UNIVERSIDAD MICHOACANA DE SAN NICOLÁS DE HIDALGO

INSTITUTO DE INVESTIGACIONES SOBRE LOS RECURSOS NATURALES

# “REDES TRÓFICAS DE INSECTOS INDUCTORES DE AGALLAS Y SUS PARASITOIDES ASOCIADOS A ENCINOS EN UN MOSAICO DE AGROSISTEMAS DE AGUACATE”.

## TESIS

Que presenta:

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Como requisito para obtener el título profesional de

**Maestra en Ciencias en Ecología Integrativa**

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Morelia, Michoacán abril de 2023.

## DEDICATORIA

A MIS PADRES:

GRISELDA DUEÑAS Y JESÚS PRIETO

# AGRADECIMIENTOS

Agradezco profundamente a mi asesora, la Dra. Yurixhi Maldonado López, por haber confiado en mí, por apoyarme en todo momento a pesar de mis equivocaciones y por no haberme abandonado, por sus llamadas de atención cuando lo merecía, además de su enorme paciencia y por el conocimiento que compartió conmigo en este proceso y desde la licenciatura.

A mi co-asesor el Dr. Pablo Cuevas Reyes, por todos los consejos que me dio, el tiempo que dedicó a atender mis dudas y por ayudarme a enamorarme de las agallas. Además de brindarme su amistad y siempre pensar en mí para proyectos futuros y oportunidades. Espero que vengan muchos años más de esta bonita amistad y que podamos hacer más ciencia juntos.

A los miembros de mi comité, el Dr. Rafa, la Dra. Sofía Vaca y el Dr. Leo, por su disponibilidad siempre para mis evaluaciones tutoriales y por las observaciones que hicieron a mi trabajo, las cuales me ayudaron a mejorarlo y también por su paciencia en las clases.

A mis compañeros del Laboratorio de Ecología de Interacciones Bióticas (LEIB), Sofi, Paloma, Joan, Isa, Jenny y Lupita. Por su apoyo en todo mi proceso de maestría, ya sea para aclarar dudas, ayudarme con cosas que no entendía, con el trabajo de campo y por supuesto, por brindarme su amistad.

También quiero agradecer a mi familia, a mi mamá, mi abue, a mi hermana y a mi padre por todo su apoyo, en general.

También un agradecimiento muy especial a los pocos amigos de fuera del laboratorio, a los pocos que siguen a mi lado a pesar de que no tuve tiempo para ellos en estos dos años.

Gracias a todas las personas que hicieron este logro posible.

# RESUMEN

Los ecosistemas forestales templados representan sitios con una gran diversidad de organismos y de interacciones bióticas. Sin embargo, se encuentran fuertemente amenazados por factores antropogénicos, principalmente por el cambio de uso de suelo. Particularmente, en Michoacán, los ecosistemas forestales templados están amenazados y han sido afectados por la conversión de bosques nativos a monocultivos de aguacate, los cuales, provocan fragmentación. Dicha fragmentación provoca cambios en las condiciones climáticas locales, afectando directamente a la incidencia y diversidad de las interacciones bióticas de insectos herbívoros como es el caso de los insectos inductores de agallas y sus parasitoides. Por lo tanto, el objetivo de este trabajo fue determinar los cambios en la estructura y diversidad de los ensamblajes tritróficos de insectos inductores de agallas y sus parasitoides asociados a encinos en sitios con diferentes proporciones de cobertura de bosque y huertos de aguacate en Michoacán. Seleccionamos dos sitios con menor cobertura de bosque que de huerto, dos sitios con igual proporción de cobertura de bosque que de huerto y otros dos sitios con una mayor cobertura de bosque que de huerto y en cada sitio realizamos muestreos sistemáticos de las agallas de *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* para obtener los datos de abundancia y riqueza para la construcción de las redes tritróficas. Descubrimos que los cambios en las variables climáticas tienen un efecto positivo sobre el vigor de las plantas, coincidiendo con que encontramos una mayor diversidad de morfoespecies de agallas en los sitios que presentan una menor cobertura de bosque que de huerto en comparación con las otras condiciones de cobertura forestal. En el caso de los parasitoides, encontramos el patrón opuesto al de las morfoespecies de agallas.

Las redes tróficas de los sitios con mayor proporción de bosque que de huerto presentan una mayor complejidad estructural sugiriendo la presencia de especies generalistas de parasitoides en comparación con las redes de los sitios con menor cobertura de bosque que de huerto, en las cuales podemos inferir la presencia de especies especialistas de parasitoides. Concluimos que la fragmentación de los bosques tiene un efecto negativo sobre las interacciones bióticas de los insectos inductores de agallas y sus parasitoides y resaltamos la necesidad de preservar los remanentes de bosque nativo de la franja aguacatera de Michoacán.

**Palabras clave:** Interacciones bióticas, Fragmentación, Ensamblajes tróficos, *Quercus*, Cultivos de aguacate, Morfoespecies de agallas.

# ABSTRACT

Temperate forest ecosystems represent sites with a great diversity of organisms and biotic interactions; however, they are surely threatened by anthropogenic factors land use change. Particularly in Michoacán, temperate forest ecosystems have been affected by the conversion of native forests to avocado monocultures, which cause fragmentation. Such, may provoke changes in local climatic conditions directly favoring the incidence and diversity of biotic interactions of herbivorous insects such as is the case of gall-inducing insects and their parasitoids. Therefore, the objective of this study was to determine the changes in the structure and diversity of tritrophic assemblages of gall-inducing insects and their parasitoids associated with oaks in sites with different proportions of forest cover and avocado orchards in Michoacan. We selected two sites with less forest cover than orchards, two sites with the same proportion of forest cover as orchards, and two other sites with greater forest cover than orchards, and at each site we systematically captured all visible galls of *Q. castanea, Q. obtusata and Q. magnolifolia* to obtain abundance and richness data for the construction of tritrophic networks. We detected that the changes in the climatic variables have a positive effect on plant vigor, according with the fact that we detected a greater diversity of morphospecies of galls in the sites that present a lower forest cover than in orchards in comparison with the other conditions of forest cover. In the case of parasitoids, we found an opposite pattern. The tritrophic networks for sites with higher proportion of forest cover than orchards present a greater structural complexity, suggesting the presence of generalist species of parasitoids in comparison with the networks of the sites with less forest than orchard cover, in which we can assume the presence of parasitoids specialist species. We conclude that forest fragmentation has a negative effect on the biotic interactions of gall-inducing insects and their parasitoids, and we highlight the need to preserve the remnants of native forest in the avocado belt of Michoacán.

**Key words:** Biotic interactions, Fragmentation, Trophic assemblages, *Quercus*, Avocado orchards, Gall morphospecies.

# INTRODUCCIÓN GENERAL

Los Ecosistemas Forestales Templados (EFTs) son el bioma forestal más extenso en México, ocupando aproximadamente el 16% de la superficie del país (CONABIO, 2022), además, se distribuyen a lo largo de todo el país, por lo regular en zonas montañosas con temperaturas promedio entre 12 y 23 °C y entre los 2000 y 3400 msnm (CONABIO, 2017). Los EFT se encuentran conformados por diversos tipos de vegetación como son los bosques de coníferas, los bosques de abeto-oyamel, los bosques de oyamel, los bosques de encinos y los bosques mixtos de pino-encino (Arasa-Gisbert et al., 2018). Además de albergar una gran biodiversidad, los EFTs prestan importantes servicios ecosistémicos como la regulación climática e hídrica (Lucas-Borja y Delgado-Baquerizo, 2019; Yuan et al., 2020), la captura de carbono (Kasper et al., 2021), la retención del suelo y la generación de oxígeno, sin mencionar que también son soporte para la protección del medio ambiente y el bienestar humano (Zimbres et al., 2017; Monárrez-González et al., 2018).

A pesar de su importancia, los EFT actualmente se encuentran fuertemente amenazados por múltiples factores, como la creciente expansión de la urbanización, la deforestación, el cambio climático global y el cambio de uso de suelo principalmente por la introducción de agrosistemas que provocan fragmentación en los ecosistemas forestales templados y amenazan su biodiversidad (Aguilar et al., 2019). Particularmente en México, el cultivo de aguacate se ha reconocido como una de las principales causas de la fragmentación en los EFTs, debido a la creciente demanda de esta fruta a nivel global en las últimas décadas (Denvir, 2022; Denvir, 2023).

## Efectos de la fragmentación de los EFT

La fragmentación es un proceso dinámico en el que el bosque se reduce progresivamente a parches de diferentes tamaños, perímetros y grados de aislamiento (Lindenmayer y Fischer, 2006; Fahrig, 2017; García-Jain et al., 2022). De esta manera los fragmentos de bosque sufren cambios bióticos y abióticos de manera rápida y abrupta, tales como cambios en las condiciones micro-climáticas como el incremento de la temperatura y la velocidad del viento, mientras que la humedad y la fertilidad del suelo disminuyen de manera considerable (Haddad et al., 2015; Fletcher et al., 2018). Por lo general, la disminución en el área de los fragmentos tiene consecuencias para la biodiversidad, alterando significativamente la dinámica de las poblaciones y la estructura y composición de las comunidades (Farwig et al., 2006; García-Jain et al., 2022).

Por ejemplo, se ha reportado que la diversidad de insectos herbívoros puede aumentar debido a la pérdida de enemigos naturales en sitios que presentan un mayor grado de fragmentación, ya que los enemigos naturales, como es el caso de los depredadores o parasitoides son extremadamente sensibles a la pérdida del hábitat (Pfeifer et al., 2017; Pérez-Solache et al., 2023). También se ha reportado el caso contrario, en el que puede que la diversidad de insectos herbívoros disminuya debido a los cambios en la cantidad de recursos para las plantas en sitios más fragmentados (Maguire et al., 2016; Maldonado-López et al., 2016).

## Efectos de la Fragmentación sobre las interacciones bióticas

Las interacciones bióticas en los EFTs están reguladas por las fuerzas “Bottom-up” y “Top-down”, que son dos mecanismos principales que controlan la estructura de estas interacciones (Heath et al., 2014; Terborgh, 2015). El mecanismo de la fuerza “Top-down” determina que los niveles tróficos superiores (e.g. depredadores y parasitoides) controlan la biodiversidad y la biomasa de los niveles tróficos inferiores a través del efecto de cascada trófica (Estes et al., 2011), proceso en el cual, una perturbación se propaga hacia arriba o hacia abajo dentro de una red de interacciones alternando efectos positivos y negativos en niveles sucesivos (Terborgh et al., 2006).

Por ejemplo, se ha observado que, en las redes tróficas de plantas-herbívoros-parasitoides, los enemigos naturales de los insectos herbívoros, como son los parasitoides, juegan un papel fundamental ya que imponen una alta mortalidad en los insectos herbívoros, regulando sus poblaciones (Maguire et al., 2016; Nicholls et al., 2018). Por otro lado, el mecanismo de la fuerza “Bottom-up” enfatiza que la biodiversidad y la biomasa están determinadas por la limitación de los recursos de los niveles tróficos inferiores, el estrés abiótico o la defensa como es el caso de los metabolitos secundarios de las plantas (Enge et al., 2012; Harvey y MacDougall, 2015). Los efectos bottom-up alteran la composición y diversidad de las especies de los niveles tróficos superiores (Haddad et al., 2015; Collins et al., 2017) y estos cambios en las plantas hospederas pueden potencialmente modificar las comunidades de insectos herbívoros y sus interacciones bióticas.

En este sentido, se ha propuesto que los cambios en la calidad y cantidad de las plantas es un factor que incide en la estructura y composición de las comunidades de insectos herbívoros (García-Jain et al., 2021). Esto coincide con la "Hipótesis del Vigor de la Planta" (HVP) (Price, 1991), la cual propone que los insectos herbívoros prefieren alimentarse de plantas con mayor tamaño y crecimiento porque estas tienen una mayor calidad nutricional, lo cual favorece el desempeño y reproducción de los insectos herbívoros (Price, 1991). La fragmentación de los ecosistemas forestales templados genera cambios en la cantidad de recursos para los insectos como el tamaño de la planta y la cobertura del dosel, así como en la calidad de la planta hospedera como el contenido de clorofila pueden afectar la preferencia, abundancia y distribución de los insectos herbívoros (Endara y Coley, 2011; Maldonado-López et al., 2016; García-Jain et al., 2021).

Un ejemplo, es que se ha observado que el vigor de la planta en bosques templados de arce azucarero entremezclado con cultivos de maíz y soya puede disminuir debido a la fragmentación provocada por los cultivos, disminuyendo la diversidad de insectos herbívoros (Maguire et al., 2016). Además, se ha encontrado que, en fragmentos pequeños de bosque, el vigor de las plantas, como es el caso de los encinos, expresado en contenido de clorofila, área de la hoja, cobertura del dosel y en diámetro a la altura del pecho, aumenta y se relaciona de manera positiva con la herbivoría, indicando que los mecanismos que impulsan las interacciones bióticas dependen de la escala, variando entre tamaños de los fragmentos y entre los tipos de hábitat (García-Jain et al., 2021).

