El Colegio de la Frontera Sur

Interacciones tróficas y biodiversidad: sistema *Piper*-orugas-parasitoides en la Península de Yucatán, México

Tesis
presentada como requisito parcial para optar al grado de
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para obtener el grado de **Doctor (a) en Ciencias en Ecología y Desarrollo Sustentable**

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Resumen

Las interacciones entre especies configuran la estructura y dinámica de las comunidades, mantienen el funcionamiento de ecosistemas, e inciden en patrones y procesos ecológicos y evolutivos. Estudios de las interacciones en un mundo cambiante, evidencian su dinámica, vulnerabilidad y su potencial para explicar y predecir los cambios que presentan poblaciones, comunidades y ecosistemas. Esta investigación describe la variación espacio-temporal del sistema tritrófico *Piper*-orugas-parasitoides, a través del análisis de la diversidad beta de especies e interacciones y parámetros de redes de interaccion, entre tres localidades y los periodos climáticos de lluvias y transición lluvia-sequía, a lo largo de remanentes de selva mediana sub-perennifolia de la Península de Yucatán.

Se encontraron 79 morfoespecies de orugas, alimentándose de seis especies de *Piper*, y hospederas de 20 especies de parasitoides, conformando un total de 116 interacciones tróficas, muchas de ellas no descritas anteriormente. La identidad de las especies e interacciones varió en escalas espacio temporales, siendo la reorganización de interacciones mayor entre periodos, y la composición de especies mayor entre localidades. Se describen dos nuevas especies de avispas parasitoides: *Aximopsis gabrielae* sp. nov**.** (Hymenoptera: Eurytomidae), endoparasitoide koinobionte en larvas de *Quadrus cerialis* (Lepidoptera: Hesperiidae), alimentándose de *Piper amalago*, y *Enicospilus carmenae* sp. nov. (Hymenoptera: Ichneumonidae), endoparasitoide koinobionte en larvas de *Zanola verago* (Lepidoptera: Apatelodidae) en *P. neesianum*, estas descripciones contribuyen a la historia natural de especies y géneros que participan. Esta investigación evidencia la importancia de implementar métodos estandarizados en el estudio de las interacciones, integrando ecología, historia natural y taxonomía, motivando al estudio de la biodiversidad en un mundo cambiante, desde una perspectiva multitrófica.

Palabras clave: *Aximopsis gabrielae***,** diversidad beta, diversidad de interacciones, *Enicospilus carmenae***,** historia natural, Lepidoptera, Piperaceae.

CAPÍTULO I INTRODUCCIÓN

1.1 Introducción General

La biodiversidad es el resultado de la variación espacial y temporal de las especies y de sus interacciones, las cuales inciden directa o indirectamente en la ecología y evolución de las especies que participan (Ehrlich y Raven 1964; Thompson 1996, 2005, 2014). Las interacciones entre especies conforman la estructura y dinámica de las comunidades (Letourneau y Dyer 2005; Andresen et al. 2018) y mantienen el funcionamiento de los ecosistemas (Duffy et al. 2007; Mougi y Kondoh 2012). Las amenazas que enfrenta la biodiversidad, como pérdida o reducción de hábitat, especies invasoras y cambio climático, también colocan en riesgo de extinción especies e interacciones (Janzen 1974; Thompson 1997; Tylianakis et al. 2010; Valiente et al. 2015), conllevando a un ciclo de reducción de diversidad, complejidad y estabilidad de las comunidades (Uchida y Drossel 2007; Mougi y Kondoh 2012; Loreau y De Manzacourt 2013; Landi et al. 2018), así como la productividad de los ecosistemas (Harvey et al. 2017; Marjakangas et al. 2020).

Estudios basados en interacciones, representan una oportunidad de integrar información de poblaciones, comunidades y ecosistemas (Ings et al. 2009), los cuales posibilitan la comprensión de patrones de diversidad (Dyer et al. 2010; López-Carretero et al. 2014; Ings et al. 2018), brindan información relevante sobre diversidad funcional (Blüthgen et al. 2008; Schmitz et al. 2015; Osorio-Canadas et al. 2018), correspondencia de rasgos (Eklöf et al. 2013; Dehling et al. 2014), especialización (Blüthgen et al. 2006; López-Carretero et al. 2016; Galiana et al. 2019), integración de teorías de nicho y redes ecológicas (Godoy et al. 2018), vulnerabilidad a extinción de especies (Petchey et al. 2008), distribución de interacciones (Giannini et al. 2013; Galiana et al. 2018), biogeografía de interacciones (Violle et al. 2014; Gravel et al. 2019), gradiente latitudinal de interacciones (Schemske et al. 2009), impacto de los cambios en el ambiente en las interacciones (Van der Putten et al. 2004; Valiente- Banuet et al. 2015), entre otros temas fundamentales en ecología y evolución, en consecuencia, su inclusión es hoy, esencial en el estudio de la biodiversidad (Janzen 1974; Dyer et al. 2014; Wilson 2017).

Enfoques recientes proponen estudiar la diversidad de interacciones como un componente en la estructura de las comunidades y brindan métodos para su medición (Bersier et al. 2002; Albrecht et al. 2007; Dormann et al. 2009; Novotný 2009; Blüthgen 2010; Dyer et al. 2010; Poisot et al. 2012; Delmas et al. 2019). Estos métodos permiten conocer, entender y predecir patrones de la diversidad (Kaiser-Bunbury y Blüthgen 2015; Poisot et al. 2015; Dormann et al. 2017), especialización (Oliveira et al. 2019) o estabilidad de comunidades (Fornoff et al. 2019), en diferentes escalas y gradientes (Tylianakis et al. 2006; Pellisier et al. 2018; Dyer y Forister 2019), que no es posible evidenciar estudiando un solo nivel trófico (Tylianakis et al. 2007; Thompson et al. 2012).

Se estima que alrededor del 75 por ciento de las especies descritas de ambientes terrestres hacen parte de interacciones tróficas entre plantas, herbívoros y enemigos naturales (Price 2002). Aunque los estudios de interacción planta-insecto y hospedero-parasitoide datan de inicios del siglo XX, es a partir de Price et al. (1980), que varios estudios reúnen evidencia sobre el efecto que ejercen niveles tróficos no adyacentes en la cadena trófica, por ejemplo, el efecto que pueden ejercer las plantas en los enemigos naturales (depredadores y parasitoides de herbívoros) (*bottom-up*), así como el efecto que pueden tener los enemigos naturales en la supervivencia y éxito biológico en las plantas (*top-down*), efectos conocidos como cascadas tróficas (Gómez y Zamora 1994; Letourneau y Dyer 1998, 2005; Dyer y Letourneau 1999a-b, 2003; Dyer et al. 2001; Boege y Marquis 2006). La descripción y estudio de estas cascadas tróficas, contribuye en la comprensión de la complejidad de las redes, así como de los patrones de diversidad de especies e interacciones en diferentes gradientes y escalas espacio-temporales (Dyer 2007; Dyer y Coley 2002).

Los estudios de interacciones planta-herbívoro han permitido entender cómo diferentes factores inciden en la variación espacio temporal de las plantas en relación a su disponibilidad como recurso (Fraenkel 1953; Feeny 1970; Baldwin y Schultz 1983;

Rosenthal y Janzen 1979; Coley y Barone 1996; Novotný y Basset 2005, Novotný et al., 2006), así como patrones de amplitud de dieta de hebívoros y su relación con gradientes latitudinales (Gauld et al.1992; Dyer et al. 2007; Novotný 2009, Novotný et al. 2010; Forister et al. 2012, 2015) o sucesionales (Boege et al. 2019). Por otra parte, los estudios de interacción parasitoide-hospedero han contribuido a la comprensión de dinámicas de poblaciones (Nicholson y Bailey, 1935); estructura de comunidaes (Force 1974; Kato 1994; Price 1994; Godfray et al. 1999; Rott y Godfray 2000; Lewis et al. 2002), así como de la relación entre estructura de redes y reducción de hábitat (Valladares et al. 2001; Tylianakis et al. 2007) y del efecto del cambio climático (Stireman et al. 2005).

