtusata* individuals between different forest/orchard coverages (Forest cover > Orchard, Forest = Orchard and Forest cover < Orchard). (a) Leaf thickness (LT); (b) Leaf dry weight (LDW); (c) Leaf fresh mass (LFM); (d) Leaf water content (LWC); (e) Leaf area (LA); (f) Specific leaf area (SLA); (g) Content of chlorophyll (CC); (h) Percentage of removed leaf area (PRLA). Asterisks indicate significant differences between the oak species and forest/orchard coverages.

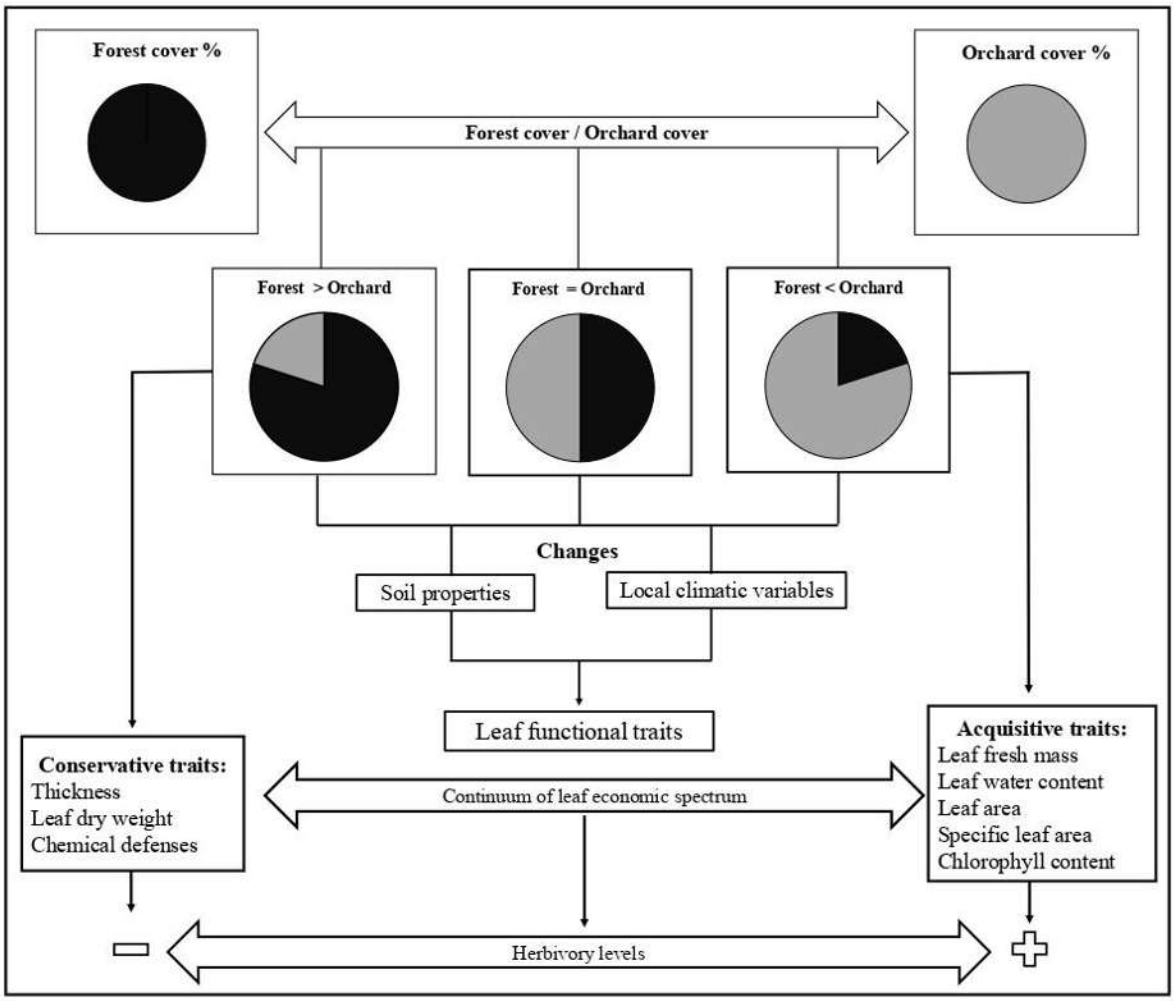
Fig. 4 Results of the principal component analyses of foliar functional traits and the herbivory percentage of *Q. castanea* (A) and *Q. obtusata* (B) and climatic variables among sites with different forest/orchard coverages. LT= Leaf thickness, LWD= Leaf dry weight, LFM= Leaf fresh matter, LWC= Leaf water content, LA= Leaf area, SLA= Specific leaf area, CC = chlorophyll content, PRLA = Percentage of removed leaf area, MAT= Mean