Se ha reportado que, en sitios fragmentados, los insectos herbívoros son altamente sensibles a los cambios en las condiciones ambientales (Maldonado-López et al., 2016;

García-Jain et al., 2021) y su abundancia aumenta como resultado de la reducción de los depredadores y parasitoides en ambientes fragmentados (Pfeifer et al., 2017).

## Insectos inductores de agallas asociados a especies de encinos

Dentro del grupo de los fitófagos, los insectos inductores de agallas (IIA) son fitófagos endófagos especialistas que son capaces de inducir modificaciones morfológicas y fisiológicas en células, tejidos u órganos vegetales a las cual se les denomina agallas (Ergan et al., 2018; Kot y Rubinowska, 2018; Ferreira et al., 2019). Las agallas se inducen a través de estímulos químico-ecológicos con sus plantas hospederas a través de secreciones salivales al momento de la alimentación (Price et al., 1988; Raman, 2021) , produciendo los fenómenos de hipertrofia e hiperplasia en las plantas hospederas (Ferreira et al., 2019; Jara-Chiquito et al., 2021) beneficiando al inductor y a su descendencia ya que las agallas les confieren recursos para alimentación (Susuki et al., 2009; Guiguet et al., 2018), un microhábitat estable (Blanche, 2000) y protección contra enemigos naturales (Price, 1998).

La capacidad de inducir agallas evolucionó en siete órdenes diferentes, siendo los más comunes y diversos Hemiptera, Hymenoptera y Diptera, y en menor proporción se incluyen los órdenes Coleoptera, Lepidoptera y Thysanoptera (Grandez-Rios et al., 2015) siendo los cinípidos (Hymenoptera: Cinipidae) los principales inductores de agallas asociados a encinos del género *Quercus* (Nieves-Aldrey y Medianero, 2011).

Los cinípidos son avispas inductoras de agallas (Hymenoptera: Cynipidae: Cynipini) (Nicholls et al., 2018; Tang et al., 2020; Vila et al., 2022), son por mucho el grupo de avispas inductoras de agallas más rico en especies con alrededor de 1400 especies conocidas comprendiendo 41 géneros en todo el mundo y, están altamente asociadas a Fagáceas, principalmente del género *Quercus* (Pujade-Villar et al., 2009; Nieves-Aldrey y Medianero, 2011). Estos organismos poseen una alta especificidad con sus plantas hospederas, ya que consideran factores como el tamaño, el vigor de la planta y el genotipo de las plantas para seleccionarlas como su huésped (Maldonado-López et al, 2016; Knuff et al., 2019; Harris y Pitzschke, 2020). La distribución de los inductores está fuertemente relacionada con la distribución de las plantas hospederas (Stone et al, 2002; Sahchar et al., 2018). Se clasifican en seis tribus: La tribu Aylacini, tribu Eschatocerini, tribu Pediaspidini, tribu Diplolepidini, y la tribu Cynipini que es la asociada a la inducción de agallas en encinos (Medianero y Nieves-Aldrey, 2011).

Los cinípidos son capaces de inducir agallas en diversos tejidos de los encinos como tallos, hojas, amentos y raíces (Stone y Hayward, 2005). Esto ocurre cuando la hembra oviposita en el tejido vegetal y libera señales químicas (Price, 2005) que inducen a la planta a formar la agalla mediante los procesos de hipertrofia que es el crecimiento anormal de las células y la hiperplasia que es la multiplicación anormal de las células (Ferreira et al., 2019; Jara-Chiquito et al., 2021). Una vez que la respuesta químico-ecológica tuvo lugar en la planta hospedera y la agalla se formó, la progenie de la hembra comenzará a desarrollarse dentro de la agalla (Stone et al., 2009). Actualmente, se conocen alrededor de 1400 especies descritas de cinípidos (Ronquist et al., 2015; Penzes et al., 2018) y cada una de ellas puede inducir una agalla con morfología única, incluso se puede considerar la morfología de la agalla para identificar al insecto inductor (Grandez-Rios et al., 2015). Las comunidades de agallas inducidas por cinípidos son de alto interés, ya que representan un sistema definido y cerrado, pero no necesariamente fácil de comprender, ya que las agallas representan un microcosmos para los cinípidos porque estas estructuras les aportan nutrientes para alimentación, protección contra depredadores y condiciones ambientales adecuadas para su desarrollo (Maldonado-López et al., 2013).

En hábitats fragmentados, se ha reportado que los árboles adultos de encinos se pueden beneficiar del incremento de luz disponible en los bordes de los fragmentos aumentando su vigor y alterando la incidencia de los insectos herbívoros, como es el caso de los insectos inductores de agallas, los cuales tienen su ciclo de vida sincronizado con la producción de órganos de la planta huésped para que se permita la inducción de las agallas, resaltando que la calidad de los encinos hospederos es significativamente mayor en encinos aislados y en fragmentos de bosque pequeños (Maldonado-López et al., 2016).

En diversos trabajos se ha abordado el efecto de la fragmentación sobre la incidencia de los insectos inductores de agallas y se ha reportado que, las poblaciones de estos organismos parecen beneficiarse de los efectos provocados por la fragmentación de los ecosistemas. Ya que se ha encontrado una mayor densidad de agallas en remanentes pequeños de bosque, en comparación con la densidad que se encuentra en sitos con fragmentos de bosque mayores (Chust et al., 2007; Maldonado-López et al., 2015; Altamirano et al., 2016)

Además de los cinípidos, algunos dípteros de la familia Cecidomyiidae, comúnmente conocidos como moscas de las agallas, son capaces de inducir estas estructuras en plantas de la familia Fagaceae como los encinos, aunque en menor medida que los cinípidos (Cole & Harris, 2002; Khaustov et al., 2022).

Uno de los grupos que pueden beneficiarse de las agallas es el de la fauna secundaria, estos organismos son aquellos que hacen uso de las agallas sin tener interacciones tróficas obligadas. Otro grupo es el de la fauna terciaria, son aquellos que son depredadores de la fauna secundaria (Serrano-Muños et al., 2022).

La fauna primaria es la encargada de establecer las agallas y también incluye diversos grupos de inquilinos y parasitoides. Por lo general, los inquilinos son otros cinípidos, principalmente de la tribu Synergini y algunas especies de cecidómidos, lepidópteros y coleópteros (Nieves-Aldrey, 1988). En cambio, los parasitoides que se conocen por atacar agallas de cinípidos, principalmente incluyendo himenópteros de la familia Chalcidoidea, quienes regulan las tasas de mortalidad (Askew et al., 2015; Serrano-Muñoz et al., 2022).

Una vez que la fauna primaria abandona las agallas, la fauna secundaria compuesta de otros organismos como arácnidos, áfidos y otros himenópteros (hormigas y avispas no parasitoides), habitan las agallas (Pujade-Villar, 2013; Serrano-Muñoz et al., 2017; Serrano-Muñoz et al., 2022). Debido al gran valor ecológico de las agallas, estas se han propuesto como “hotspots” de la diversidad de artrópodos. (Pujade-Villar, 2013; Serrano-Muñoz et al., 2022). En este sentido, las comunidades asociadas a las agallas están estructuradas por varios niveles tróficos, formando complejas redes de interacciones (Sánchez et al., 2013).

## Redes de interacciones tróficas

Los insectos herbívoros forman parte fundamental de las redes tróficas y comprenden la mayor porción de la biodiversidad. Las redes tróficas, son uno de los conceptos centrales dentro de la literatura ecológica (Lindeman, 1942) y los modelos de redes de interacciones tróficas constituyen un marco adecuado y a la vanguardia para estudiar la estructura de las comunidades. Gracias a esta herramienta, los ecólogos pueden concentrar su atención en las conexiones tróficas entre las especies y el flujo de energía y poder entender cómo se organizan los organismos dentro de las comunidades (Lawler y Morin, 1993), las cuales están asociadas con plantas hospederas específicas están influenciadas por las fuerzas ejercidas por el primer nivel trófico, así como por las presiones de los niveles tróficos superiores, especialmente los insectos herbívoros, interactúan de forma indirecta a través de las interacciones con depredadores o parasitoides (de Siqueira Neves et al., 2011).

Jordano (2009), define las redes de interacciones planta-animal como el conjunto de dos tipos de elementos, los nodos o vértices que representan a las especies y los enlaces sobre ellos, dónde cada nodo es conectado por los enlaces. En ese sentido, las interacciones en la comunidad pueden ser representadas de manera gráfica para ayudarnos a visualizar la compleja red de interacciones y además de proveer herramientas para la búsqueda de patrones que nos permitan comprender la complejidad de las interacciones en las comunidades (Jordano et al., 2009). Específicamente, las redes de interacción planta-animal son redes bipartitas que están conformadas por dos conjuntos distintos de nodos (plantas y animales) que nos muestran las interacciones entre los nodos de los distintos grupos (Newman et al., 2004).

La mayoría de las redes tróficas ilustradas en interacciones bióticas se han encaminado a la construcción de redes cuantitativas (vanVeenet et al., 2006; Hirao, 2008; Novotny et al., 2010). Sin embargo, pocos estudios se han realizado estudiando interacciones antagónicas sobre la estructura hospedero-parasitoides, como el caso de los áfidos (Jafari et al., 2020; Venancio et al., 2020) y menos se han realizado estudiando insectos inductores de agallas, especialmente en sistemas templados. Por ejemplo, Maldonado-López et al., (2022), realizaron redes de interacciones tritróficas en un complejo híbrido de dos especies de encinos en bosques templados mexicanos, ellos pudieron corroborar que la hibridación de los encinos genera cambios en su composición genética y que eso a su vez, influye en las redes tróficas de los encinos con los insectos inductores de agallas y sus parasitoides asociados.

## Fragmentación de los EFTs por cultivos de aguacate

Más de 100,000 ha de ecosistemas forestales templados se han transformado debido al cambio de uso de suelo para agricultura en nuestro país. La demanda global del aguacate ha incrementado de manera significativa en las últimas décadas (Denvir.2022; Denvir, 2023), la variedad más cotizada es el aguacate Hass, el cual se cultiva en los ecosistemas forestales templados de México en la zona denominada Franja aguacatera, la cual comprende varios estados de la república mexicana., siendo Michoacán y Jalisco los únicos estados que cuenta con permiso de exportación, dándose en Michoacán aproximadamente el 85% de la producción nacional y el equivalente a aproximadamente 2.98 billones de dólares (Statista, 2022).Lamentablemente, el desarrollo de la franja aguacatera en Michoacán ha generado una alta tasa de conversión de los EFTs a huertos de aguacate de aproximadamente 700 ha/año, generando un mosaico de remanentes de bosque entremezclados con huertas de aguacate (Cho et al., 2021; Pérez-Solache et al., 2023).

La fragmentación de los EFTs a causa de la producción aguacatera se caracteriza por generar cambios como en los factores bióticos y abióticos (Haddad et al., 2015) como el aumento de la temperatura, la radiación solar y la velocidad del viento, mientras que la humedad y la fertilidad del suelo disminuyen (Tuff et al., 2016; Bernaschini et al., 2019). Además, provoca cambios en los ensamblajes tróficos de distintos grupos funcionales como los insectos inductores de agallas y sus parasitoides (Rossetti et al., 2017; Cusser et al., 2019).

Por lo tanto, en el presente trabajo se determinaron los cambios en la estructura y diversidad de los ensamblajes tróficos de insectos inductores de agallas y sus parasitoides asociados a *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* así como los efectos del vigor de la planta en la diversidad de insectos inductores de agallas en sitios con diferente proporción de cobertura de bosque que de huerto en la Franja Aguacatera del estado de Michoacán. Para ello, se plantearon las siguientes preguntas: I) Existirá alguna relación entre los cambios en las proporciones de cobertura vegetal y la diversidad de IIA y sus parasitoides asociados a tres especies de encinos? II) El vigor de la planta se verá afectado por los cambios en las proporciones de cobertura vegetal? Y, finalmente, III) Se verán influenciados los ensamblajes tróficos de IIA y sus parasitoides por los cambios en las proporciones de cobertura vegetal?

## HIPÓTESIS

- La diversidad de insectos inductores de agallas y parasitoides asociados a *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* será mayor en sitios con mayor cobertura de bosque templado y menor cobertura de huertas de aguacate.
- Las redes tróficas más complejas tendrán mayor diversidad de morfoespecies de insectos inductores de agallas y parasitoides y mayor conectancia en sitios con mayor proporción de cobertura de bosque templado y menor cobertura de huertas de aguacate.
- El vigor de los individuos de *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* expresado en tamaño, cobertura del dosel y contenido de clorofila será mayor en sitios con mayor cobertura de bosque templado y menor cobertura de huertas de aguacate.
- Existirá una relación positiva entre el vigor de los individuos *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* y la diversidad de insectos inductores de agallas y sus parasitoides en sitios con mayor cobertura de bosque templado y menor cobertura de huertas de aguacate.