Diferentes estudios demuestran cómo las interacciones fluctuan de acuerdo a la fenología de plantas e insectos, la cual determina la probabilidad de encuentro e interacción planta-herbívoro (Coley et al. 1985; Coley y Baron 1996) o parasitoide-hospedero (Godfray et al. 1994) y cómo la heterogeneidad espacial influye en la probabilidad de ocurrencia de la interacción de acuerdo con disponibilidad de recursos, calidad de habitat, conectividad, entre otros factores (Araújo y Ronzenfeld 2014; Pellissier et al. 2018). Por todo lo anterior, el campo de investigación de las interacciones planta-herbivoro-enemigo natural, representa un marco de referencia teórico y metodológico que permite entender diferentes dimensiones de la biodiversidad (Dyer et al. 2014).

Para conocer la variación espacial y temporal de las interacciones investigué el sistema tritrófico *Piper*-orugas-parasitoides. El género *Piper* con una distribución pantropical, es uno de los mas diversos dentro de las angiospermas, con más de 1300 especies en el Neotrópico (Quijano-Abril et al. 2006; Jaramillo et al. 2008); algunas de sus especies son endémicas, y pueden ser dominantes en tierras bajas (Jaramillo 2006) formando asociaciones de varias especies (Gentry 1982). Por otra parte, las pocas especies estudiadas presentan una muy alta diversidad fitoquímica (Dyer y Palmer 2004) y son consideradas un elemento clave en ecosistemas, por proveer alimento a una gran diversidad de herbívoros (Marquis 1991; Vanin et al. 2008), incluyendo orugas de las familias Geometridae, Erebidae, Papilionidae y Apatelodidae (Beccaloni et al. 2008; Janzen y Hallwachs 2012; Dyer y Gentry 2019). Estas orugas a su vez son hospederos de de moscas y avispas parasitoides (p.e. Whitfield et al. 2009; Tape et al. 2014). Estudios recientes han demostrado que la diversidad química de *Piper* puede reducir la respuesta inmune de orugas y promueve el reclutamiento de parasitoides (Richards et al., 2010, 2015; Glassmire et al., 2016; Salazar et al., 2016; Slinn et al. 32018), estos hallazgos permiten considerar *a priori* las asociaciones *Piper*, orugas, parasitoides, como un sistema tritrófico.

Existen algunos estudios en *Piper* que permiten conocer la incidencia que tienen factores abióticos (Connahs et al. 2009; Cosmo et al. 2019), o bióticos (Richards et al. 2015; Salazar et al. 2016; Glassmire et al. 2016) en la comunidad de herbívoros y parasitoides asociados; sin embargo, no hay muchos estudios que permitan conocer la dinámica espacio-temporal del sistema tritrófico *Piper*-orugas-parasitoides.

1.2 Objetivo general y objetivos particulares

1.2.1. Objetivo general

Describir la diversidad espacial y temporal de especies e interacciones en el sistema *Piper*-orugas-parasitoides en la Peninsula de Yucatán (México).

1.2.2 Objetivos particulares

1. Determinar la variación de diversidad de especies e interacciones en el sistema *Piper*-orugas-parasitoides en tres localiades lo largo de un transecto suroeste-noreste de la Península de Yucatán en los periodos de lluvias y transición lluvias-sequía.

2. Describir algunas especies e interacciones que componen el sistema *Piper*-orugas-parasitoides integrando datos geográficos, ecológicos, taxonómicos e historia natural.

1.3 Metodología general

1.3.1 Área de estudio y localidades de muestreo

El estudio se realizó en la Península de Yucatán (PY). Esta región, según su geomorfología, clima, suelo, vegetación y fauna, conforma la Provincia Biogeográfica Península de Yucatán, la cual presenta afinidad mesoamericana con respecto al Neotrópico (Duno de Stefano et al. 2012; Morrone 2017).

El clima en la PY es tropical sub-húmedo, con una temperatura promedio de 26°C y presenta una marcada estacionalidad, con estación de lluvias de junio a octubre, transición lluvia-sequía de noviembre a febrero y sequía de marzo a mayo, y presenta un promedio de precipitación total anual entre 600 y 1400 mm (Orellana et al. 2009). Los suelos son cársticos y tiene un relieve semiplano con elevaciones inferiores a 350 m. La vegetación es un mosaico heterogeneo que incluye todas las combinaciones entre selva baja caducifolia al norte, hasta selva alta perennifolia al sur, incluyendo selva mediana subperennifolia, el cual es el tipo de vegetación predominante en toda la región (Martínez y Galindo-Leal 2002; Islebe et al. 2015). En la PY se registran dieciséis especies de *Piper* (Villaseñor 2016), siendo éstos parte de los registros más septentrionales del género en el Neotrópico (Quijano-Abril et al. 2006). Varios estudios han documentado la diversidad y estacionalidad de los lepidópteros en la PY (Pozo et al. 2003, 2008; Montero-Muñoz 2013; Essens et al. 2014), y otros más permiten conocer la diversidad de algunas familias de avispas parasitoides (Delfín-González y Chay-Hernández 2010; González-Moreno et al. 2015, 2018).

Los sitios de muestreo se eligieron sobre un transecto suroeste-noreste de aproximadamente 600 km, cubriendo la mayor heterogeneidad de la selva mediana subperennifolia, en la que se distribuyen especies de *Piper* de esta región (Figura 1, Tabla 1).

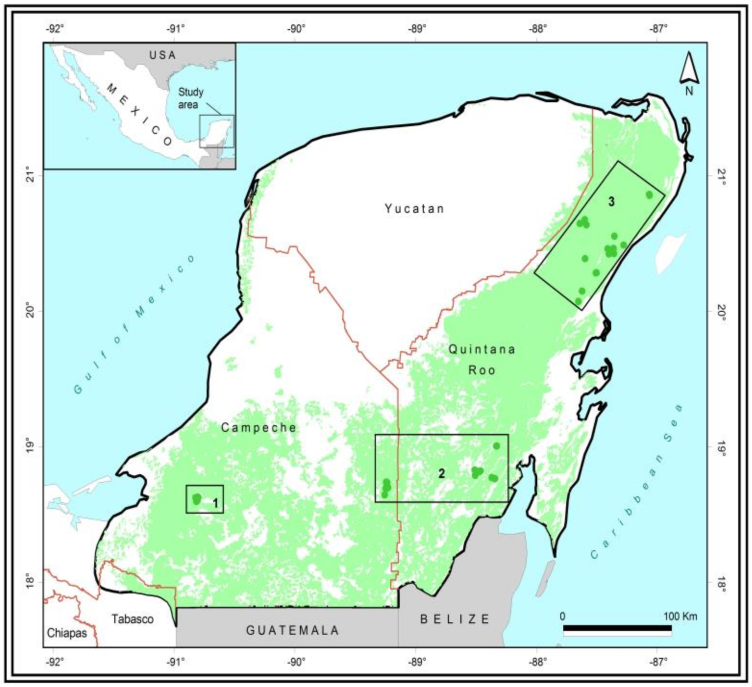

Figura 1. Área y localidades de estudio a lo largo de un gradiente suroeste-noreste en selva mediana sub-perennifolia de la Peninsula de Yucatán (Mexico). 1. El Tormento (ET); 2. Nuevo Becal- Bacalar (NBB); 3. Tulum-Puerto Morelos (TPM)