729 annual temperature, MAP= Mean annual precipitation, WQT=Wettest quarter temperature,

730 PWQ= precipitation of the wettest quarter and PDQ= precipitation of the driest quarter.

731

732 **Fig. 1**



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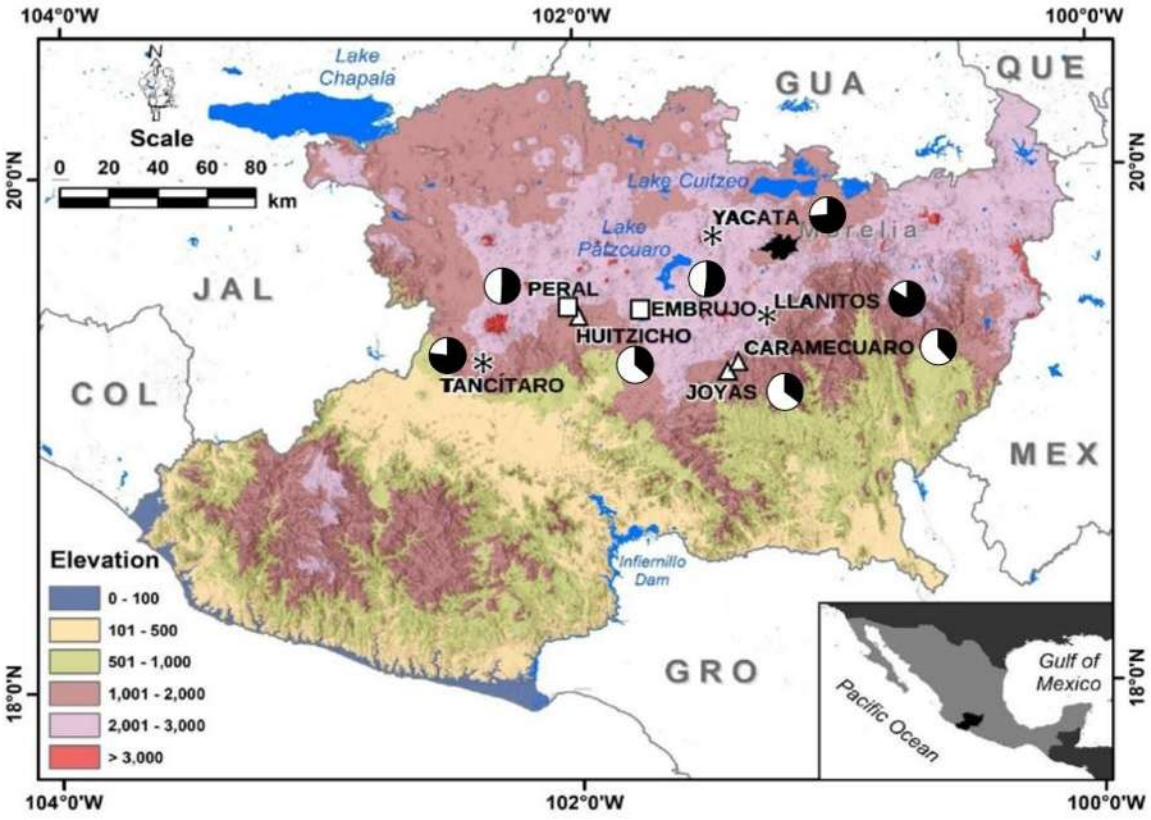
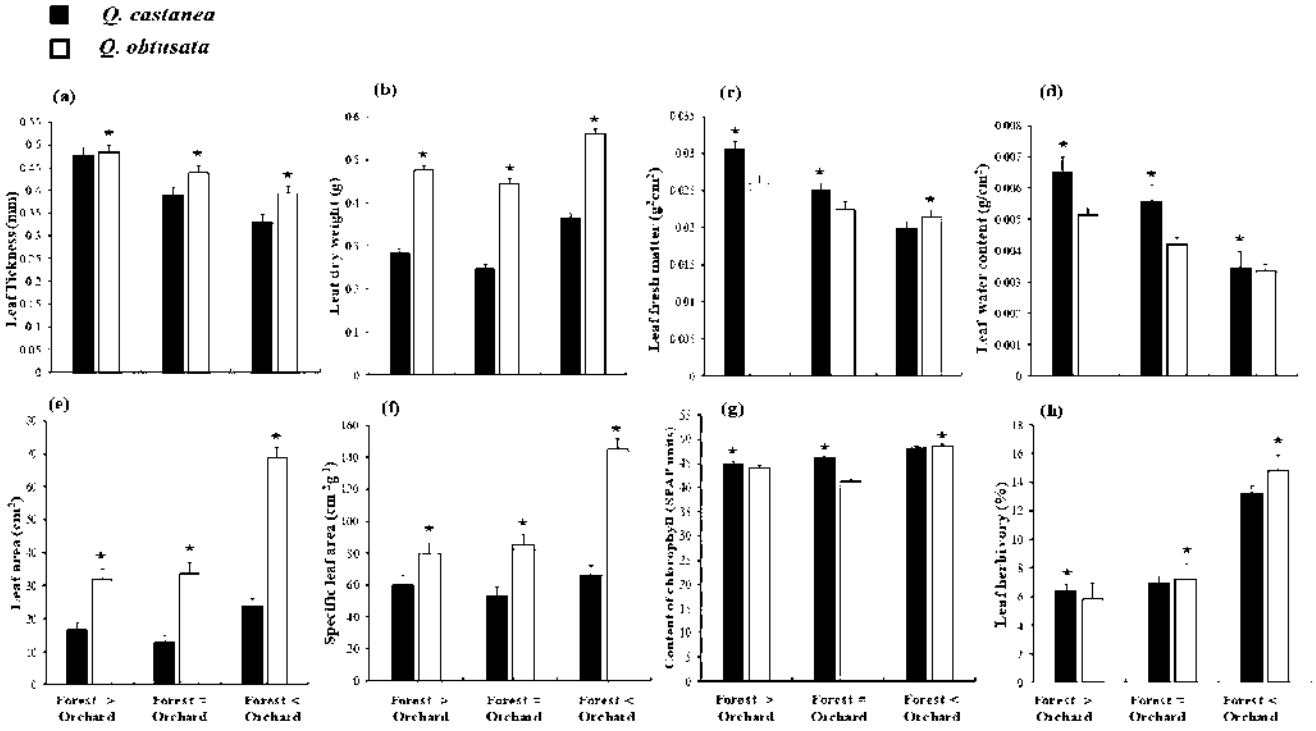
735 **Fig. 2**


104°0'W
102°0'W
100°0'W
20°0'N
18°0'N
Lake Chapala
Scale
0 20 40 60 80
km
GUA
QUE
Lake Cuitzeo
YACATA
Morelia
Lake Pátzcuaro
JAL
PERAL
EMBRUJO
LLANITOS
HUITZICHO
CARAMECUARO
TANCÍTARO
JOYAS
COL
MEX
Elevation
0 - 100
101 - 500
501 - 1,000
1,001 - 2,000
2,001 - 3,000
> 3,000
Infiernillo Dam
GRO
Gulf of Mexico
Pacific Ocean