# OBJETIVOS

**Objetivo General:** Determinar los cambios en la estructura y diversidad de ensamblajes tróficos en insectos inductores de agallas y parasitoides asociados a *Quercus castanea*, *Quercus obtusata* y *Quercus magnoliifolia* en sitios con diferente proporción de cobertura de bosque y huertos de aguacate en el estado de Michoacán.

## Objetivos Particulares:

- Determinar los cambios en la riqueza, abundancia y composición de insectos inductores de agallas y sus parasitoides asociados a *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* en sitios con diferente proporción de cobertura de bosque y huertos de aguacate en el estado de Michoacán.
- Determinar la dominancia, similitud y equitatividad de insectos inductores de agallas y sus parasitoides asociados a *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* en sitios con diferente proporción de cobertura de bosque y huertos de aguacate en el estado de Michoacán.
- Identificar los cambios en los ensamblajes tróficos de insectos inductores de agallas y sus parasitoides asociados a *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* en sitios con diferente proporción de cobertura de bosque y huertos de aguacate en el estado de Michoacán.
- Determinar los cambios en el vigor de la planta de *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* y su relación con la diversidad de insectos inductores de agallas y parasitoides en sitios con diferente proporción de cobertura de cobertura de bosque y huertos de aguacate en el estado de Michoacán.

# CAPÍTULO

# Tri-trophic networks of gall-inducing insects and their parasitoids associated to oak species in Mexican avocado agrosystems: importance of native forest coverage and local climatic variables

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## Abstract

Despite temperate forest ecosystems (TFEs) are sites with great diversity of biotic interactions, they are highly threatened by many anthropogenic factors being land use change the main one. In México, TFEs have been strongly affected by the conversion of native forests to avocado orchards generating forest fragmentation, affecting trophic networks such as gall-inducing insects (GII) and their parasitoids. We determined the changes in structure and diversity of trophic assemblages of GII and their parasitoids associated with *Q. castanea*, *Q. obtusata* and *Q. magnoliifolia*, as well as the effects of plant vigor on GII diversity in sites with different proportions of forest cover and avocado orchard in México. We assessed also the effects of local climate variables on the plant vigor and the GII diversity. In each study site, we selected 20 individuals with gall presence for each oak study species. We found that plant vigor traits (DBH, canopy cover and chlorophyll content) and GII diversity of the three oak species decrease as forest cover increases. An opposite trend was detected to parasitoid diversity for areas with greater forest cover. GII diversity was a positive relationship with temperature, but a negative relationship with precipitation was found in all study sites. Plant-GII networks were different among sites and among three oak species, being the network for areas with lower forest cover showing higher values of nestedness, specialization and modularity than networks for areas with greater forest cover. Network of GII and parasitoids of areas with lower forest cover had higher modularity and nestedness and showed lower diversity of interactions than networks for areas with greater forest cover. The most complex trophic network corresponded to sites with greater forest cover than orchards suggesting the presence of generalist parasitoid species in comparison with the less complex network which is the one for sites with lower forest cover than orchard, suggesting dominance of specialist parasitoid species. Therefore, we highlight the need to conserve and manage the forest remnants in the avocado belt.

**Key words**: Temperate forests; avocado orchards; oaks, gall-inducing insects; parasitoids; trophic networks

## Introduction

Temperate forest ecosystems (TFEs) are conformed by different tree species such as fir, fir-oyamel, oak and pine-oak forests (Arasa-Gisbert et al., 2018), and harbor great biodiversity. The oaks or *Quercus* is a very diverse genus of tree species, distributed mainly in temperate forests from the northern hemisphere (Cavender-Bares, 2016), being Mexico an important center of oak diversification and endemisms (Hipp et al., 2018) with about 170 species (32-40 % of diversity worldwide), of which, 109 are endemic (Valencia, 2004; Hipp et al., 2020). Oak forests supply important ecosystemic services such as carbon capture, climatic and hydric regulation and pollutant purification (Lucas-Borja & Delgado-Baquerizo, 2019; Yuan et al., 2020; Kasper et al., 2021). Nevertheless, these forests are strongly threatened by anthropogenic activities such as urbanization, deforestation, global warming and land use change to agrosystems (Watson et al., 2016; Aguilar et al., 2019). Agrosystems intensification result in a loss of landscape heterogeneity, as well as habitat loss and formation of forest fragments interspersed with crops, which reduces biodiversity and affects biotic interactions, control of pests and diseases (Tscharntke et al., 2007; Campbell et al., 2018; Pérez-Solache et al., 2023).

Fragmentation is a dynamic process where the matrix of forest is progressively reduced in several fragments of different sizes and perimeters and degrees of isolation experiencing rapid and abrupt abiotic (i.e. increment of temperature and light incidence and reduction of soil fertility, humidity and precipitation) and biotic changes (i.e. reduction of species diversity and disrupt biotic interactions) (Haddad et al., 2015; Rossetti et al., 2017; Fletcher et al., 2018; Salomão et al., 2019). Insect herbivores are highly sensitive to habitat loss (Maldonado-López et al., 2016; García-Jain et al., 2021), due their abundance, richness, and distribution are shaped by changes in microclimatic conditions caused by forest fragmentation, and by the presence of predators and natural enemies such as parasitoids (Pfeifer et al., 2017; Schüepp et al., 2014). Insect herbivore abundance is also regulated by the reduction in the amount of plant resource for insect herbivores (e.g. plant size and abundance, canopy cover) and by host plant quality (e.g. water and chlorophyll content) (bottom-up effects), as result of forest fragmentation (Schüepp et al., 2014; Pfeifer et al., 2017). Thus, "The plant vigor hypothesis" proposes that herbivorous insects prefer feeding on plants with larger size and growth because they have higher nutritional quality that favors their offspring (Price, 1991). It has been reported that plant vigor can change in fragmented habitats, decreasing the diversity of insect herbivores (Maguire et al., 2016) such as gall-inducing insects (GII) and their complex community associate to them. Particularly, some biotic (i.e. plant species richness, life form of host plant, plant age, plant density, plant size) and abiotic factors (i.e. soil fertility, temperature, humidity and radiation) have also been proposed to explain the GII species richness at different scales (Fernandes & Price 1992; Fernandes 1996; Cuevas-Reyes et al., 2004a, b; de Araújo et al., 2013).

In this sense, host plants, GII and their parasitoids conform a very complex tri-trophic interaction, where top-down and bottom-up effects regulate the assemblages of different populations at each trophic level. Galls induced by insects in oaks, benefit the inducers progeny by providing food resources (Stone, 2002; Susuki et al., 2009, Guiguet et al., 2018), stable microhabitat (Blanche, 2000) and protection against natural enemies such as parasitoids (Price, 1998). Parasitoid wasps are one of the main natural enemies that causes high mortality of oak galls (Hosseini et al., 2022), where their specialization to their hosts can vary greatly, from generalist strategies to specific-specialist interactions such as in the families Braconidae, Chalcididae, Eulophidae and Ichneumonidae families (Hanson et al., 2014; Maldonado-López et al., 2022). It has been reported that in fragmented oak forests, GII diversity increases due to changes in local climatic conditions provoked by forest fragmentation (Maldonado-López et al., 2016).

Tri-trophic interactions such as plant-GII and their parasitoids are very diverse and represents complex networks, being approached in the past decades by quantitative ecological networks (Delmas et al., 2019; Oliveira et al., 2019; Maldonado-López et al., 2022). The use of quantitative ecological networks to study tri-trophic interactions, enables a better understanding of the complexity of communities, providing a clear functional description of community structure and diversity (Landi et al., 2018). Most of GII network studies has been carried in tropical systems (de Araújo et al., 2017; Araújo et al., 2019), few studies in Nearctic and Palearctic regions (Nyman et al., 2015; Barbour et al., 2016) and even less studies that consider the three trophic levels (Maldonado-López et al., 2022).

Many TFEs in México are fragmented due to agricultural activities (Molina-Sánchez et al., 2019; Pérez-Solache et al., 2023). Particularly, in the TEFs of Michoacán state in Mexico, the avocado orchards are recognized as the main driver of habitat deforestation and biodiversity loss due to the increasing demand worldwide (Cho et al., 2021; de la Vega-Rivera & Merino-Pérez, 2021). México is the lead country in avocado production with more than 241,140 ha and more than 1715 ha/year of forest conversion rate to avocado orchard generating earnings over 2,500,000 dollars per year (González-Estudillo et al., 2017; Cho et al; 2021). Most studies of networks have reported highly diverse communities associate to GII (Espírito-Santo & Fernandes, 2007; Kuzmanich et al., 2018;

Serrano-Muñoz et al., 2022), but few have evaluated the changes in the structure and composition of the networks of oak-GII-parasitoids in temperate agrosystems. Therefore, the aim of this study was to determine the changes in the structure and diversity of trophic assemblages of GII and their parasitoids associated with *Q. castanea*, *Q. obtusata* and *Q. magnoliifolia,* as well as the effects of plant vigor on GII diversity in sites with different proportions of forest cover and avocado orchard in Michoacán. We addressed the following questions: (i) Is the plant vigor affected by the proportion of coverage of forest and avocado orchards? (ii) Is there a relationship between plant vigor and GII diversity across different proportion of coverage of forest and avocado orchards? and (iii) Are the structure and composition of tri-trophic networks influence by the distinct proportion of coverage of forest and avocado orchards? We expect that, in areas with higher proportion of orchard cover, environmental conditions will be harsher (i.e., high incidence of light and temperature and drier climatic conditions). As a consequence, individuals of *Q. castanea*, *Q. obtusata* and *Q. magnoliifolia* will present networks of trophic assemblages of GII and their parasitoids with lower values of diversity of interactions, nestedness, modularity and lower values of specialization in these habitats. The opposite being expected for areas with a higher proportion of forest cover in relation to avocado orchards.

## Material and methods

### *Study sites*

This study was carried in the "avocado belt" in the center-west of the Michoacán state, Mexico, characterized by a landscape of pine-oak forest fragments mixed with avocado orchards (Barsimantov & Antezana, 2012). We determined the dynamics of forest cover change and avocado orchards using medium and high-resolution satellite images (Landsat, SPOT, Sentinel and Rapid Eye with TM 5, ETM + and OLI sensors) to define the location and extent of the main TFEs coverages and avocado orchards (Neinavaz et al., 2020; Pérez-Solache et al., 2023). Based on this information, we selected six study sites with different proportion of forest and avocado orchards cover (Hass variety) and where *Q. castanea*, *Q. obtusata* and *Q. magnoliifolia* were present, and we classified them as follows: two sites with higher proportion of orchards: (i) Tacámbaro, Rancho las Joyas (35% forest cover and 65% orchard cover) (19° 13’4.6” N; 101° 25’ 4.6” W) and (ii) Caramécuaro: (38% forest cover and 62% orchard forest) (19°15’387.3” N; 101° 23’43.7” W), two sites with similar coverage of forest and avocado orchard: (i) Tacámbaro, Rancho el Embrujo: (52% forest cover and 48% orchard cover) (19°15’53.77” N; 101° 27’ 41.34” W) and (ii) Tacámbaro, Exhacienda (51% forest cover and 49% orchard cover) (19°15’1.91” N; 101°28’42.59” W) and two sites with more proportion of forest: (i) Acuitzio, Llanitos (84% forest cover and 16% orchard cover) (19°26’58.54” N; 101°16’38.91”W) and (ii) Acuitzio, La Yácata (74% forest cover and 26% orchard cover) (19°26’16.06”N; 101°18’0.14”W). We included in the Supplementary Materials the map of the distribution of the study sites in the avocado belt in Michoacán state, México (Figure S1). A 1000 m radius buffer area was established at each study site. All study sites have organic management without the application of synthetic pesticides. In addition, all study sites have similar size, ranging from 60 to 80 ha and a similar age that oscillates between 15 and 20 years after felling (Pérez-Solache et al. 2023).

## Study species

*Quercus castanea Neé* belongs to the Lobatae section (red oaks), and its geographical distribution is restricted to mountain ranges from Mexico: The Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del sur and the Trans-Mexican volcanic belt. This tree occurs between 1180 and 2600 masl (Valencia, 1995; Valencia-Cuevas et al., 2015). This oak species grows up to 15 m height and its leaves are oblanceolate, oblong, lanceolate and obovate, lustrous, rough and of grayish green color (Valencia, 1995).

*Quercus obtusata* Humb. & Bonpl. belongs to the *Quercus* section (white oaks) and is distributed only in Mexico, at altitudes between 1430 and 2900 masl in the Central Plateau of México and Trans-Mexican volcanic belt (Valencia, 2004). This tree species grows up to 30m height and its leaves are obovate o elliptical, with a green, lustrous and tomentous underside (Arizaga, 2009).

*Quercus magnoliifolia* Neé belongs to the *Quercus* section (white oaks) and is distributed from Mexico to Central America, between 600 and 2800 masl (Valencia, 1995). This species grows up to 25 m height and its leaves are obovate, almost glabrous and of lustrous green (Arizaga, 2009).