Tabla 1. Localidades de muestreo

Localidad	***Ubicación geográfica***	***Área aprox.***
El Tormento (ET)	18º 16.4' N, 90º 46.6' W Escárcega, Campeche	1400 ha
Nuevo Becal-Bacalar (NBB)	18º 41.4’ N, 89º 14.77' W Nuevo Becal, Campeche 18º 49.3' N, 88º 27.7' W San Felipe de Bacalar, Quintana Ro	>5000 ha
Tulum-Puerto Morelos (TPM)	20º 16.8' N. 87º 30.3' W Tulum, Quintana Roo 20º 51.58' N. 87º 3.84' W Puerto Morelos, Quintana Roo	<1000 ha

ET es una reserva forestal establecida en 1961. Esta localidad está dominada por *Manilkara zapota* (L.) P. Roven (Sapotaceae), *Vitex gaumeri* Greenm. (Lamiaceae) y *Brosimum alicastrum* Sw. (Moraceae) (Secretaría de Agricultura y Recursos Hidráulicos, SARH 1981). NBB está compuesta por dos áreas en los municipios de Nuevo Becal y San Felipe de Bacalar, que abarcan > 5000 ha. Estas localidades son similares y contienen bosques subperennifolios que han experimentado una extracción selectiva de madera caracterizada por un nivel medio de perturbación, con un dosel superior dominado por *Spondias mombin* L. (Anacardiaceae), *Pouteria campechiana* (L.) Baehni (Sapotaceae) y *B. alicastrum*. Nuevo Becal colinda con la Reserva de la Biosfera de Calakmul, establecida en 1989 (Secretaría de Medio Ambiente Recursos Naturales y Pesca, SEMARNAP 1989) y la reserva forestal en San Felipe de Bacalar fue establecida en 1971 (SARH, 1981). TPM es una zona turística con pequeños fragmentos de menos de 500ha de bosque subperennifolio con altos niveles de perturbación causada por ciclones, incendios forestales y deforestación. El dosel superior de los fragmentos de bosque está dominado por *B. alicastrum*.

1.3.2 Métodos de muestreo

En cada una de las tres localidades, se establecieron al menos 10 parcelas en cada periodo climático (lluvias y transición lluvias-sequía). Las parcelas fueron circulares con 10 m de diámetro centradas en un individuo de *Piper* y estuvieron separadas al menos 300m entre sí, y 50 m de cualquier borde de bosque para evitar pseudoreplicación y efecto de borde (Figura 2).

Figura 2. Diseño de muestreo en parcelas circulares

Registro individual de *Piper,* orugas y parasitoides. En cada parcela se registraron todos los individuos de cada especie de *Piper* y se recolectaron las orugas alimentándose en las hojas en bolsas plásticas (con hojas de la planta), para ser transportadas al laboratorio para ser críadas en condiciones de luz, humedad y temperatura ambiente, hasta la emergencia de lepidópteros o parasitoides.

Identificación taxonómica. Las especies de *Piper* fueron previamente identificadas en campo y verificadas en el Herbario de ECOSUR (CIQR). Las orugas fueron fotografiadas en campo o laboratorio para identificación. Lepidópteros en estado de oruga y adultos fueron identificados por C. Pozo y L. Dyer y/o utilizando recursos en línea (Janzen y Hallwachs 2012, http://janzen.sas.upenn.edu; Dyer y Gentry 2019, http://www.caterpillar.org). Parasitoides del orden Diptera fueron identificados por J. Stireman y avispas parasitoides por J. Whitfield, M. Gates y D. Campos. Los especímenes recolectados y criados se depositaron en la Colección de Lepidópteros (ECO-CH-L) y la Colección de Artrópodos (Insectos y Arañas) (ECO-CH-AR), ambas del Museo de Zoología de ECOSUR. Con el fin de completar la identificación taxonómica de lepidópteros y parasitoides se extrajo el ADN con el protocolo estándar de Ivanova et al. (2006), y se obtuvieron secuencias del gen de la subunidad 1 del citocromo mitrocondrial (COI), de acuerdo con el protocolo descrito en Hebert et al. (2003). Posteriormente, estas secuencias se usaron para establecer comparaciones con librerias disponibles en BOLD System, y obtener identificaciones taxonómicas de acuerdo con la metodología de Ratnasinghan y Hebert (2013).

1.3.3 Esquema de la tesis

Los resultados de este trabajo se presentan en el capítulo 2. En la sección 2.1 se determinó la variación espacial y temporal de diversidad de especies e interacciones, en el sistema *Piper*-orugas-parasitoides (Objetivo 1). En las secciones 2.2 y 2.3 se describen especies integrando datos geográficos, ecológicos, taxonómicos e historia natural (Objetivo 2). En el capítulo 3 se presenta la discusión general. En la sección 3.1 la variación espacio temporal de especies e interacciones; en la sección 3.2 se discute la estructura de comunidades en el sistema *Piper*, orugas, parasitoides y en sección 3.3 se presentan recomendaciones y perspectivas.

CAPÍTULO 2 RESULTADOS

2.1 Campos-Moreno DF, Dyer LA, Salcido D, Massad TJ, Pérez-Lachaud G, Tepe EJ, Whitfield JB and Pozo C. 2021. Importance of interaction rewiring in determining spatial and temporal turnover of tritrophic (Piper-caterpillar-parasitoid) metanetworks in the Yucatán Península, México. Biotropica. 53(4):1071–1081. https://doi. org/10.1111/btp.12946

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ORIGINAL ARTICLE

Importance of interaction rewiring in determining spatial and temporal turnover of tritrophic (*Piper*-caterpillar-parasitoid) metanetworks in the Yucatán Península, México

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Abstract

Natural history studies documenting spatial and temporal variation of species assemblages and their interactions are critical for understanding biodiversity and community ecology. We characterized caterpillar–parasitoid assemblages on shrubs in the genus *Piper* across remnants of semi-evergreen forest in the Yucatán Península during the rainy and rainy–dry seasons. We collected caterpillars feeding on *Piper* leaves and reared them to adults or parasitoids to: (i) describe tritrophic interactions between *Piper*, caterpillars, and parasitoids, (ii) compare empirical metanetworks among sites and seasons, and (iii) investigate patterns in species and interaction turnover across spatial and temporal scales to understand the contribution of species composition and interaction rewiring to overall interaction turnover. We found six *Piper* species supporting 79 species of caterpillars, which in turn hosted 20 species of parasitoids. In total, there were 116 realized trophic interactions. Species and interactions exhibited substantial turnover at temporal and spatial scales. Total interaction turnover was more pronounced across seasons in all sites (>93%), than it was between sites (<91%). We also found that interaction rewiring contributed more to overall interaction turnover than species turnover. The spatial and temporal variation in metanetworks documented here contribute to understanding fine-scale temporal and spatial turnover in tropical species and interactions and raise important questions about the lability of consumer specialization and the short-term effects of interaction rewiring on the stability of biotic communities. Our results highlight the importance of tropical food web studies that are based on natural history using consistent field methods to document bi- and tripartite interactions.

Abstract in Spanish is available with online material.

KEYWORDS
beta diversity, caterpillar–parasitoid assemblages, natural history, temporal–spatial variation, tritrophic interactions

1 | INTRODUCTION

Understanding how the composition and structure of species assemblages vary across spatial and temporal scales has been the focus of decades of study in community ecology (Legendre, 2014; MacArthur, 1965; Ricklefs, 1987; Whittaker, 1960). Discovery of species and their interactions is critical to developing a deeper understanding of multiple dimensions of biodiversity (Dyer et al., 2014; Janzen, 1974; Wilson, 2017). Over half of all described species are involved in multitrophic interactions between plants, herbivores, and natural enemies (Price, 1994, 2002); studying these relationships is therefore fundamental to understanding community dynamics and diversity patterns (Letourneau et al., 2005; Singer & Stireman, 2005). Studies of plant–herbivore and host–parasitoid interaction networks contribute to understanding evolutionary and ecological outcomes of interactions (Abdala-Roberts et al., 2019), such as host specificity (Dyer et al., 2007), diet breadth (Forister et al., 2012), community structure (Force, 1974; Lewis et al., 2002; Memmott et al., 1994), and stability (Sauve et al., 2014; Thébault & Fontaine, 2010). Network analyses also contribute to the description and understanding of interactions (Newman, 2003, 2018) and can answer questions focused on how interactions generate predictable community patterns (Dormann et al., 2017) and local community stability (Fornoff et al., 2019) or how specialization changes over space or time (Oliveira et al., 2019).