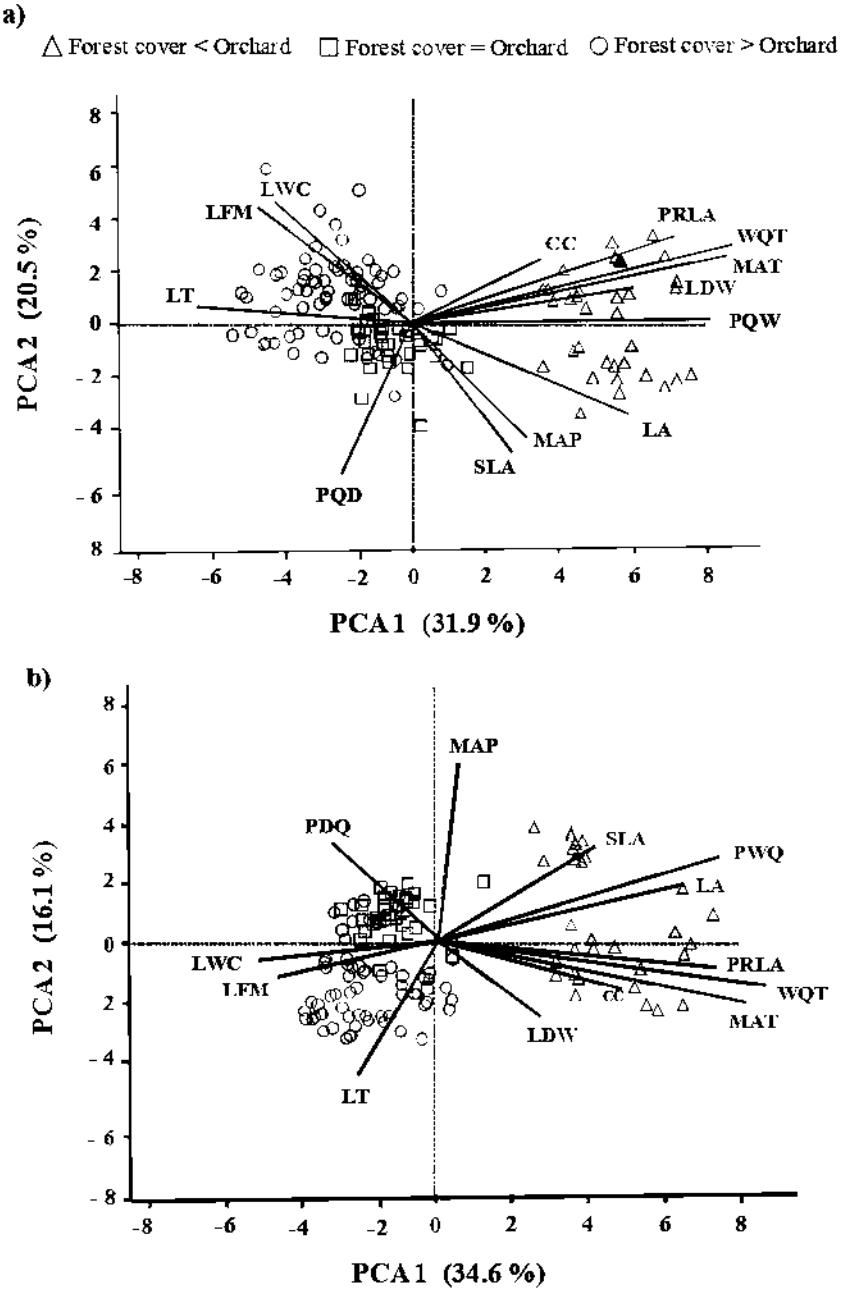
736

737 **Fig. 3**


Q. castanea
Q. obtusata
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Leaf Thickness (mm)
Leaf dry weight (g)
Leaf fresh matter (g/cm²)
Leaf water content (g/cm²)
Leaf area (cm²)
Specific leaf area (cm²g⁻¹)
Content of chlorophyll (SPAD units)
Leaf herbivory (%)
Forest > Orchard
Forest = Orchard
Forest < Orchard