## Sampling design

In each study site, 20 individuals for each study species (*Q. castanea*, *Q. obtusata* and *Q. magnoliifolia*) with presence of galls were collected and permanently marked with aluminum tags. In each individual, a systematic stratified sampling design was used by collecting six branches in each stratum of the crown (i.e. lower, medium and higher)

(Maldonado-López et al., 2022). Sampling was performed monthly from July to February of 2021 to estimate gall richness, the proportion, abundance and density of galls. The alternation of generations in a single year is a typical characteristic of gall-inducing cynipids, where the sexual generation develops in spring, while the asexual generation occurs in summer and autumn (Stone et al., 2002; Maldonado-López et al., 2015; 2022). In Michoacán, the oaks lose their leaves in the dry season which is from March to June (i.e. spring), while in the wet season where the oaks keep their leaves is from July to February (i.e. summer and autumn). Therefore, in our sampling, we included only galls from the asexual generation of cynipids. In the field, all leaves and branch galls were separated and placed in plastic containers, covered with tricot fabric to transport them to laboratory, where we wait for the emergence of gall inducers and adult parasitoids (Pérez-López et al., 2016; Maldonado-López et al., 2022). All emerged insects from each sampled gall were stored in alcohol at 70%, until their taxonomic identification (i.e., parasitoid insects) by taxonomic keys of Graham (1969), Graham & Gijswijt (1998) and Gibson et al., (1997). All galls were referred as a morphospecies according to their external morphology since each insect species is capable of inducing a unique gall form, indicating that gall morphospecies are a reliable approach to estimate diversity and structure of GII communities (Cuevas-Reyes et al., 2004; de Araújo et al., 2013; Pérez-López et al., 2016; Maldonado-López et al., 2022). To the extent possible, emerged GII were stored in ethanol vials.

### *Plant vigor traits*

We evaluated the plant vigor on the same trees where the galls were collected of the three oak studied species, and we measured the following traits: (i) diameter at breast height (DBH) as an estimator of plant size (Cuevas-Reyes et al., 2004; Maldonado-López et al., 2014; García-Jain et al., 2021); (ii) canopy cover as an indicator of leaf availability (Maldonado-López et al., 2015) using the app “Canopeo”, which is free and is capable of outputting data from canopy cover percentage of each oak tree from pictures or video (Patrignani and Ochsner, 2015; Reed et al., 2021); and (iii) the chlorophyll content as an indicator of photosynthetic capacity, primary productivity and nutritional status, quantified by SPAD 502 (Minolta) collecting ten randomly selected leaves (García-Jain et al., 2021; Costa Santos et al., 2022).

### *Trophic networks*

Graphical representation of the quantitative trophic networks of each oak species (*Q.castanea*, *Q. obtusata* and *Q.magnoliifolia*) were constructed based on abundance and richness of each GII morphospecies and their respective parasitoids associated in each study site with different coverage of forest cover and avocado orchard using the “Food web designer” software (Saint & Traugott., 2015). In each quantitative trophic network, oak species was the first trophic level, GII species were the second trophic level, and the parasitoid species as the third trophic level.

The metrics that described the networks topology were calculated for each oak species (*Q.castanea*, *Q. obtusata* and *Q.magnoliifolia*) in tripartite networks for each study site. The following descriptors were used: (i) diversity, (ii) connectance, (iii) specialization, vulnerability (iv) generality (iv) modularity and (v) nestedness.

The diversity index was calculated based on the Shannon index (Kaartinen &

Roslin, 2012). Connectance was calculated as the proportion of the possible interactions that occurs over the number of possible links that take place within the network (Dormann et al., 2009). Network specialization was calculated using the index $H_2$' which can result on values from 0 to 1, 0 being absolute generalization and 1 being absolute specialization (Dormann, 2009). The vulnerability was considered as the mean number of GII that attack each oak individual and the mean number of parasitoids that attack each GII morphospecies. The generality metric was used to determine the mean effective number of individuals of oak species attacked per each gall morphospecies, and the mean number of GII morphospecies attacked by each parasitoid species. The modularity index was calculated to identify within each trophic network, the presence of groups (or modules) of species of a particular trophic level, which interacts more frequently with another group of species from other trophic level. This index takes values from 0 to 1, where the highest values indicate the existence of modules or semi-independent groups of interactors within the general network. We finally calculated the nesting index using the NODF metric, which is based on the overlap at decreasing fill that identifies the species with the highest number of interactions in each trophic level (Almeida-Neto et al., 2008).

In order to test the significance of network descriptors obtained for the three different networks, we used 500 simulated networks generated by the null models (Dormann & Strauss, 2014). We generated the null models using *nullmodel* algorithm (Dormann et al., 2009) and all network analyses were performed in the *Vegan* and *Bipartite* packages (Dormann et al., 2008) in R software (ver.4.0.5)

*Relationships between local climate variables, plant vigor and GII and parasitoid diversity*

We also evaluated the climatic variables that can influence the plan vigor traits, GII and parasitoid diversity. We obtained 19 bioclimatic variables available in WorldClim2.1 data set (http://worldclim.org/version2) (Fick & Hijmans, 2017; Marchi et al., 2019) for each study site. These climatic variables represent annual trends, seasonality, and extreme or limiting environmental factors for organisms (Otgonbayar et al., 2022). Then, we performed a paired correlation analysis for each climatic variable to eliminate redundant variables (the criterion was eliminated one variable from each pair with r > 0.80 retaining the more general climatic variable) (Vaca-Sánchez et al., 2021). The selected variables were: Annual Mean Temperature (AMT), Mean Temperature of Wettest Quarter (MTWQ), Annual Precipitation (AP), Precipitation of Wettest Month (PWM), Precipitation of Driest Month (PDM) and Precipitation of Driest Month (PDM).

## Statistical analysis

A spatial autocorrelation analysis was performed using the Moran's I coefficient, which is optimum for identifying clustered, dispersed or random land cover conformations as a function of spatial location (Kowe et al., 2019). This analysis has values range from -1 to 1, where values close to 0 indicate a random spatial distribution and values close to -1 or 1 show high negative or positive spatial autocorrelation of the data (García-Jaín et al., 2021; Pérez-Solache et al., 2022). Moran's I coefficient values were close to 0 for all parameters related to plant vigor (DBH = 0.051; canopy cover = 0.021; chlorophyll content = 0.06), gall-inducing insect diversity (gall abundance = 0.067; gall richness = 0.03) and parasitoid diversity (parasitoid abundance = -0.19, parasitoid richness= -0.11, in *Q. castanea*, *Q.*

*obtusata* and *Q. magnoliifolia*, confirming the spatial independence of each study sites in all analyses.

### *Plant vigor, GII and parasitoid diversity*

We performed generalized linear mixed model (GLMM) to determine the effects of sites with different coverage of forest and orchards (forest > orchard *vs*. forest = orchard *vs*. forest < orchard), oak species (*Q. castanea vs*. Q. *obtusata vs. Q. magnoliifolia*) and the interaction of forest cover/avocado orchard * oak species on plant vigor (i.e., diameter at breast height, canopy cover and chlorophyll content), gall diversity (abundance and richness) and parasitoid diversity (abundance and richness). We performed out a separate model for each of the response variables. Sites with different coverage of forest and orchards and oak species were considered as fixed factors (explanatory variables), study sites were considered a random factor and DBH, canopy cover, chlorophyll content, gall abundance and richness, parasitoid abundance and richness as response variables.

Multivariate analyses were used to evaluate the differences in GII morphospecies composition among the study sites. Thus, the six GII morphospecies communities were ordered by non -metric multidimensional scaling (NMDS) using the abundance similitude matrix and the Bray-Curtis index as a distance metric. Then, a non-parametric permutation procedure (ANOSIM) was used to check whether gall morphospecies composition differed among the six study sites. The ANOSIM was based on a binary matrix gall morphospecies occurrence in each study site and the Bray–Curtis index was used as a distance metric, realizing 5000 permutations. Pairwise ANOSIMs were performed between all pairs of sites as a post-hoc test. These analyses were developed using PAST software (Hammer et al., 2001).

To build the rarefaction curves, we included all gall morphospecies registered in the three oak study species (*Q.* castanea, *Q. obtusata* and *Q. magnoliifolia*) per each forest coverage category using the software Estimates 9.1.0 (Cowell, 2013). The same procedure was used to obtain the rarefaction curves for parasitoid richness among forest coverage categories. The scale of the independent variable (X axis) was represented by the estimated number of GII morphospecies and the parasitoid richness respectively. A data set was standardized and compared using the number of individuals as sampling effort (Gotelli & Cowell, 2001) for the application of the rarefaction method. We used a 95% of confidence intervals in each rarefaction curve to determine if the richness of gall morphospecies and the parasitoids differed among forest coverage categories.

### *Relationships between local climate variables, plant vigor and GII and parasitoid diversity*

To evaluate the association between plant vigor traits, GII abundance and richness, parasitoid diversity (richness and abundance) and local climatic variables in the three forest/orchard coverage categories (forest > orchard *vs.* forest = orchard *vs.* forest < orchard), a principal component analysis (PCA) was performed. With this analysis, we obtained a PCA biplot that showed the association of the individuals from different forest coverage categories with the different climate variables (i.e. AMT, MTWQ, AP, PWM, PDM), plant vigor traits (i.e. DBH, canopy cover and chlorophyll content), gall diversity (abundance and richness) and parasitoid diversity (abundance and richness) (SAS, 2000; Stokes et al., 2000). Besides, Spearman’s correlation analyses were performed to determine the relationship among climate variables, plant vigor traits, GII and parasitoid diversity.

## Results

### *Plant vigor traits*

According to the GLMM analyses, we found significant differences in all plant vigor traits among different avocado forest/orchard covers for the three oak study species (Table 1). A general pattern was detected, individuals of *Q. castanea*, *Q. obtusata* and Q. *magniliifolia* had greater DBH, canopy cover and chlorophyll content in sites with higher proportion of orchards (Figure 1). Particularly, individuals of *Q. castanea* had higher DBH followed by *Q. magnoliifolia* and *Q. obtusata* in all study sites (Fig. 1a). In all study sites, *Q. obtusata* individuals exhibited the greatest canopy cover compared to *Q. castanea* and *Q. magnoliifolia* (Fig. 1b). Finally, *Q. magnoliifolia* individuals had the lowest chlorophyll content at all study sites compared to *Q. castanea* and *Q. obtusata* (Fig. 1c).

### *GII and parasitoid diversity*

We collected a total of 21,886 galls which correspond to different 31 GII morphospecies from *Q. castanea*, *Q. obtusata* and *Q. magnoliifolia* in the three forest coverage categories. We also reared a total of 1,001 parasitoids belonging to 10 species, 5 genera (*Aprostocetus*, *Eurytoma*, *Ormyrus*, *Sycophila* and *Torymus*) and 4 families (Eulophidae, Eurytomidae, Ormyridae and Torymidae). We found a total of 191 parasitoid species associated with GII morphospecies of *Q. castanea*, 343 parasitoid species associated with GII morphospecies of *Q. obtusata* and 467 parasitoid species associated with GII morphospecies of *Q. magnoliifolia*.

We found significant differences among GII abundance ($\chi^2$= 11490.8; *d.f* =2, *P* <

0.0001) (Supplementary Materials, Figure S2a) and species richness ($\chi^2$ = 311.0*; d.f* = 2; *P* < 0.0002) (Supplementary Materials, Figure S2b) among areas with different proportions of forest and orchards for the three oak species (*Q. castanea* and *Q. obtusata* and *Q. magnoliifolia*). In particular, *Q. magnoliifolia* and *Q. obtusata* had higher GII abundance in sites with higher proportion of orchards. Contrary, *Q. castanea* recorded the highest GII abundance in sites with similar coverage of forest and avocado orchard (Figure S2a). GII richness was higher in sites with higher proportion of orchards for three oak species in comparison with the other study sites (Figure S2b).

Parasitoid abundance ($\chi^2$= 331.6; *d.f* =2; *P* < 0.0001) and parasitoid richness ($\chi^2$= 108.2040; *d.f* = 2; *P* < 0.0001) differed among forest coverage categories. The general pattern indicated that parasitoid diversity increases as forest cover increases for the three oak species studied. Particularly, *Q. obtusata* presented the higher parasitoid abundance in all forest coverage categories (Supplementary Material, Figure S2c). Parasitoid species richness was higher on GII associated to *Q. magnoiifolia* in all study sites (Supplementary Material, Figure S2d).

Rarefaction curves showed that GII richness was significantly higher in sites with higher proportion of orchards than in sites with more proportion of forest (Figure 2a). Also, the rarefaction analysis indicated that parasitoid richness increases in sites with grater forest cover than in sites with higher proportion of orchards (Figure 2b).