Networks of trophic interactions are not static; they fluctuate in response to abiotic and biotic factors that vary spatially and temporally (Cagnolo et al., 2011; Poisot et al., 2015). For example, seasonal changes in the identity and strength of plant–herbivore–enemy interactions occur via predictable changes in host plant availability and quality as well as consumer activity (Hopkins & Memmott, 2003; Hunter, 2003). Seasonally cued phenophases of plants or insects, including reproduction, growth, and diapause, can moderate the presence or abundance of host species and the timing or likelihood of interactions (Godfray et al., 1994; van Nouhuys & Lei, 2004; Wolda, 1988). Seasonal changes affect plant quality and defensive chemistry, which may determine the presence or strength of chemically mediated plant–insect interactions (Coley, 1998; Dyer, 2007; Murakami et al., 2008). Spatial factors also contribute to species co-occurrence patterns through suitable habitat, plant community structure, and connectivity, all of which determine the likelihood of interactions occurring in any given habitat (Cronin & Reeve, 2014; Thies et al., 2003). There is a rich history of studies linking spatial and seasonal fluctuations in biotic communities with a focus on species beta diversity (Whittaker, 1960, 1972; MacArthur, 1965; Ricklefs, 1987; see reviews in Koleff et al., 2003 and Calderón-Patrón & Moreno, 2019). In the last decade, these patterns have been explored through beta diversity analysis of species interactions (see Novotny, 2009; Poisot et al., 2012) and network analysis, which provide quantitative indices that allow comparisons between networks across spatial and temporal gradients (Pellissier et al., 2018; Tylianakis & Morris, 2017). Such studies focusing on network ecology and diversity patterns in relation to community processes and ecosystem function are critical to biodiversity conservation efforts (Kaiser-Bunbury & Blüthgen, 2015; Moreno et al., 2018).

Species interactions are dynamic, and there are substantive knowledge gaps concerning the heterogeneity of these networks across spatial and temporal scales. Despite the value of documenting variation of insect assemblages on plants, natural history studies describing plant–caterpillar–parasitoid interactions are still relatively uncommon (Dyer et al., 2010). Seasonal turnover in plant–herbivore interactions may be largely influenced by interaction turnover due to reassembly or reorganization of interactions among the same pool of co-occurring species (i.e., CaraDonna et al., 2017; Lepesqueur et al., 2018; Saavedra et al., 2017), referred hereafter as *interaction rewiring*, rather than turnover in species composition. Yet, there is much to be explored regarding spatial and seasonal effects on interaction beta diversity and rewiring (Bartley et al., 2019), as well as the contribution of each trophic level to overall structure of metanetworks.

This study was conducted in the Yucatán Península (YP), which is considered a biodiversity hotspot (Myers et al., 2000) and includes the northernmost distribution records of the tropical shrub, *Piper* (Piperaceae; Quijano-Abril et al., 2006), with sixteen recorded species (Villaseñor, 2016). Several studies have documented the diversity and seasonality of Lepidoptera in the YP (Essens et al., 2014; Montero-Muñoz et al., 2013; Pozo et al., 2003, 2008), and others have focused on some families of parasitic wasps (Delfín-González & Chay-Hernández, 2010). It is particularly useful for conservation to continue these surveys in this biologically important region, as well as to link surveys to studies that document tritrophic interactions between plants, caterpillars, and parasitoids.

Because species turnover across seasons and habitat types is high for tropical insects (Janzen, 1993; Wolda, 1988), we hypothesized that *Piper*–caterpillar–parasitoid networks would be characterized by high beta diversity of species and interactions across seasons and sites. In this study, we collected caterpillars feeding on *Piper* leaves and reared them to adults or parasitoids to: (i) describe tritrophic interactions between *Piper*, caterpillars, and parasitoids, (ii) compare empirical metanetworks among sites and seasons, and (iii) investigate patterns in species and interaction turnover across spatial and temporal gradients to understand the contribution of species composition and interaction rewiring to overall interaction turnover.

2 | METHODS

2.1 | Study system

The tropical genus *Piper* is characterized as a “species swarm” because it is abundant, locally diverse, and many ecologically similar species of *Piper* frequently occur together (Gentry, 1982). There are more than 1300 species of *Piper* in the Neotropics (Quijano-Abril et al., 2006), and there is a wealth of natural history of these plants yet to be discovered. Existing natural history studies on a handful of *Piper* species indicate that the genus shows a great phytochemical diversity (Dyer & Palmer, 2004) and supports complex communities of arthropods (Marquis, 1991; Tepe et al., 2014; Vanin et al., 2008), including hundreds of species of caterpillars mostly in the families Geometridae, Erebidae, Hesperiidae, and Nymphalidae (Beccaloni et al., 2008; Dyer & Gentry, 2019; Janzen & Hallwachs, 2012), which are parasitized principally by flies in the family Tachinidae and wasps in the families Braconidae, Ichneumonidae, and Eulophidae (Arias-Penna et al., 2019; Cosmo et al., 2019; Glassmire et al., 2016; Whitfield et al., 2009). There is also substantive geographic and seasonal variation in ecological communities associated with *Piper* (Connahs et al., 2009, 2011; Cosmo et al., 2019; Glassmire et al., 2016). These characteristics make the study of caterpillar–parasitoid assemblages associated with *Piper* ideal for understanding the variation of species and interactions across temporal and spatial scales.

2.2 | Study area and sampling localities

The Yucatán Península, México is characterized by a warm sub-humid climate with a mean annual temperature of 26°C. Soils are karstic, and the landscape does not rise above 350 m a.s.l. Precipitation is highly seasonal with a rainy season from June to October, a rainy–dry transition season from November to January and a dry season from February to May. Total annual precipitation across the YP ranges from 600 to 1800 mm (Orellana et al., 1999). The dominant ecosystems on the YP include deciduous forest, semi-deciduous dry forest, and semi-evergreen forest (Martínez & Galindo-Leal, 2002).

In order to cover the greatest heterogeneity of semi-evergreen forest, we chose three localities along a ~600 km long south–north transect of the YP (Figure S1). The study localities are briefly described below. El Tormento (ET) in southwestern YP is a forest reserve with 1400 ha (18°16.4′N, 90°46.6′W) that was established in 1961. This locality is dominated by *Manilkara zapota* (L.) P. Roven (Sapotaceae), *Vitex gaumeri* Greenm. (Lamiaceae), and *Brosimum alicastrum* Sw. (Moraceae) (SARH, 1981). The second locality (NBB) in southeastern YP is composed of two areas encompassing >5000 ha, Nuevo Becal (18°41.4′N, 89°14.77′W) and San Felipe de Bacalar (18°49.3′N, 88°27.7′W). These areas are close together and are similar containing semi-evergreen forest that has experienced selective timber extraction characterized by a medium level of disturbance. Nuevo Becal is adjacent to the Calakmul Biosphere Reserve established in 1989 (SEMARNAP, 1989) and the forest reserve near San Felipe de Bacalar was established in 1971 (SARH, 1981), with an upper canopy dominated by *Spondias mombin* L. (Anacardiaceae), *Pouteria campechiana* (Kunth) Baehni (Sapotaceae), and *B. alicastrum*. The third locality in northeastern YP was Tulum–Puerto Morelos (TPM), a tourist area (20°16.8′N, 87°30.3′W). This locality has small fragments <500 ha of semi-evergreen forest with high levels of disturbance caused by cyclones, forest fires, and deforestation. The upper canopy of the forest fragments is dominated by *B. alicastrum*.