738

739 **Fig. 4**


a)
△ Forest cover < Orchard
□ Forest cover = Orchard
○ Forest cover > Orchard
PCA2 (20.5 %)
PCA1 (31.9 %)
LWC
LFM
LT
PQD
CC
PRLA
WQT
MAT
LDW
PQW
LA
MAP
SLA
b)
PCA2 (16.1 %)
PCA1 (34.6 %)
MAP
PDQ
SLA
PWQ
LA
LWC
LFM
LT
LDW
PRLA
WQT
MAT
CC

740

Discusión general

La fragmentación por cambio de uso de suelo a agrosistemas provoca cambios en la calidad y atributos funcionales foliares en las plantas (Tuff, et al. 2016; Reinmann y Hutyra 2017; Bernaschini, et al. 2019), ya que los fragmentos presentan condiciones no óptimas para las plantas como alta temperatura y baja humedad relativa, disponibilidad de agua y fertilidad (Murcia 1995; Bernaschini et al. 2019). En nuestro estudio, los atributos funcionales relacionados con la disponibilidad de agua como grosor foliar, masa fresca foliar y contenido de agua foliar fueron mayores en los fragmentos de bosque de mayor tamaño, lo cual explica que fungen como reservorios de agua (Power 2010). Por otra parte, los atributos relacionados al crecimiento como peso seco de la hoja, área de la hoja y área foliar específica fueron mayores en el bosque menor a huertos debido a que son sitios abiertos, hay mayor disponibilidad de luz y arrastre de fertilizantes de magnesio, nitratos y sulfatos (Borgy et al. 2017; Faucon et al. 2017). Además, de que en esos sitios hubo mayor precipitación que favorecen el vigor de las plantas (Borgy et al. 2017).

Las condiciones no óptimas reducen la calidad de la planta y aumentan las defensas físicas y químicas (Cuevas-Reyes et al. 2013; Maldonado- López et al. 2015). Por ejemplo, la baja disponibilidad de agua, alta temperatura y la incidencia de radiación UV disminuyen la absorción y la cantidad de nitrógeno y carbono en las hojas provocando un cambio en la asignación de recurso en la planta a compuestos de defensa (metabolitos secundarios) como terpenos, alcaloides y fenoles (Niinemets 2015; Piasecka et al. 2017) modificando la preferencia de los insectos herbívoros (Kolb et al., 2016). La herbivoría puede ser influenciada por el aislamiento de los fragmentos, el tamaño de estos, así como por la composición de los remanentes de bosque (Tscharntke et al. 2002; Maguire et al. 2015). Se ha encontrado que los remanentes de bosque más conectados y más grandes comúnmente albergan una comunidad de herbívoros más diversa y abundante, pero tienden a tener menores niveles de herbivoría, esto debido al control por parte de sus depredadores naturales (fuerzas top-down) (Valdés-Correcher et al. 2019). En nuestro estudio, la herbivoría fue mayor en los sitios donde el área de fragmentos de bosque es menor a la de los huertos, para ambas especies de encinos. Nuestros resultados pueden deberse a que la fragmentación de la vegetación original afecta los procesos top-down, es decir, existe pérdida de enemigos naturales de los herbívoros como parasitoides (Schüepp et