The results of the similarity of GII community showed that NMDS ordination explained 74 % of the variance between sampling points (axis 1 = 54 % and axis 2 = 20 %), where each point is a two-dimensional representation of the composition of GII morphospecies in a single tree based on global NMDS (Figure 3). We found differences in the composition of GII morphospecies associated to *Q. castanea* (ANOSIM $r = 0.32$, n = 25, $P < 0.001$) (Fig. 3a), *Q. magnoliifolia* (ANOSIM $r = 0.62$, n = 25, $P < 0.001$) (Fig. 3b) and *Q. obtusata* (ANOSIM $r = 0.39$, n = 25, $P < 0.001$) (Fig. 3c) between the different avocado forest/orchard cover. Also, the results of post-hoc pairwise ANOSIM tests showed different composition of GII morphospecies between the different avocado forest/orchard covers. Particularly, sites with higher proportion of orchards had totally different GII species assemblages in comparison to sites with similar forest/orchard and higher forest/orchard cover ($P < 0.05$).

On the other hand, the results of parasitoid community similarity showed that NMDS ordination explained 82% of the variance between sampling points (axis 1 = 59% and axis 2 = 23%), where each point is a two-dimensional representation of the parasitoid composition in a single tree based on global NMDS (Figure 4). We found differences in the composition of parasitoids associated to *Q. castanea* (ANOSIM $r = 0.16$, n = 25, $P < 0.001$) (Fig. 4a), *Q. magnoliifolia* (ANOSIM $r = 0.20$, n = 25, $P < 0.001$) (Fig. 4b) and *Q. obtusata* (ANOSIM $r = 0.17$, n = 25, $P < 0.001$) (Fig. 4c) between the different avocado/orchard covers. Also, the results of post-hoc pairwise ANOSIM tests showed different composition of parasitoids between the different avocado forest/orchard cover. Particularly, the sites with higher proportion of orchards had totally different assemblages in comparison with similar forest/orchard and higher forest/orchard cover ($P < 0.05$).

### *Relationship of GII and parasitoid diversity, plant vigor traits and climatic variables*

The variation of the plant vigor traits, abundance and species richness of GII and parasitoids of *Q. castanea*, *Q. magnoliifolia* and *Q. obtusata* was explained by the differences in the forest-orchards covers and their variation of climatic variables, according to the PCA biplot (Figure 5), where individuals growing in different avocado forest/orchard covers were separated as follows: the PC1 axis explained 43.1 % of the total variance and are associated with the right side: DBH, GII abundance and richness, CC, PWM, AMT, MTWQ and canopy cover with individuals growing in sites with higher proportion of orchards. The PC2 axis explained 17.7 % of the variance and is related with the left side: PDM and AP were related to individuals of similar coverage of forest and avocado orchard, as well as in sites with more proportion of forest. In general, according to the Spearman's correlations for the three oak species, we observed significant relationships. For the DBH, we detected positive relationships with CC, AMT, MTWQ and negative correlations with PDM and GII richness (Table 2). In the case of the CC, have positive correlations with AMT, MTWQ, PDM, PWM and GII richness. We also detected that parasitoid diversity presented significant and positive correlations only with AP and PDM, but a negative correlation with CC, ATM, MTWQ, PWM and GII diversity (Table 2).

### *Tri-trophic Networks*

Overall, we found that oak tri-trophic networks had greater connectance and lower modularity as forest cover increases in the different study sites. Oak species from sites with higher proportion of orchards showed tri-trophic networks with lower connectance and greater modularity, suggesting dominance from specialist parasitoid species. On the other hand, sites with greater forest cover had oak tri-trophic networks with greater connectance and lower modularity, suggesting dominance form generalist parasitoid species (Figure 6).

### *Oak-GII networks*

In relation to the networks from the three oak study species and their associated GII, topological descriptors ranged greatly among cover categories. (Table 3). First, the network constructed for areas with lower forest cover than orchard presented greater values in two topological descriptors being modularity (0.511) and nestedness (62.67) in comparison with the networks with greater forest cover, showing off a network with GII that interact strongly with the three oak species. Second, the network for areas with similar forest cover than orchard presented the highest values in two topological descriptors, generality (1.019) and vulnerability (0.019) indicating a generalist but less diverse network in comparison with the network for areas with lower forest cover than orchard. Finally, the network constructed for areas with greatest forest cover than orchard presented higher values in three topological descriptors like connectance (0.372), Shannon index (1.563) and specialization (0.987) in comparison with the networks with lower forest cover than orchard, demonstrating a strongly connected and diverse generalist network (Table 3).

Null model comparisons showed that the observed values of connectance, Shannon index, generality and vulnerability were lower than expected by chance for the networks of all three coverage conditions. Contrary, modularity and nestedness were higher than expected by chance for all networks (Table 3).

### *GII-parasitoid networks*

For the networks constructed for GII and their associated parasitoid species, including the three oak study species we found: First, the network made for areas with lower forest cover than orchard presented higher values for three topological descriptors, connectance, (0.225), modularity (0.453) and specialization (0.645) resulting into a network with presence of specialized parasitoid species in comparison with the networks for sites with greater forest cover than orchard. Second, the existing network for areas with similar forest cover than orchard showed greater values in two topological descriptors such as nestedness (33.65) and Shannon index (3.164), showing off a diverse but not well connected network in comparison with the networks for other cover categories, and third the network for areas with greater forest cover than orchard presented the highest values in two topological descriptors like generality (15.70) and vulnerability (15.70, showing off a very diverse network with complex interactions in comparison with the networks for areas with lower forest cover than orchard. (Table 3).

Compared to null models, observed values for connectance and Shannon index were lower than expected by chance for all three networks and modularity, generality and vulnerability observed values were higher than expected by chance in all three networks. In the case of nestedness, we found higher values than expected by chance in the networks for lower forest cover than orchard and similar forest cover than orchard, while in the network for sites with greater forest cover than orchard we found that the nestedness values were lower than expected by chance (Table 3)

## Discussion

### *Effects of forest-orchard cover on plant vigor traits*

Our study showed that plant vigor traits increase as forest cover decreases for the three oak studied species. The general pattern for the three oak species, *Q. castanea*, *Q. obtusata* y *Q. magnoliifolia* was presenting higher values of plant vigor traits in sites with lower forest cover than avocado orchards. This result agrees with the reported by Pérez-Solache et al. (2023), which detected that oaks with a greater diameter at breast height, canopy cover and chlorophyll content occur in areas where the forest cover is lower and the coverage of avocado orchards is greater. These results suggest an effect of forest fragmentation modifying local climate variables, which leads to a greater plant vigor on the most fragmentated sites in comparison with the sites that are less fragmented. It has been reported that environment strongly influences trait expression in plant (i.e., DBH, CCV, leaf area and CC) (Hamann et al., 2021), being abiotic factors such as solar radiation, wind speed, temperature and humidity the main causes on plant vigor changes (Maldonado-López et al., 2015; Arroyo-Rodríguez et al., 2016; García-Jaín et al. 2022). This fact suggests that environment changes associate to fragmented landscapes can favor the plant vigor traits, having larger trees, with higher canopy coverage and chlorophyll concentration in areas with higher proportion of orchards (Karban, 2007; Magrach et al., 2014; Maldonado-López et al., 2015). An alternative explanation to this pattern could be attributed to artificial fertilization used in sites with greater avocado orchard cover (Blondeel et al., 2019). The literature reported that artificial fertilization increases chemical compounds (i.e., magnesium, nitrates, sulfates and nitrogen) in soil, which can reach the adjacent forest remnants making them available for oaks (Bravo-Espinoza et al., 2012; Mao et al., 2017; Pérez-Solache et al., 2023). This artificial fertilization of the soil might increase oak plant vigor in the forest remnants adjacent to the avocado orchard and therefore, modifying their interactions with insect herbivores such as herbivory (García-Jain et al., 2022; Pérez-Solache et al., 2023).

### *Effects of plant vigor on GII and parasitoid diversity in different forest-orchard cover*

We found a higher GII diversity in areas with higher proportion of orchards. Contrary, the higher parasitoid diversity was detected in areas with higher proportion of forest cover. In the first case, one possible explanation to this result could be attributed to "Bottom-up forces" (i.e. plant-herbivore), because a recent studies suggest that the main mechanism that regulate the insect herbivore distribution and diversity is the variation in host plant quality (i.e. plant vigor), which increases in anthropized habitats (Maldonado-López et al., 2015, Rosetti et al., 2017, García-Jain et al., 2022; Pérez-Solache et al., 2023). This fact is consistent with the "Plant vigor hypothesis" (Price, 1991), which states that herbivorous insects prefer to feed on large and more vigorous plants, because of their greater nutritional quality which benefits offspring performance. Therefore, plant vigor can increase (i.e., DBH, CCV and CC) as result of abruptly changes in abiotic conditions such as temperature and precipitation associated to fragmented landscapes, but chemical defense against herbivores can decrease in these anthropized conditions (Coley et al., 1985, Barbour et al., 2015; García-Jain et al., 2022). Alternatively, this result can also be supported by "The crowding effect" (Debinski & Holt 2000), which stands that, after a forest clearing the herbivorous insects can possibly relocate in adjacent forest fragments increasing populations density, resulting into a relatively positive effect of fragmentation on herbivorous insect populations (Maldonado-López et al., 2015; García-Jain et al., 2022).

In the second case, the parasitoid diversity decreases as forest cover does, therefore, we can expect that their populations will be lost in fragmented habitats with small forest remnants (Anderson et al., 2022). This fact can be explained because parasitoids are particularly sensitive to environmental changes (i.e., temperature and humidity) caused by forest fragmentation (Maldonado-López et al., 2016; García-Jain et al., 2021) due to their greater requirements in forest area (Gravel et al., 2011; García-Jain et al., 2022).

We also found a positive relationship between the GII diversity and the temperature indicating a clearly effect of the local climatic variables over the GII community present in the remnants of forest present in the avocado agrosystems mosaic. This result is in accord to the reported in the ecological literature, that showed that GII communities generally present greater diversity in environments with higher temperature and lower levels of precipitation (Fernandes & Price, 1992; Price et al., 1998; Cuevas-Reyes et al., 2003; de Araújo et al., 2014). This pattern can be attributed to the fact that the gall induction by insects possibly emerged and radio in xeric habitats, which are characterized by having high temperatures and low levels of precipitation. These environmental conditions can avoid gall desiccation and decreased the incidence of pathogens such as fungus, favoring their survival and establishment in these habitats. (i.e., environmental protection) (Price et al., 1998; Stone & Schönrogge 2003; Cuevas-Reyes et al., 2004).

### *Tri-trophic Networks*

We found a diverse and modular oak-GII networks for areas with lower forest cover than orchard and very diverse but generalist networks in areas with greater forest cover. Our results indicate the presence of specialist parasitoid species in areas with lower forest cover than orchard in comparison with areas with greater forest cover than orchard, where we found the presence of generalist parasitoid species.

Concerning to oak-GII networks, we found great modularity and diversity of GII. These results might be explained by the fact that, areas with lower forest cover than orchard presented the most vigorous oaks, which increase with forest fragmentation, representing more resource availability for GII populations (Anderson et al., 2022; Santos-Neto et al., 2022). GII are more abundant and richer in these areas, therefore, it might alter network structure because species abundance and richness determine network size and influences as well some network topological descriptors such as connectance, vulnerability, generality, modularity and interactions diversity (Tylianakis et al., 2007; Osorio et al., 2015). In this sense, plant vigor might impact GII diversity by influencing their performance and survival (bottom -up forces) (Sobek et al., 2009). Our results agree with Maldonado-López et al., (2015), who found a greater gall-inducing cynipid diversity in small forest fragments due to changes in plant vigor caused by forest fragmentation.

Regarding to GII- parasitoid networks, we found that parasitoid species diversity decreases as forest cover does. These results might be explained by the fact that parasitoid species are highly sensitive to changes in microclimatic conditions (Batista Matos et al., 2013). Therefore, GII diversity increases as consequence of loss on parasitoid reduction due to changes in environmental conditions (i.e., increased temperature, and lowered humidity), caused by forest fragmentation (top-down effects) (Pfeifer et al., 2017; Schüepp et al., 2014). So, higher trophic levels seemed to be more sensitive to effects of forest fragmentation, due to their higher resource requirements in comparison with lower trophic levels organisms (Martinson & Fagan, 2014; Murphy et al., 2016; Rossetti et al., 2017). These results concord with Anderson et al. (2022), that found that parasitism rates decrease with forest fragmentation in specialist parasitoids.

In the same direction, our results concord with Bernaschini et al. (2021) which found that, in herbivore-parasitoid interactions, species in the upper trophic levels, such as parasitoids, might be directly affected by changes in microclimatic conditions and indirectly by the response of their herbivore host to such changes. Our results indicated that bottom- up and top-down forces work alongside to structure herbivore communities, like Gall Inducing Insects (Castagneyrol et al., 2014, 2017; Vaca-Sánchez et al., 2023).

Our findings confirm that temperate forest ecosystems conversion to avocado orchard increase plant vigor traits (DBH, CCV and CC) in areas with lower forest cover than avocado orchards. Similarly, GII diversity increases as forest cover reduces, but parasitoid diversity increases as forest cover does. Also, on tri-trophic antagonistic interactions (oak-GII-parasitoid networks), we found a more complex in interactions network for areas with greater forest cover than orchard but the presence of specialist parasitoid species in the network for areas with lower forest cover than orchard, related to a greater diversity of GII. Therefore, we highlight the urgent need for forest remnants conservation in the "Avocado Belt" in Michoacán because of the important ecosystem services they provide such as carbon capture, mitigation of climate change effects and soil retention and the great biodiversity of GII and parasitoids they harbor so we can avoid local species extinction.