2.3 | Sampling *Piper*–caterpillar–parasitoid interactions

We sampled *Piper* plants and caterpillars in the three localities across two seasons (rainy and rainy-dry), from December 2017 to February 2019. Ten to eleven plots were sampled in each site and season, for a total of 62 plots. Plots were 10 m in diameter and were centered on a randomly selected *Piper* shrub. To avoid pseudo-replication and edge effects, each plot was separated by at least 300 m from other plots and was at least 50 m from any forest boundary following methods in Dyer et al. (2010). All *Piper* shrubs within a plot were surveyed, and caterpillars found feeding on leaves were collected. All the caterpillars were carried to the laboratory and reared under ambient conditions feeding on leaves of the same species from which they were collected until adult Lepidoptera or parasitoids emerged.

All *Piper* species were identified by EJT, and determinations of individuals from the plots were verified against the collections in the Herbarium at ECOSUR (CIQR). Caterpillars were photographed in the field or laboratory, and larvae and adults were identified to genus or species by CP and LD, and using online resources (Janzen & Hallwachs, 2012; http://janzen.sas.upenn.edu; Dyer & Gentry, 2019; http://www.caterpillars.org). Insect parasitoids in the order Hymenoptera were identified to genus or species by DC and JW; Tachinids in the order Diptera were identified to genus by J.O. Stireman III. Specimens of Lepidoptera were deposited in the Lepidoptera collection (ECO-CH-L) and Hymenoptera and Diptera in the Arthropod Collection (ECO-CH-AR), both collections of the Zoological Museum at ECOSUR. To assist in species delineation and identification of morphospecies, morphology-based taxonomy and DNA sequences were both used following Boege et al. (2019). We used CO1 sequences (Hebert et al., 2003) for comparisons with libraries available in the Barcode of Life Data (BOLD) system following Ratnasingham and Hebert (2013).

2.4 | Metanetworks

A metanetwork is analogous to a metacommunity (Baiser et al., 2013; Leibold et al., 2004; van Nouhuys & Hanski, 2002), we referred to them here as a *Piper* shrub metacommunity interlinked by caterpillar–parasitoid assemblages. Tripartite networks were constructed for each site and season. Network analysis was conducted using the bipartite package in R (Dormann et al., 2009). To calculate network indices, quantitative bipartite matrices of *Piper*–caterpillar and caterpillar–parasitoid interactions were constructed and the following network parameters were calculated: interaction diversity (ID), weighted connectance (C_{qw}), and weighted specialization (H'_2). These parameters summarize important aspects of plant–arthropod interactions that might vary over space and time, including the degree of consumer specialization and interaction diversity at the network level (Blüthgen et al., 2006; Kaiser-Bunbury & Blüthgen, 2015).

2.5 | Quantifying spatial and temporal beta diversity

The sample sizes for our study reflect snapshots of the actual densities of caterpillars and associated parasitoids on *Piper*, since all individuals in a plot were collected. While sample sizes and associated rarefaction approaches are important for overall diversity estimates for species and interactions (Jordano, 2016), the goal of our approach was to compare the diversity of interactions found in these snapshots and not to estimate the diversity of species across sites and seasons. Rather, we completed counts of all interactions at a given plot and time to create observed empirical metanetworks of trophic interactions between individuals of *Piper* surveyed, caterpillars collected, and parasitoids reared to compare among sites and seasons. Simulations and empirical studies have demonstrated that similar sample sizes of network parameters obtained through similar sampling efforts are effective for comparisons across biotic and abiotic gradients (Dyer & Forister, 2019; Forister et al., 2015). Because of the small number of interactions at the plot scale, we created larger scale networks by randomly joining data from three different plots within each site and season and pooling species and interactions in all possible randomized three-plot combinations, a method that allows for sampling at the smallest scale and estimations of potential networks at larger scales (Dyer & Forister, 2019).

Pairwise comparisons were made among these plot aggregates for calculations of beta diversity both for species and interactions across spatial and temporal units. Beta diversity was calculated as Jaccard dissimilarity $\beta_J = (b + c)/(a + b + c)$, where a represents the number of shared species between two samples, and the exclusive number of species is represented by b in the first sample and c in the second sample (Koleff et al., 2003; Magurran et al., 2010). We calculated total species turnover (β_S) and then calculated turnover separately for each trophic level: plants (β_{Plants}), caterpillars ($\beta_{\text{Caterpillars}}$), and parasitoids ($\beta_{\text{Parasitoids}}$). Second, following Poisot et al. (2012), we estimated interaction turnover (β_{WN}) composed of two additive components: (1) interaction turnover due to differences in the composition of interacting species (β_{ST}) and (2) interaction rewiring (β_{OS}). For both species and interaction turnover, we calculated values across seasons and sites. Seasonal turnover was calculated as the turnover across seasons for each site, and site-level turnover was calculated for each pairwise site comparisons. We generated 1000 null matrices that preserved marginal totals using the vegan package in R (Oksanen et al., 2020) to compare with our observed networks and to evaluate the biological significance of observed values. Although hypothesis testing was not the goal of this observational study, we used a simple Bayesian regression to compare beta diversity estimates across sites and seasons with a Gaussian error distribution, identity link, and uninformative Gaussian priors in the brms package in R using the probabilistic language Stan (Bürkner, 2017).

3 | RESULTS

3.1 | Community composition

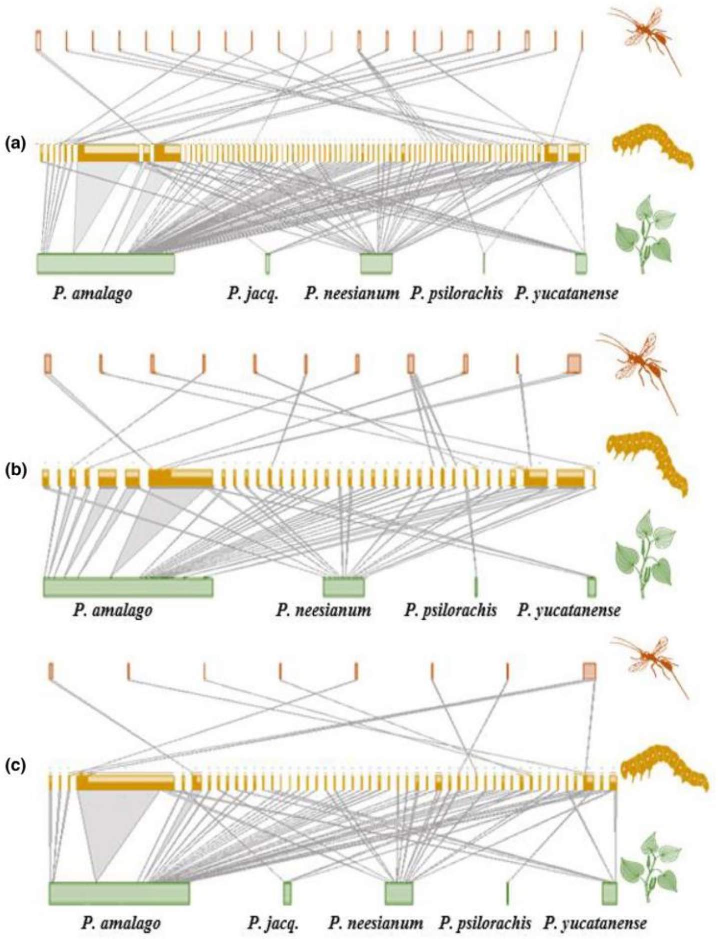
We surveyed a total of 1654 *Piper* shrubs (412 in ET, 617 in NBB, and 625 in TPM), and six *Piper* species were found: *P. amalago* L., *P. jacquemontianum* Kunth, *P. marginatum* Jacq., *P. neesianum* C. DC., *P. psilorhachis* C. DC., and *P. yucatanense* C. DC in the study sites (Table S1). We collected 264 caterpillars, comprising 29 identified species in 12 families and 50 Morphos (Table S1). We found 20 species of parasitoids reared from 14 species of Lepidoptera (Table S2). The parasitoids comprised four genera and four Morphos in the dipteran family Tachinidae and eight genera and 16 Morphos in eight hymenopteran families, mostly Braconidae, Ichneumonidae, Eurytomidae, and Chalcididae (Table S1).