al. 2014; Pfeifer et al. 2017; Anderson et al. 2019) y aves insectívoras (Ruiz-Guerra et al. 2012). Al disminuir estos depredadores, la abundancia y riqueza de insectos herbívoros incrementa sus poblaciones y los niveles de herbivoría (Anderson et al. 2019). Un patrón similar es lo encontrado por Maldonado-López et al. (2014) que reporta en *Q. castanea* mayor herbivoría en fragmentos de bosque pequeños, asumiendo que es posiblemente debido a una reducción en la abundancia de depredadores y parasitoides herbívoros ya que no se encuentra una correlación fuerte con la calidad nutricional y el metabolismo secundario (Maldonado-López et al. 2014). Por otra parte, un meta-análisis de De Carvalho Guimarães et al. (2014) concluye que el borde presenta espacios abiertos para la colonización de nuevas especies de plantas y animales que favorecen la apertura de nuevos nichos y con ello un aumento en la riqueza de insectos herbívoros generalistas ya que son sitios de recuperación posterior a la perturbación (Benítez-Malvido y Lemus-Albor 2005). Además, la migración de los insectos se da de los huertos hacia el borde de los fragmentos de bosque, producto de los pesticidas (Médiène et al 2011) lo cual podría estar ocurriendo en los fragmentos de bosque propiciando mayor herbivoría. También, el bosque menor a huertos y los bordes presentaron cambios en la cantidad (e.g. conectividad del hábitat, apariencia de la planta hospedera) y calidad (palatabilidad, calidad nutricional, defensa química) de la planta ya que se obtuvo mayor área foliar, contenido de clorofila, DAP y cobertura del dosel posiblemente al arrastre de fertilizantes y la mayor disponibilidad de luz (recursos) presentes en los fragmentos y bordes que podrían estar asignando las plantas al crecimiento, y de esa forma los insectos herbívoros podrían estar eligiendo por la mayor cantidad y calidad de las plantas (procesos bottom-up) (Nowak y Komor et al 2010; Rossetti et al. 2017).

Nuestros resultados, muestran que la calidad de la planta analizada como área foliar, diámetro a la altura del pecho, cobertura del dosel y clorofila, fue mayor y estuvo asociada en la cobertura de bosque menor a huerto y en el borde en ambas especies de encinos (*Q. castanea* y *Q. obtusata*). Esto se explica ya que los fragmentos pequeños y el borde presentan condiciones abiertas para la incidencia solar que se puede desarrollar mayor fotosíntesis y por consecuencia hojas más grandes, diámetro, cobertura del dosel y clorofila (Shinozaki et al. (1964a, b; Lohbeck et al. 2015; Reinmann y Hutyra 2017). Como lo reportado por Núñez (2014) que menciona que los encinos necesitan una mayor cantidad de luz que otras especies para desarrollar sus follajes. Otro ejemplo es Reinmann y Hutyra (2017) que encuentran que la calidad de la planta es

importante para el consumo foliar de los insectos en los fragmentos y el borde del bosque templado y que existe mayor disponibilidad de luz que ocasiona mayor tasa fotosintética y por consecuencia mayor crecimiento de la biomasa y la tasa de crecimiento anual (calidad) en *Quercus* spp. Un resultado similar fue lo encontrado por Maldonado-López et al. (2015) quienes encuentran que la cobertura y el DAP es mayor en el borde en una comunidad de encinos incluidas nuestras dos especies de estudio (*Q. castanea* y *Q. obtusata*) en el bosque templado. Otra posible causa es que pueda deberse a un posible arrastre de fertilizantes de las huertas hacia los fragmentos pequeños de vegetación de bosque nativo y borde (Pellissier et al. 2014) que podrían estar aumentando la calidad de estos árboles ya que se encontró mayor contenido de Mg^{+2}, NO_3^- y SO_4^{-2} en estas condiciones (Uzêda et al., 2016; Fried et al. 2018).

A las huertas a lo largo de su vida se les aplican fertilizantes para mejorar su producción (Boutin y Jobin 1998). Sin embargo, no siempre los fertilizantes son fijados en las huertas, sino que existe arrastre por la acción del viento y lluvia hacia el bosque adyacente (Fried et al. 2018). Prueba de ello, son los trabajos en condiciones controladas de Pellissier y colaboradores (2014), los cuales encuentran una mayor área foliar específica y altura del dosel en comunidades de plantas adyacentes a parcelas a las que fueron aplicados fertilizantes nitrogenados; llevando a un déficit de calcio y fósforo en las plantas. Este desbalance de nutrientes puede generar cambios en la asignación de recursos de crecimiento en las plantas expresado en mayores tasas de crecimiento, altura, DAP y producción de hojas (Blondeel et al. 2019); lo cual es soportado por lo propuesto por la Hipótesis de Asignación de Recursos (Coley et al. 1985), que predice un crecimiento más rápido y mayor producción de hojas más grandes en sitios con mayor disponibilidad de recursos, como un aumento en la disponibilidad de nitrógeno. Así, estos sitios representan islas potenciales de gran disponibilidad de nutrientes del suelo que afectan el crecimiento de los encinos; resultando ser más vigorosos (Baxendale et al. 2014).