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**Table 1**. Summary of the effects of forest-orchard cover, as well as oak species and their interactions (forest- forest-orchard cover × oak species) on plant vigor according to each generalized mixed model performed.

| **Source** | | | | |
|---|---|---|---|---|
| **Response Variable** | **Explanatory Variable** | ***d.f.*** | ***F*** | ***P<*** |
| DBH (cm) | Forest-orchard cover | 2 | 9.4 | 0.0091* |
| | Oak species | 2 | 33.1 | 0.0001* |
| | Forest-orchard cover x Oak species | 4 | 12.1 | 0.0169* |
| Canopy cover (%) | Forest-Orchard cover | 2 | 47.44 | 0.0001* |
| | Oak species | 2 | 34.72 | 0.0001* |
| | Forest-Orchard cover x Oak species | 4 | 12.76 | 0.0012* |
| Chlorophyll content (SPAD Units) | Forest-Orchard cover | 2 | 44.58 | 0.0001* |
| | Oak species | 2 | 17.16 | 0.0002* |
| | Forest-Orchard x Oak species | 4 | 10.17 | 0.04* |

* Significant values

**Table 2**. Spearman's correlation coefficients of plant quality traits, gall and parasitoid diversity and climatic variables.

| | **Plant vigor traits** | | | **Climate variables** | | | | | **GII diversity** | | **Parasitoid diversity** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **DBH** | **CCV** | **CC** | **AMT** | **MTWQ** | **AP** | **PWM** | **PDM** | **GII richness** | **GII abundance** | **Parasitoid richness** | **Parasitoid abundance** |
| **DBH** | --- | | | | | | | | | | | |
| **CCV** | -0.16 | --- | | | | | | | | | | |
| **CC** | 0.37* | 0.06 | --- | | | | | | | | | |
| **ATM** | 0.22* | 0.11 | 0.52* | --- | | | | | | | | |
| **MTWQ** | 0.22* | 0.11 | 0.52* | 0.1 | --- | | | | | | | |
| **AP** | -0.5 | -0.8 | -0.43 | -0.56 | -0.82 | ---- | | | | | | |
| **PWM** | 0.41* | 0.22 | 0.57 | 0.82 | 0.82 | -0.56 | --- | | | | | |
| **PDM** | -0.33* | -0.17 | 0.57* | 0.74 | -0.95 | 0.74 | -0.95 | --- | | | | |
| **GII richness** | 0.22* | -0.07 | 0.22* | 0.34* | 0.34* | -0.28* | 0.39* | -0.38* | --- | | | |
| **GII abundance** | 0.06 | 0.11 | 0.11 | 0.21* | 0.21* | -0.08 | 0.21* | -0.21* | 0.19 | --- | | |
| **Parasitoid Richness** | -0.40* | 0.09* | -0.40* | -0.33* | -0.33 | 0.11 | -0.49 | 0.49 | -0.14 | -0.06 | --- | |
| **Parasitoid abundance** | -0.25* | -0.13* | -0.29* | -0.28* | -0.30 | 0.11 | -0.35 | 0.43 | -0.09 | -0.009 | 0.46 | --- |

Diameter at breast height (DBH), Canopy cover (CCV), Chlorophyll content (CC). Climate Variables: Annual Mean Temperature (AMT), Mean Temperature of Wettest Quarter (MTWQ), Annual Precipitation (AP), Precipitation of Wettest Month (PWM), Precipitation of Driest Month (PDM).

* Significant correlations

**Table 3** Network topology analyses results for plant-GII and GII-parasitoid networks in three different forest cover categories in the avocado belt in Michoacán, México.

| **Forest cover** | **Network** | **Descriptor** | **Observed** | **Null models** | *P* ≤ |
|---|---|---|---|---|---|
| Forest < Orchard | Plant-GII | Connectance | 0.333 | 0.898 | 0.004* |
| | | Modularity | 0.511 | 0.008 | 0.009* |
| | | Nestedness | 62.67 | 1.279 | 0.001** |
| | | Shannon index | 1.45 | 2.294 | 0.001* |
| | | Generality | 1 | 3.299 | 0.003* |
| | | Vulnerability | 1 | 3.299 | 0.003* |
| | | Specialization | 1 | 0.001 | 0.001* |
| | Gall-parasitoid | Connectance | 0.225 | 0.356 | 0.007* |
| | | Modularity | 0.463 | 0.117 | 0.007* |
| | | Nestedness | 14.65 | 14.07 | 0.06 |
| | | Shannon index | 2.516 | 3.071 | 0.001* |
| | | Generality | 7.349 | 5.194 | 0.001* |
| | | Vulnerability | 7.349 | 5.069 | 0.001* |
| | | Specialization | 0.646 | 0.078 | 0.001* |
| Forest = orchard | Plant-GII | Connectance | 0.361 | 0.575 | 0.002* |
| | | Modularity | 0.172 | 0.013 | 0.001* |
| | | Nestedness | 60.29 | 11.32 | 0.006* |
| | | Shannon index | 0.593 | 0.949 | 0.001* |
| | | Generality | 1.019 | 1.609 | 0.001* |
| | | Vulnerability | 1.019 | 1.610 | 0.001* |
| | | Specialization | 0.962 | 0.0235 | 0.001* |
| | Gall-parasitoid | Connectance | 0.2 | 0.290 | 0.007* |
| | | Modularity | 0.367 | 0.221 | 0.003* |
| | | Nestedness | 33.65 | 26.54 | 0.006* |
| | | Shannon index | 3.164 | 3.442 | 0.002* |
| | | Generality | 5.498 | 4.413 | 0.06 |
| | | Vulnerability | 5.498 | 4.891 | 0.019* |
| | | Specialization | 0.397 | 0.140 | 0.001* |
| Forest > orchard | Plant-GII | Connectance | 0.372 | 0.882 | 0.004* |
| | | Modularity | 0.495 | 0.019 | 0.006* |
| | | Nestedness | 49.21 | 1.539 | 0.001* |
| | | Shannon index | 1.563 | 2.353 | 0.001* |
| | | Generality | 1.015 | 3.463 | 0.004* |
| | | Vulnerability | 1.015 | 3.459 | 0.004* |
| | | Specialization | 0.987 | 0.006 | 0.001* |
| | Gall-parasitoid | Connectance | 0.169 | 0.251 | 0.008* |
| | | Modularity | 0.185 | 0.088 | 0.001* |
| | | Nestedness | 13.02 | 14.98 | 0.12 |
| | | Shannon index | 3.138 | 3.294 | 0.002* |
| | | Generality | 15.70 | 8.913 | 0.001* |
| | | Vulnerability | 15.70 | 8.894 | 0.001* |
| | | Specialization | 0.483 | 0.151 | 0.001* |

## Figure legends

**Figure 1.** Plant vigor traits of *Q. castanea, Q. magnoliifolia* and *Q. obtusata* individuals growing in sites with different proportions of forest cover and avocado orchards. Different letters indicate statistically significant differences (*P* <0.05).

**Figure 2**. Rarefaction curves. a) GII species and b) parasitoids species of oak species studied for each forest coverage category.

**Figure 3.** Non-metric multidimensional scaling (NMDS) ordinations illustrating the similarity of GII composition among the different proportions of forest cover-orchards. a) Similarity of GII morphospecies composition of *Quercus castanea*, b) *Q. obtusata* and c) *Q. magnoliifolia*. Each point is a two-dimensional (axis 1 and axis 2) representation of arthropod species composition on an individual tree based on global, non-metric multidimensional scaling (NMDS).

**Figure 4.** Non-metric multidimensional scaling (NMDS) ordinations illustrating the similarity of parasitoid composition among the different proportions of forest cover orchard. a) For *Quercus castanea*, b) *Q. obtusata* and c) *Quercus magnoliifolia*. Each point is a two-dimensional (axis 1 and axis 2) representation of parasitoid species composition on an individual tree based on global, non-metric multidimensional scaling (NMDS)

**Figure 5.** Results of principal component analyses of plant quality traits, GII and parasitoid diversity and climatic variables among individuals of three forest-cover orchards. DBH= Diameter Brest Height, Canopy cover, CC= Chlorophyll content, AMT= Annual Mean Temperature, MTWQ= Mean Temperature of Wettest Quarter, AP= Annual Precipitation, PWM= Precipitation of Wettest Month and PDM= Precipitation of Driest Month.

**Figure 6.** Quantitative tri-trophic networks of oak study species, GII morphospecies and parasitoids in different proportions of forest cover-orchards. a) Trophic network of sites with higher proportion of orchards. b) Trophic network of sites with similar coverage of forest and avocado orchard c) Trophic network of sites with higher proportion of forest. Line thickness represents the number of interactions (based on abundance).

**Figure 1**

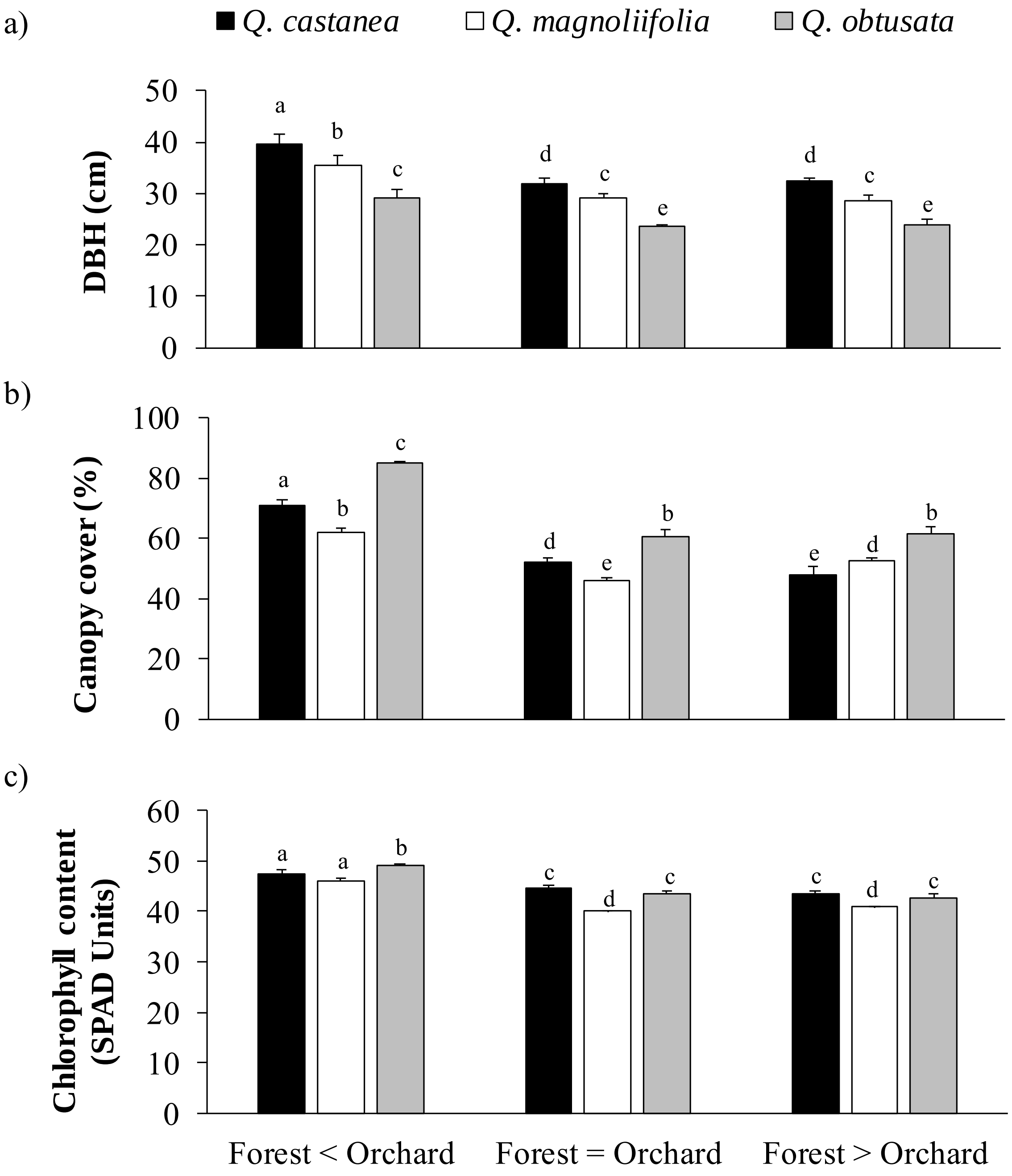
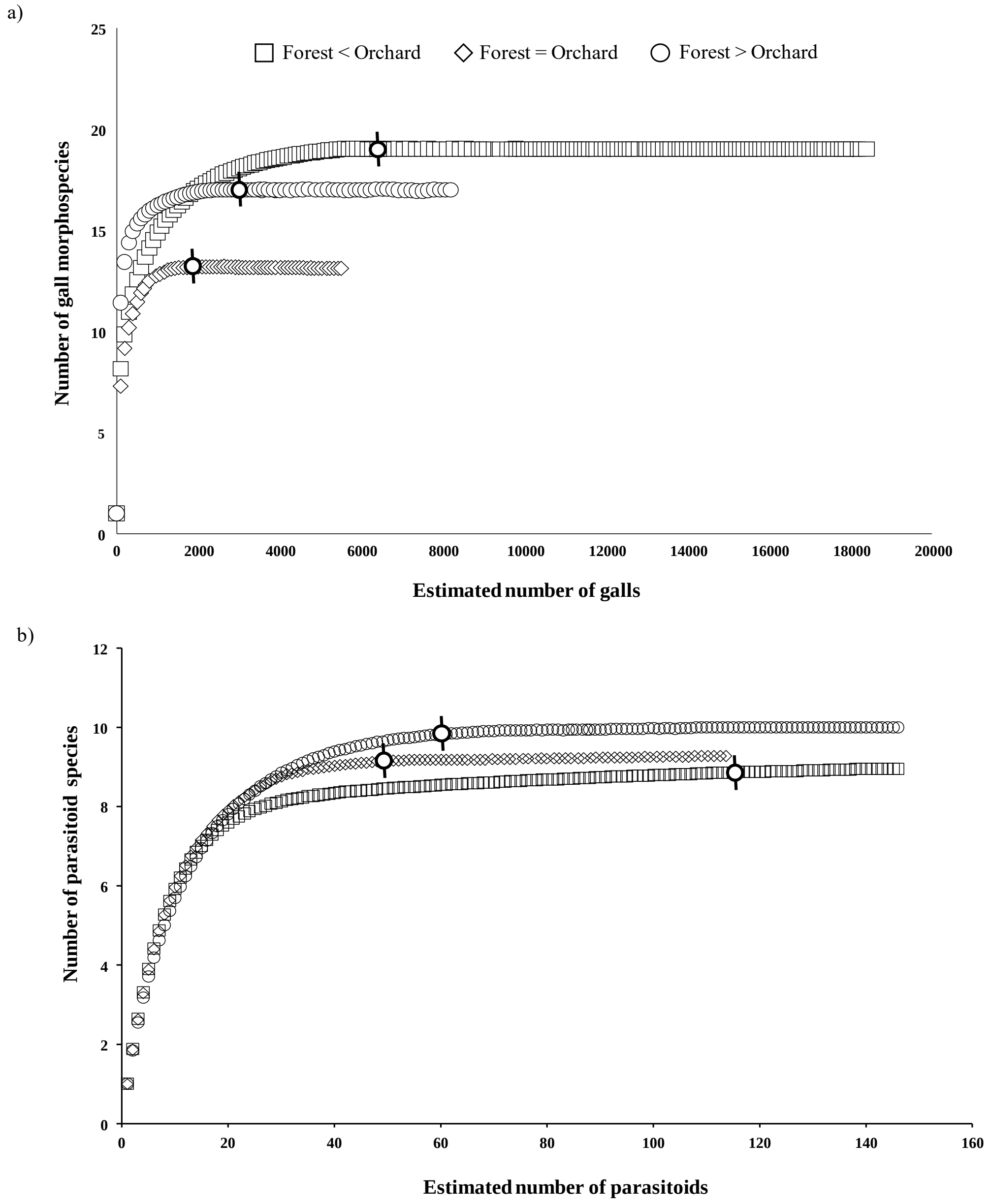