Piper neesianum was the most common focal plant species in the plots, followed by *P. amalago* and *P. yucatanense* (Figure S2A–C, Table S1). Together these three species represented 97% of plant individuals surveyed. Caterpillars found were mainly in the families Geometridae, Erebidae, and Hesperiidae. The genus *Eois* (Geometridae) accounted for 35% of all individuals followed by *Gonodonta nitidimacula* (Erebidae) with 14% of individuals and *Quadrus cerialis* (Hesperiidae) with 7% of individuals (Figure S2D–F, Table S1). The parasitoids reared were mostly Tachinidae (45%) and Braconidae (35%; e.g., Figure S2G–I, Table S1). Overall, 116 realized trophic interactions were documented (Table S2). *Piper amalago* was the most connected plant species, comprising more than 50% of plant–caterpillar interactions. Thirty percent of them involved *P. amalago-Eois* sp. Seventy-six percent of parasitoids were reared from caterpillars feeding on *P. amalago* (Table S2). Species and interaction richness varied across sites and seasons and were highest during the rainy–dry season except at ET (Table S3). Species and interactions exclusive or unique to a given metanetwork that were not shared in other site or season metanetworks were high for caterpillars and parasitoids (>86%) as well for bipartite interactions between *Piper*–caterpillars and caterpillars–parasitoids (>90%; Table S4).

3.2 | Metanetworks

We summarized various subsets of the total metanetwork (Figure 1a). These subsets included metanetworks across seasons at the regional scale (combining all sites; Figure 1b,c), and site-level metanetworks (Figure 2a–c). *Piper*–caterpillar connectance (C_{qw}), interaction diversity (ID), and specialization (H'_2) varied across sites and seasons (Table S5).

FIGURE 1 Regional *Piper*–caterpillar–parasitoid metanetworks by season in the Yucatán Península, México. (a) Total; (b) Rainy season; (c) Rainy–dry transition season. Nodes in the network represent species, and edges represent interactions between species. The width of the bar nodes indicates the abundance of each species. Edge thickness represents the relative weight of the interaction (the abundance of each interaction)



3.3 | Temporal and spatial patterns of beta diversity

3.3.1 | General patterns in species and interaction turnover across temporal and spatial scales

Species and interactions exhibited substantial temporal and spatial turnover (Tables 1 and 2). This turnover was significantly different from results predicted by null models (Tables S6, S7, Figures S3, S4; also see Bayesian results, Figure S5).

3.3.2 | Seasonal patterns

Observed species turnover across seasons within each site (β_s) differed significantly from null model results (Table S6, Figure S3). Turnover of caterpillars ($\beta_{\text{caterpillar}}$) and parasitoids ($\beta_{\text{parasitoid}}$) were greater than plant turnover (β_{plant}; Table 1). Total interaction turnover differed significantly between seasons for all sites, and this value differed significantly from null model results (Table S6, Figure S3). The Bayesian model comparing interaction turnover among seasons supports this pattern (Figure S5).

3.3.3 | Spatial patterns

Interaction (β_{WN}) and species turnover (β_S) were high across sites for all trophic levels, while rewiring (β_{os}) was low (Table 2). Species turnover between sites differed significantly from null model results (Table S7, Figure S4). Species turnover at each trophic level contributed equally to site-level turnover, but β_{plant} between ET-NBB was smaller (β_{plant} = 0.61). Total interaction turnover differed between sites, and this value differed significantly from null model results (Table S7, Figure S4). The greatest spatial dissimilarity among species and interactions occurred between NBB and TPM (β_S = 0.95, β_{WN} = 0.91), whereas ET and

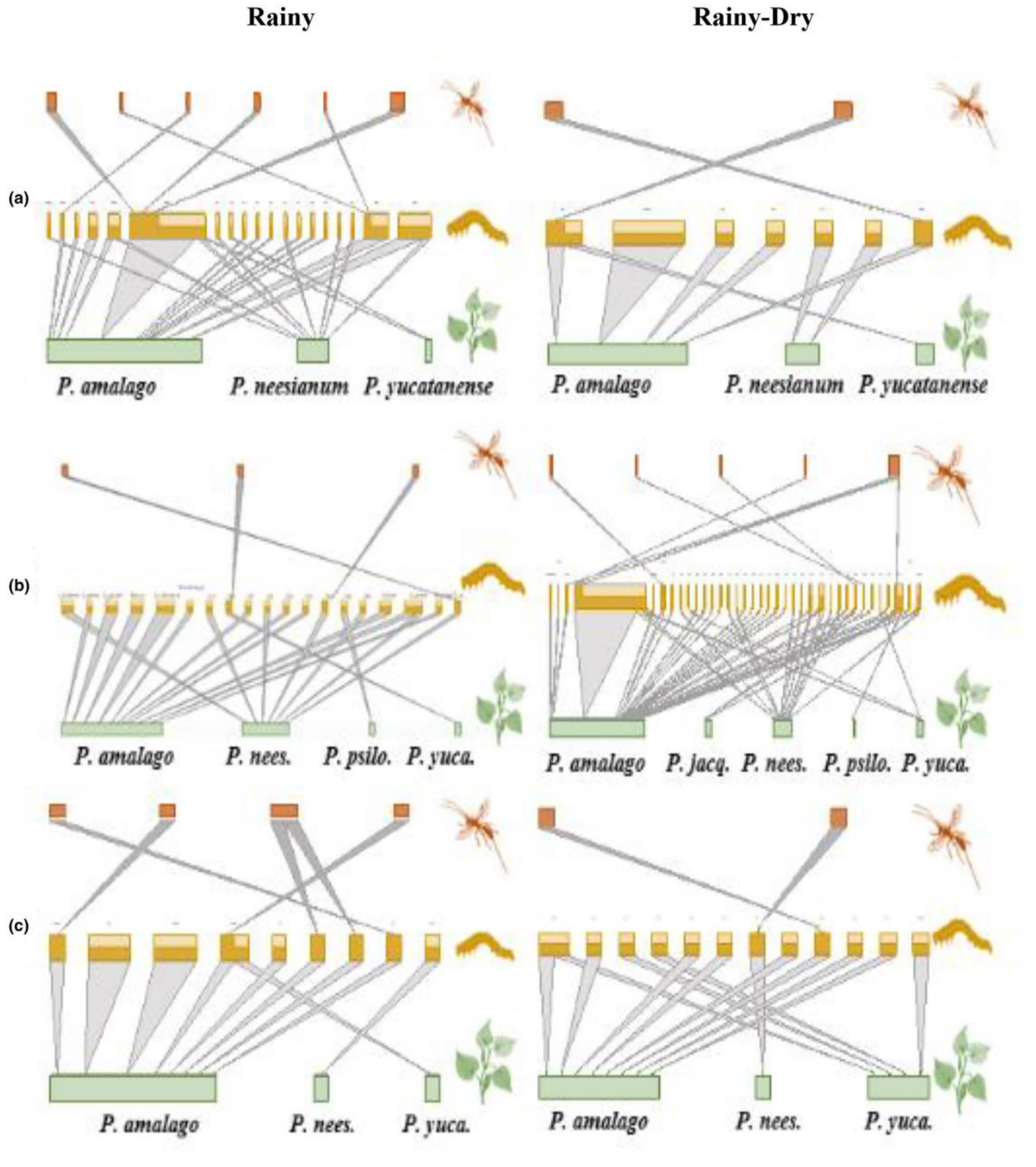


FIGURE 2 *Piper*–caterpillar–parasitoid metanetworks by site across seasons. (a) El Tormento; (b) Nuevo Becal–Bacalar; (c) Tulum–Puerto Morelos. The width of each bar indicates the abundance of each species. Nodes in the network represent species, and edges represent interactions between species. The width of the bars nodes indicates the abundance of each species. Edge thickness represents the relative weight of the interaction (the abundance of each interaction)

NBB were the most similar (β_S = 0.77, β_{WN} = 0.87). Interaction turnover was high between sites mainly due to changes in community composition, but interaction turnover between ET and TPM was due largely to rewiring (Table 2).