La fragmentación de la cobertura vegetal por el cambio de uso de suelos provoca estrés en las plantas que se refleja en cambios asimétricos y morfológicos de acuerdo a la capacidad de tolerar el estrés abiótico (Zvereva et al., 1997; Freeman et al., 2004; Cuevas-Reyes et al. 2013; Cuevas-Reyes et al. 2018b). En nuestro estudio, la AF fue mayor en los fragmentos de bosque pequeño en el borde apoyando estos resultados. Además, la AF en plantas responde a factores como disturbios del hábitat (Maldonado-López et al.2019), fertilidad del suelo (Cuevas-

Reyes et al.2018b), y la herbivoría (Cuevas-Reyes et al. 2011a, b, 2018), condiciones y eventos presentes en los fragmentos de bosque pequeño en nuestro trabajo. De igual forma, las hojas fueron más anchas y alargadas y asimétricas en los fragmentos de bosque más pequeños y borde. Los cambios en la morfología y AF foliar pueden deberse al efecto de la deficiencia de agua (Freeman et al., 2004), diferencias ambientales (Álvarez et al. 2009; González-Rodríguez & Oyama, 2005) y la fragmentación (Martínez-Munguía et al. 2015) concordando con nuestro estudio ya que en los fragmentos más pequeños de bosque estuvo asociado el bajo contenido de agua foliar, la materia fresca foliar y la alta temperatura. Se sugiere también que estos cambios podrían ser por la posible mayor disponibilidad de luz y fertilizantes nitrogenados encontrados en el bosque menor a huertos y el borde como Mg^{+2}, NO_3^- de acuerdo a la hipótesis de disponibilidad de recurso que ocasiona que las hojas sean más grandes (Coley et al. 1985). En general, detectamos cambios en la morfología foliar y altos niveles de AF en las dos especies de encinos en los fragmentos de bosque pequeño y mayor cobertura de huertos sugiriendo que existe una respuesta fenotípica debido a las condiciones ambientales y propiedades del suelo cambiantes locales debido a la mayor cobertura de huertos.

Por otra parte, nuestras dos especies de encinos mostraron una relación positiva entre herbivoría y AF. Algunos estudios han encontrado ese patrón (Cornelissen et al. 2003; Cuevas-Reyes et al.2018b; Aguilar-Peralta et al. 2020) siendo la AF en las hojas la causa de la herbivoría (hipótesis del estrés de las plantas) que menciona que la calidad nutricional de la hoja y la concentración de metabolitos secundarios influye en la selección de la hoja por parte de los insectos herbívoros, es decir, el insecto preferirá una hoja con mayor calidad nutricional y menores concentraciones de metabolitos secundarios que está dada por la AF (Cornelissen and Stiling 2011). De nuestras variables de calidad de la planta medidas no encontramos relación con la AF, lo cual podría sugerirnos que el insecto herbívoro no elige las hojas asimétricas por la calidad nutricional. Otra explicación de la relación herbivoría y AF es la herbivoría generando AF (hipótesis de herbivoría generando estrés) es decir, que la presión de los insectos herbívoros y alto consumo ocasiona que la hoja se vuelva asimétrica (Møller and Shykoff 1999). Sin embargo, en nuestro trabajo no podemos decir que la herbivoría cause la AF. Es necesario realizar estudios que incluyan otras variables de calidad nutricional de la hoja y los metabolitos secundarios, así como la medición de la AF bajo un escenario de herbivoría no acumulada. Además, la herbivoría estuvo correlacionada con el DAP, cobertura, clorofila y tamaño de la