a)
■ Q. castanea
□ Q. magnoliifolia
▨ Q. obtusata
DBH (cm)
0
10
20
30
40
50
a
b
c
d
c
e
d
c
e
b)
Canopy cover (%)
0
20
40
60
80
100
a
b
c
d
e
b
e
d
b
c)
Chlorophyll content (SPAD Units)
0
10
20
30
40
50
60
a
a
b
c
d
c
c
d
c
Forest < Orchard
Forest = Orchard
Forest > Orchard

**Figure 2**


a)
□ Forest < Orchard
◇ Forest = Orchard
○ Forest > Orchard
Number of gall morphospecies
0
5
10
15
20
25
0
2000
4000
6000
8000
10000
12000
14000
16000
18000
20000
Estimated number of galls
b)
Number of parasitoid species
0
2
4
6
8
10
12
0
20
40
60
80
100
120
140
160
Estimated number of parasitoids

## Figure 3

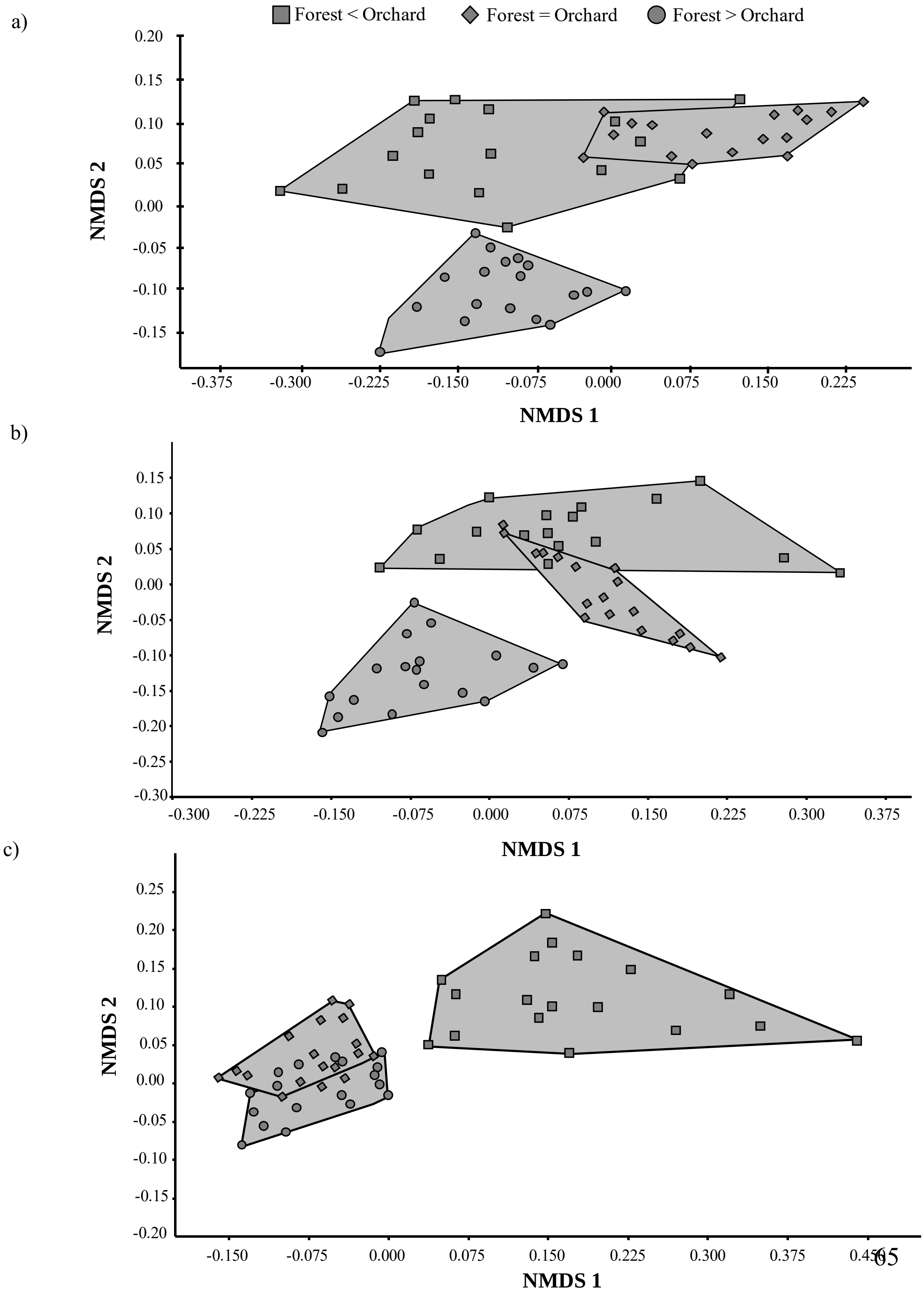
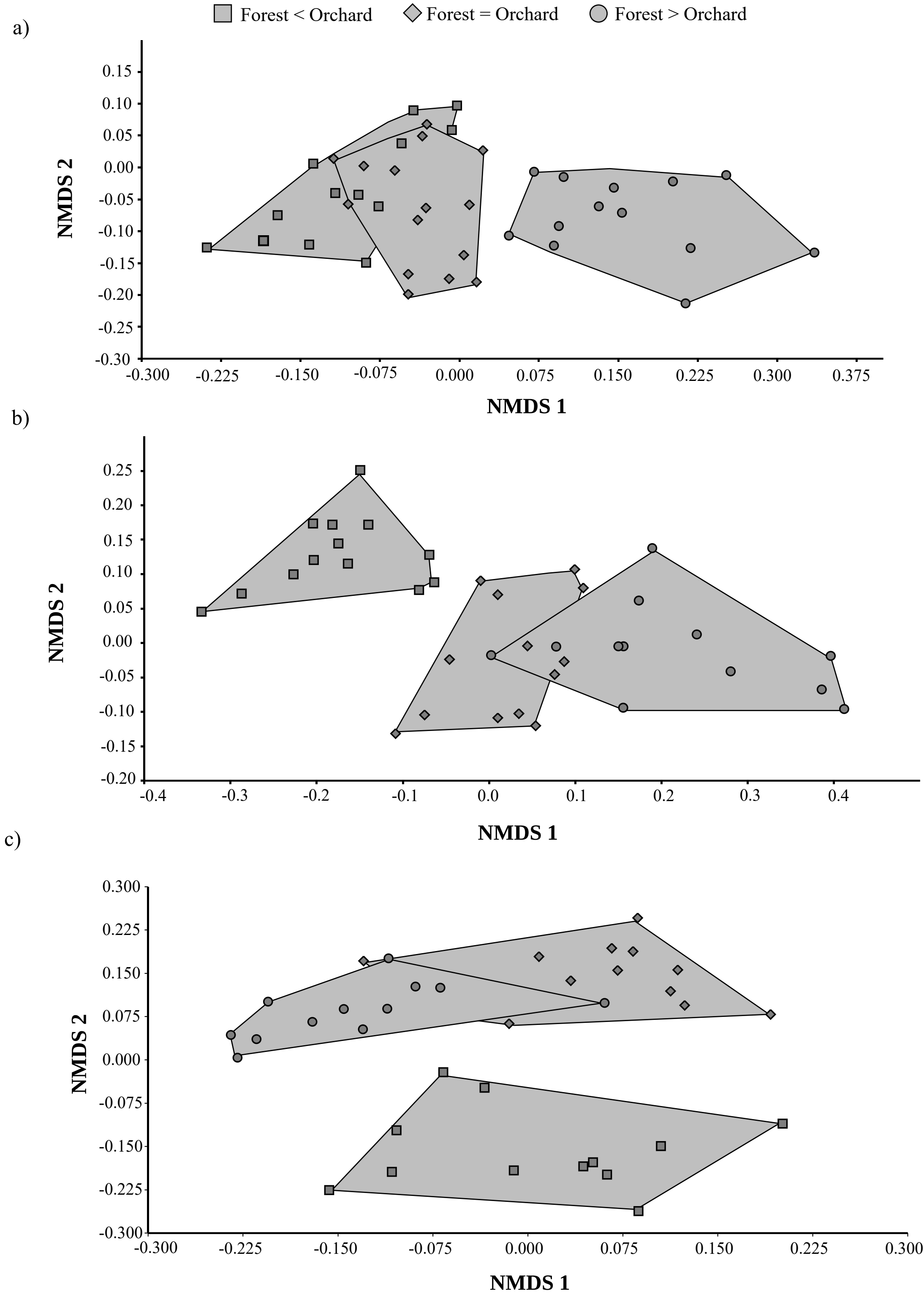
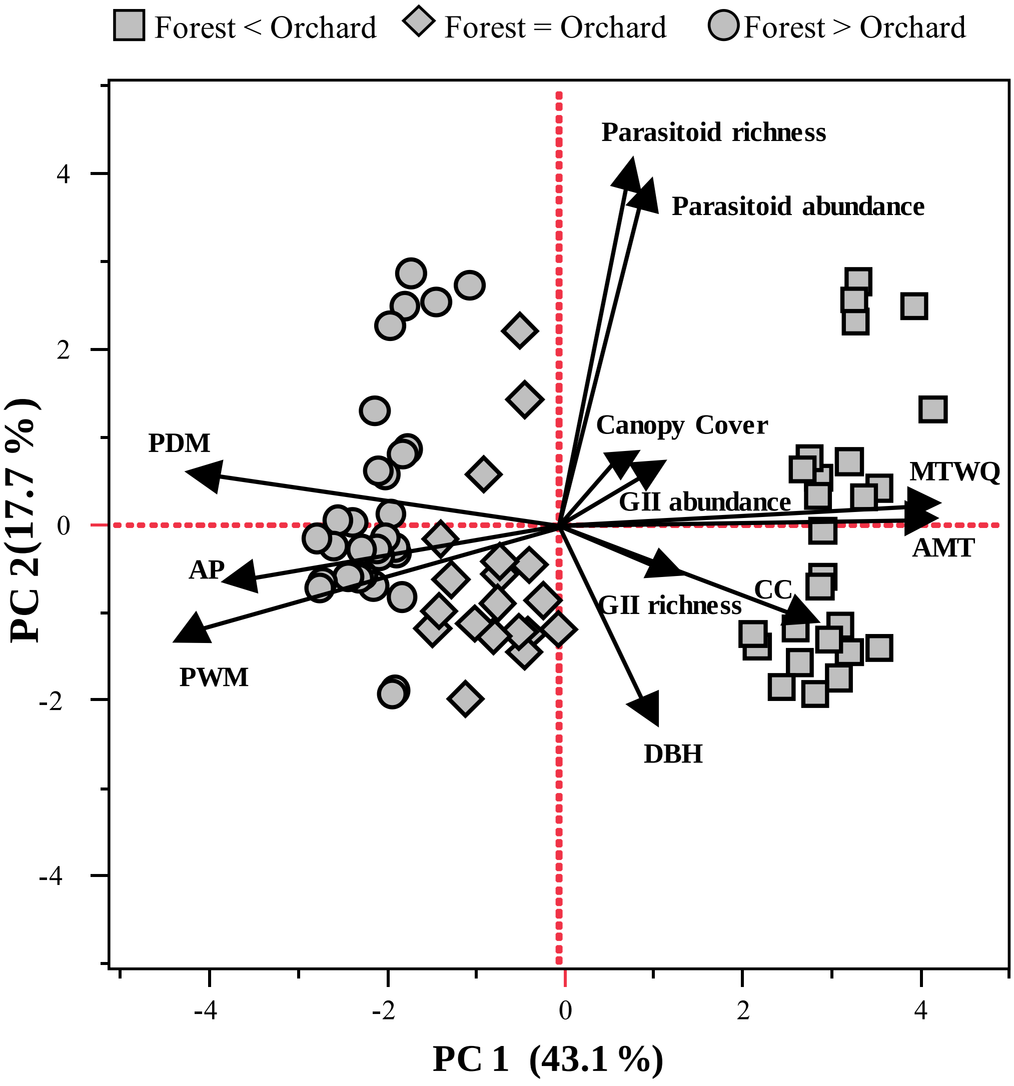