4 | DISCUSSION

The metanetworks documented here contribute to understanding fine-scale temporal and spatial turnover in tropical species and

TABLE 1 Interaction turnover (β_{wn}) and their components (β_{os} and β_{st}) and species turnover (β_s, β_{plant}, $\beta_{caterpillar}$, and $\beta_{parasitoid}$) across seasons (rainy R – rainy-dry RD) within each site

	R-RD						
	Interaction turnover			Species turnover			
Site	β_{wn}	β_{os}	β_{st}	β_s	β_{plant}	$\beta_{caterpillar}$	$\beta_{parasitoid}$
ET	0.94	0.60	0.34	0.59	0.26	0.75	1
NBB	0.93	0.62	0.31	0.99	0.99	0.99	1
TPM	0.95	0.75	0.20	0.77	0.6	0.88	0.86

Abbreviations: ET, El Tormento; NBB, Nuevo Becal–Bacalar; TPM, Tulum–Puerto Morelos.

TABLE 2 Interaction turnover (β_{wn}) and their components (β_{os} and β_{st}) and species turnover (β_s, β_{plant}, $\beta_{caterpillar}$, and $\beta_{parasitoid}$) between sites

	Interaction turnover			Species turnover			
Sites	β_{wn}	β_{os}	β_{st}	β_s	β_{plant}	$\beta_{caterpillar}$	$\beta_{parasitoid}$
ET–NBB	0.87	0.36	0.51	0.77	0.61	0.89	0.91
ET–TPM	0.90	0.58	0.32	0.86	0.79	0.89	0.95
NBB–TPM	0.91	0.37	0.54	0.95	0.92	0.96	0.99

Abbreviations: ET, El Tormento; NBB, Nuevo Becal-Bacalar; TPM, Tulum–Puerto Morelos.

interactions, including new records of bi- and tripartite interactions. Our data show that the *Piper*–caterpillar–parasitoid metanetworks changed across sites and seasons, corroborating similar results in tropical (Dáttilo et al., 2019; Lepesqueur et al., 2018) and temperate systems (Dell et al., 2019).

The results of this study showed differences in species richness and abundance for *Piper* and caterpillar species across seasons, leading to differences in metanetwork topologies and parameters (e.g., C_{qw} and H'_2). Similar studies have demonstrated that variation in abundance at lower trophic levels has bottom-up effects on the frequency and strength of interactions, supporting the abundance–asymmetry hypothesis (Vázquez et al., 2007), as we observed in this study. This variation in plant abundance can also affect the size, diversity, and robustness of interaction networks (Fornoff et al., 2019), network topology (Oliveira et al., 2019), and community stability (Pereira-Martins et al., 2019; Rooney & McCann, 2012).

4.1 | Total interaction turnover (β_{wn}) versus species turnover (β_s)

Overall, interaction turnover across sites and seasons exhibited high values and less variable dissimilarity (β_{wn} = 0.87–0.95) compared to species turnover (β_s = 0.59–0.99), which reflects the prevalence of interaction rewiring across space and time. A high degree of interaction turnover is common among interaction networks, and similar magnitudes and ranges have been reported primarily for mutualistic, but also antagonistic networks, across spatial (Carstensen et al., 2014; Kemp et al., 2017), temporal (CaraDonna et al., 2017; Lepesqueur et al., 2018; Olesen et al., 2011), and land-use gradients (Morrison & Dirzo, 2020). Interaction turnover in plant–herbivore networks has mixed results, Kemp et al. (2017) showed that species composition influenced interaction turnover across spatial gradients, while Lepesqueur et al. (2018) showed that interaction rewiring is the primary driver of interaction turnover across seasons. Results here provide further support that dominant drivers of interaction and species turnover in plant–herbivore networks will differ for temporal or spatial metanetworks.

Species turnover across all pairwise site comparisons, except for ET-TPM, contributed most to interaction turnover. The high turnover of *Piper* species between sites is partly responsible for this pattern and reflects the patchy distribution of *Piper* species in the YP. In particular, NBB is unique for its proximity to a reserve and selective logging, which creates a more heterogeneous landscape that may support higher species richness (e.g., via forest gaps that create a mix of resource availability beneficial to a diverse mix of species; Richards & Coley, 2007). High parasitoid turnover could be explained because most of the parasitoids reared were koinobiont endoparasitoids, which are host specialists (Godfray, 1994; Hawkins, 2005) and sensitive to variation in resource availability (Elias et al., 2013; Nascimento et al., 2015; Tylianakis et al., 2005).

4.2 | Interaction rewiring highest in seasonal than site-level metanetworks

The components of beta diversity that contributed most to interaction turnover for seasonal and site metanetworks differed. Following patterns observed in other temporal networks (CaraDonna et al., 2017; Lepesqueur et al., 2018), interaction rewiring contributed most to interaction turnover in our seasonal networks while changes in species composition contributed most to interaction turnover between site metanetworks. Interaction rewiring across seasons indicates that species are interacting with a different subset of hosts despite their persistence in both rainy and rainy-dry seasons. Several factors contribute to seasonal changes in resource utilization, such as host nutritional quality or abundance, which may in turn affect consumer preference for or detection of hosts. In the case of herbivores, seasonal changes in host plant macronutrients or secondary compounds act to modify palatability, digestibility, or sequestration by herbivores, which can modulate interactions with parasitoids and herbivore specialization (Forister et al., 2012; Novotny et al., 2010; Renner & Zohner, 2018).

In our study, interactions were possibly rewired as consumer adaptations to changes in resource over time. The relatively high caterpillar turnover was likely a consequence of greater availability of *Piper* leaves, peaking at the end of the rainy season. Annual gross productivity in semi-evergreen forest of YP is correlated with seasonal variation in evapotranspiration and precipitation, and more leaf material is available at the end of the rainy season (Uuh-Sonda et al., 2018). Further, univoltine caterpillars are more prone to persist in the rainy to dry season transition (Janzen, 1993; Morais et al., 1999), and seasonality patterns of species abundances have been found for Lepidoptera in this zone of the YP (Essens et al., 2014; Montero-Muñoz et al., 2013; Pozo et al., 2008). Also, Scherrer et al. (2016) showed that in the tropical Cerrado, mean caterpillar diet breadth increased in the dry season when leaves were older. Similar patterns are expected for plant–caterpillar–natural enemy interactions where phenology drives host shifts of higher trophic levels (Calixto et al., 2021; Coley, 1998; Connahs et al., 2011; Stireman & Singer, 2002, 2003). This trophic interaction rewiring can promote stability of communities (Bartley et al., 2019; Robinson & Strauss, 2020; Rooney & McCann, 2012; Saavedra et al., 2017) and contribute to resilience and complexity of communities in fluctuating environments (Kondoh, 2003; Nuwagaba et al., 2015; van Baalen et al., 2001).