hoja en nuestro estudio, lo cual soporta la hipótesis del vigor de la planta de Price (1991) la cual menciona que plantas con mayor calidad tendrán una mayor abundancia de insectos herbívoros debido a que presentan una posible mayor cantidad de recursos, calidad nutricional y menor cantidad de metabolitos secundarios. Por lo tanto, en nuestro trabajo creemos que los mayores porcentajes de herbivoría en *Q. castanea* y *Q.obtusata* se deben a la calidad de la planta. Este patrón podría atribuirse a una mayor disponibilidad del recurso para los herbívoros; donde la herbivoría podría ser modulada por una mayor cantidad en la disponibilidad de recursos de plantas hospederas (fuerzas bottom-up) (e.g. conectividad del hábitat, apariencia de la planta hospedera) y la calidad del recurso de las plantas hospederas (palatabilidad, calidad nutricional, defensa química) (Maron and Crone 2006; Ruiz-Carbayo et al. 2020). Adicionalmente, se ha observado que los insectos eligen la forma de la hoja que está relacionada con la palatabilidad, por ejemplo, en mariposas *Heliconius* las hembras eligen un tipo de hoja para ovipositar resultado de la apariencia visual (Dell'Aglio et al. 2016; Higuchi and Kawakita 2019).

El cultivo de aguacate ha ido en aumento debido a la derrama económica que genera, sin embargo, esto ocasiona una pérdida del bosque templado, donde algunos de los organismos afectados son los encinos (SAGARPA 2017; Scanes 2018; SADER-ASERCA-SIMA 2019). Por ello, es necesaria la incentivación del gobierno a los productores del sector forestal por pago de servicios ambientales del bosque, así como la creación de áreas naturales protegidas, debido a la función ambiental que representan (Bravo et al. 2009). En este estudio, a pesar de que las dos especies de encinos muestreadas pertenecen a secciones distintas, *Quercus castanea* (encino rojo) y *Quercus obtusata* (encino blanco) y su rango de plasticidad y tolerancia al estrés biótico y abiótico es diferente, ya que *Q. castanea* es menos tolerante al estrés por sequía que se refleja en su distribución (Cavender-Bares et al 2004; Renninger et al. 2013; Aranda et al. 2014) y es menos defoliada que *Q. obtusata* (Dillaway and Stringer, 2003; Ohio DNR, 2005), ambas se vieron afectados por la fragmentación. Por lo que se recomienda que se conserven los fragmentos de bosque adyacentes a los huertos ya que son sitios de reservorio de agua y alojamiento de insectos benéficos que mantienen la diversidad y los servicios ecosistémicos además del mantenimiento y la producción de los cultivos, así como la mitigación del cambio climático.

La fragmentación por agrosistemas modifica los atributos funcionales de las hojas de los encinos, ya sea por las modificaciones de las condiciones ambientales o la lixiviación de

fertilizantes al bosque cambiando el contenido de nutrientes en la hoja de los encinos y por consecuencia la palatabilidad de los insectos herbívoros (Borgy et al. 2017; Faucon et al. 2017), la fragmentación del bosque por agrosistemas podría estar disminuyendo los depredadores de los insectos herbívoros lo que podría aumentar su distribución (Schüepp et al. 2014; Pfeifer et al. 2017; Anderson et al. 2019), a su vez los encinos en los fragmentos pequeños podrían tener consecuencias en su sobrevivencia y reproducción a largo plazo al ser mayormente defoliados lo que podría mermar sus poblaciones (Moreira et al 2019). Se concluye que la conversión de bosque templado a huertas de aguacate tiene importantes consecuencias en las propiedades del suelo incrementando la cantidad de nitratos. Además del cambio en las condiciones ambientales que influencian la cantidad y calidad del recurso de *Q. castanea* y *Q.obtusata* afectando las interacción bióticas como la herbivoría en fragmentos de bosque pequeño y mayor cobertura de huertos.

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