a)
■ Forest < Orchard
◆ Forest = Orchard
● Forest > Orchard
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
NMDS 2
-0.375
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
NMDS 1
b)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
NMDS 2
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
0.300
0.375
NMDS 1
c)
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
NMDS 2
-0.150
-0.075
0.000
0.075
0.150
0.225
0.300
0.375
0.450
NMDS 1

**Figure 4**



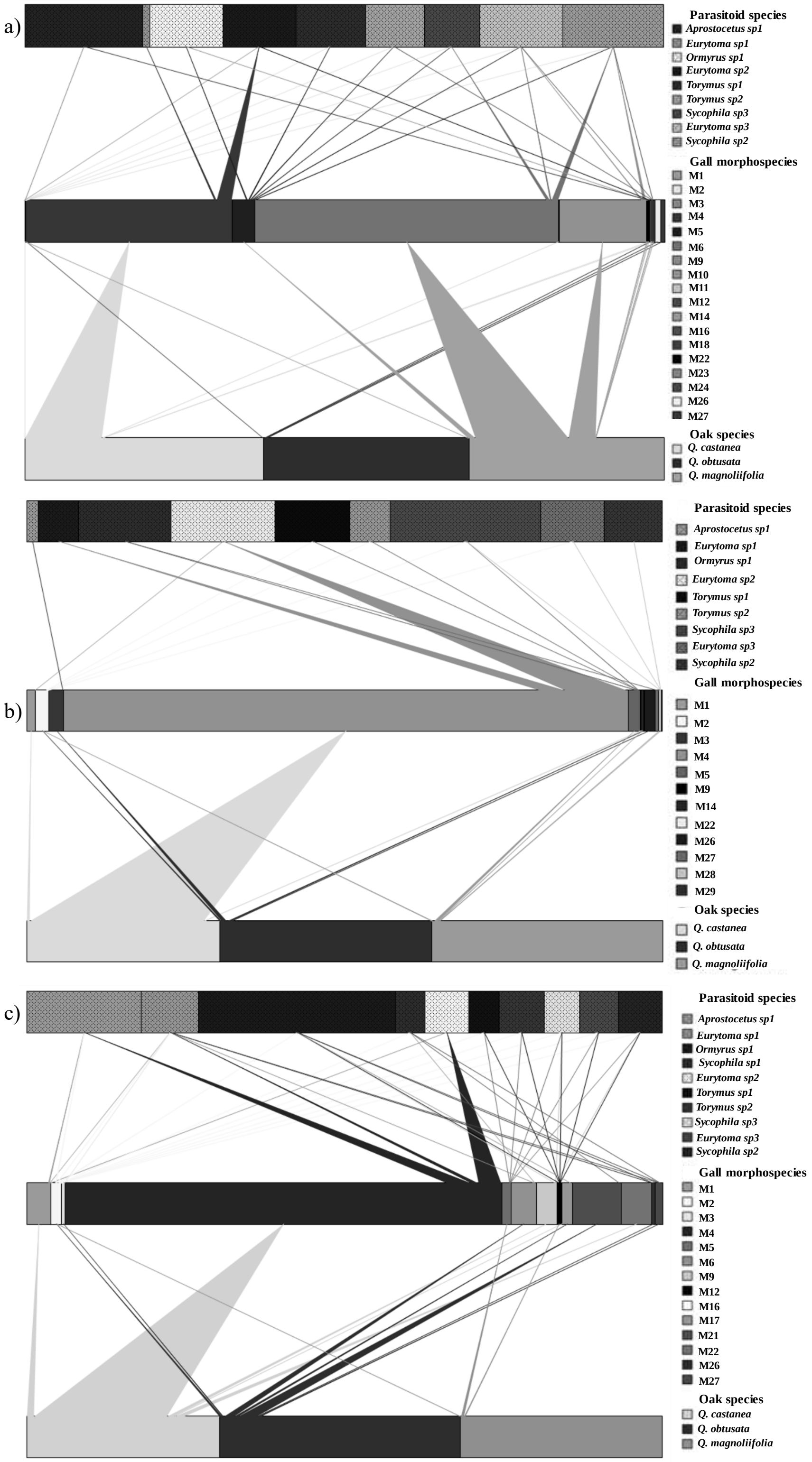
Forest < Orchard
Forest = Orchard
Forest > Orchard
a)
NMDS 2
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
0.300
0.375
NMDS 1
b)
NMDS 2
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
NMDS 1
c)
NMDS 2
0.300
0.225
0.150
0.075
0.000
-0.075
-0.150
-0.225
-0.300
-0.300
-0.225
-0.150
-0.075
0.000
0.075
0.150
0.225
0.300
NMDS 1

**Figure 5**



■ Forest < Orchard
◆ Forest = Orchard
● Forest > Orchard
Parasitoid richness
Parasitoid abundance
Canopy Cover
GII abundance
MTWQ
AMT
PDM
AP
PWM
GII richness
CC
DBH
4
2
0
-2
-4
-4
-2
0
2
4
PC 2(17.7 %)
PC 1 (43.1 %)

**Figure 6**


a)
Parasitoid species
Aprostocetus sp1
Eurytoma sp1
Ormyrus sp1
Eurytoma sp2
Torymus sp1
Torymus sp2
Sycophila sp3
Eurytoma sp3
Sycophila sp2
Gall morphospecies
M1
M2
M3
M4
M5
M6
M9
M10
M11
M12
M14
M16
M18
M22
M23
M24
M26
M27
Oak species
Q. castanea
Q. obtusata
Q. magnoliifolia
b)
Parasitoid species
Aprostocetus sp1
Eurytoma sp1
Ormyrus sp1
Eurytoma sp2
Torymus sp1
Torymus sp2
Sycophila sp3
Eurytoma sp3
Sycophila sp2
Gall morphospecies
M1
M2
M3
M4
M5
M9
M14
M22
M26
M27
M28
M29
Oak species
Q. castanea
Q. obtusata
Q. magnoliifolia
c)
Parasitoid species
Aprostocetus sp1
Eurytoma sp1
Ormyrus sp1
Sycophila sp1
Eurytoma sp2
Torymus sp1
Torymus sp2
Sycophila sp3
Eurytoma sp3
Sycophila sp2
Gall morphospecies
M1
M2
M3
M4
M5
M6
M9
M12
M16
M17
M21
M22
M26
M27
Oak species
Q. castanea
Q. obtusata
Q. magnoliifolia

# DISCUSIÓN GENERAL

Encontramos un efecto positivo de la fragmentación de los EFTs sobre el vigor de las plantas ya que los individuos más vigorosos de las tres especies de encinos se encontraron en sitios con una menor cobertura de bosque que de huerto. Este resultado puede deberse a dos posibles explicaciones: La primera es que la fragmentación provocada por los huertos de aguacate genera cambios en las variables climáticas locales, aumentando la temperatura, la velocidad del viento y disminuyendo la humedad en estos sitios. Se ha reportado que, los cambios en las variables climáticas pueden favorecer a los atributos del vigor de las plantas (Karban,2007; Magrach et al., 2014; Maldonado-López et al., 2015; Arroyo-Rodríguez et al., 2016). La segunda posible explicación es que, en los huertos de aguacate se utiliza la fertilización artificial, la cual, llega a los bosques adyacentes a los huertos a través de lixiviados y permite que los encinos presentes en los remanentes de bosque puedan hacer uso de diversos compuestos químicos como el magnesio, los nitratos, sulfatos y el nitrógeno (Bravo-Espinoza et al., 2012; Mao et al., 2017; Pérez-Solache et al., 2023).

Ese incremento en el vigor de las plantas provoca modificaciones en las interacciones que tienen las mismas con los insectos herbívoros. En los sitios de menor cobertura de bosque que de huerto, encontramos una mayor diversidad de IIA. Esto puede explicarse con la “Hipótesis del Vigor de la planta” de Price (1991), que nos dice que entre más vigorosos sean las plantas, serán más atacados por los insectos herbívoros, el cual incrementa en sitios antropizados (Maldonado-López et al., 2015, Rosetti et al., 2017, García-Jain et al., 2022; Pérez-Solache et al. 2023). Sin embargo, encontramos el patrón opuesto para los parasitoides, porque encontramos una mayor diversidad en sitios con una mayor proporción de bosque que de huerto y estos resultados pueden deberse a que particularmente, los organismos de los niveles tróficos superiores son altamente sensibles a los cambios de temperatura y humedad debido a que tienen mayores requerimientos de cobertura forestal (Gravel et al., 2011; Maldonado-López et al., 2016; García-Jain et al., 2022).

Finalmente, para las redes de interacción tritrófica, encontramos una red más compleja en términos de conectancia y diversidad de interacciones en sitios con una mayor cobertura de bosque que de huerto en comparación con las redes tróficas de los sitios que presentan una menor cobertura forestal. Aunque existe una mayor diversidad de IIA en sitios con menor cobertura de bosque que de huerto y esto puede deberse a los cambios en las condiciones ambientales que provocan un aumento en el vigor de los encinos hospederos (Anderson et al., 2022; Santos-Neto et al., 2022) y a su vez, a la pérdida de enemigos naturales como los parasitoides por las altas temperaturas (Batista Matos et al., 2013; Bernaschini et al., 2021). Lo que sugiere que en los sitios que tienen una menor cobertura de bosque que de huerto, dominan especies de parasitoides especialistas y, caso contrario, en sitios con una mayor cobertura de bosque que de huerto, dominan especies de parasitoides especialistas.

# CONCLUSIONES

Este trabajo nos permite concluir que efectivamente existen consecuencias de la fragmentación sobre el vigor de las plantas, la diversidad de IIA y parasitoides además de en sus interacciones tróficas. En el caso del vigor de la planta observamos un efecto positivo ya que en los sitios donde domina la cobertura de huertos, el vigor de los encinos es mayor y lo mismo ocurre con la diversidad de IIA. Sin embargo, la diversidad de parasitoides se reduce significativamente en sitios de mayor cobertura de bosque que de huerto. De maneracontraria, la red tritrófica de interacciones más compleja, corresponde a los sitios con una mayor cobertura de bosque que de huerto. Por lo tanto, resaltamos la importancia de conservar los remanentes de bosque que quedan dentro de la franja aguacatera del estado de Michoacán, debido a la gran diversidad que albergan de IIA y para evitar la extinción local de las especies de los parasitoides.

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