5 | CONCLUSIONS

In conclusion, this diverse tropical system of tritrophic metanetworks is characterized by substantial seasonal and spatial variation. Our results rise questions about the short-term effects of interaction rewiring on the stability of biotic communities, as well as larger questions about specialization in plant–insect interactions. These results highlight the importance of tropical food web studies that are based on empirical data and natural history using consistent field methods to document trophic interactions across spatial and temporal scales.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.70rxwdbx8 (Campos-Moreno et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Supplementary Information

Importance of interaction rewiring in determining spatial and temporal turnover of tritrophic (*Piper*-caterpillar-parasitoid) metanetworks in the Yucatán Península, México.

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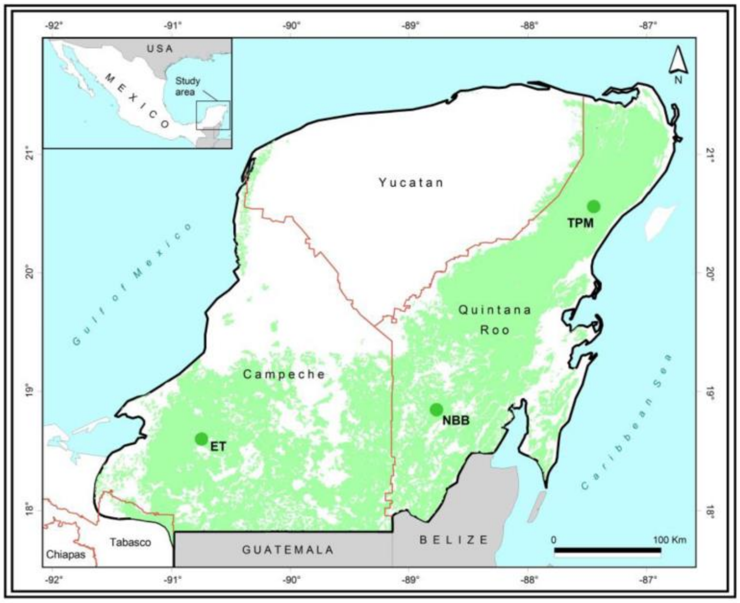

Figure S1. **Study area and localities along semi-evergreen forest in the Yucatán Península, México**. El Tormento (ET); Nuevo Becal- Bacalar (NBB); Tulum-Puerto Morelos (TPM).

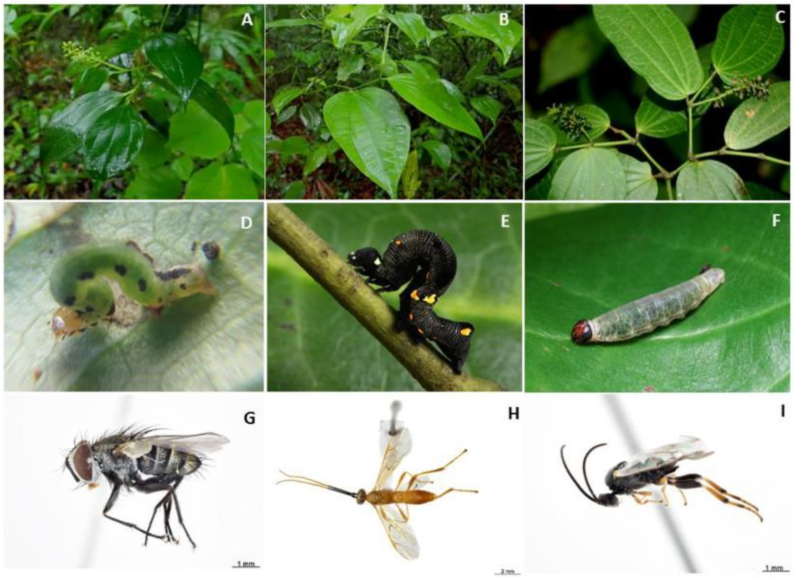

Figure S2. Most common species surveyed and reared. A *Piper neesianum*; **B**. *P. amalago*; **C** *P*. *yucatanense*; **D**. *Eois sp.* (Geometridae); **E**. *Gonodonta nitidimacula* (Erebidae); **F**. *Quadrus cerialis* (Hesperiidae); **G**. *Hyphantrophaga sp.* (Tachinidae) **H.** *Aleiodes sp.* (Braconidae: Rogadinae); **I**. *Apanteles sp.* (Braconidae: Microgastrinae). Photos by E. Tepe, H. Bahena-Basave & D. Campos.

Table S1 Overall species abundance for each trophic level of *Piper*-caterpillar-parasitoid interactions in surveys in the Yucatan Peninsula, México. (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos (R) Rain; (RD) Rain-Dry Transition

Trophic level	Family	Species	ET		NBB		TPM	
			R	**RD**	**R**	**RD**	**R**	**RD**
Plant	**Piperaceae**	*Piper amalago* L.	109	61	52	189	122	163
		P. jacquemontianum Kunth			7	6		
		P. marginatum Jacq		2				
		P. neesianum C.DC	89	92	67	241	124	125
		P. psilorhachis C.DC	18		4	20		
		P. yucatanense C.DC	7	34	7	24	32	60
Caterpillar	**Apatelodidae**	*Apatelodes torrefacta* Smith, 1797	1		2			
		Drepatalodes zacki D. Herbin & J. Monzon- Sierra 2015			1			
		Ephoria sp.				1		
		Zanola verago Cramer, 1777			1			
	Crambidae	*Patania solis*						
	Erebidae	*Crambidia myrolsea* Dyar, 1917	1					
		Dysschema gaumeri Druce, 1894	1		2			
		Eudesmia menea Drury, 1782	4			2	3	
		Illice sp				1		
		Lycomorphodes sordia Butler, 1877				3		
		Pachydota saduca Druce, 1895						
		Robinsonia sabata Druce, 1895	11		1	4	1	1
		Metalectra sp.				1		
		Gonodonta nitidimacula Guenée, 1852	26	4	3	4	2	
		Gonodonta sp.			3			
		Acanthodica grandis Schaus, 1924				1		
		Lascoria sp.				1		
	Geometridae	*Physocleora sp.*				2		
		Eois sp.	3	2	2	79	3	2
	Hesperiidae	*Quadrus cerialis* (Stoll, 1782)	8	1	3	7		
		Quadrus lugubris Felder, 1869				1		
	Limacodidae	*Semyra sp.*		2				
	Nepticulidae	*Stigmella sp.*						1
	Nymphalidae	*Consul electra* Maza, 1987			1	1		1
		Consul fabius Cramer, 1779				1		
		Heliconius petiverana Doubleday, 1847	1					
	Papilionidae	*Heraclides thoas* (Linnaeus, 1771)		2	2			
	Riodinidae	*Argyrogrammana holosticta* Godman & Salvin, 1878				2		
	Unknown	Morpho 1				1		
		Morpho 10				1		
		Morpho 11						1
		Morpho 12						1
		Morpho 13		1				
		Morpho 16				1		
		Morpho 17				1		
		Morpho 18			1			
		Morpho 19	1					
		Morpho 2	1					
		Morpho 20			1			1
		Morpho 22				1		
		Morpho 23				1		
		Morpho 26				1		
		Morpho 29	1					
		Morpho 3					1	

		Morpho 30	1					
		Morpho 31	1					
		Morpho 32			1			
		Morpho 34				1		
		Morpho 35	1					
		Morpho 38				1		
		Morpho 39			1			
		Morpho 4				2		
		Morpho 40	1					
		Morpho 44				1		
		Morpho 45				3		
		Morpho 46						1
		Morpho 47				4		
		Morpho 48			1			
		Morpho 50	1					
		Morpho 51					1	
		Morpho 52						1
		Morpho 53			1			
		Morpho 54					1	
		Morpho 55						1
		Morpho 56			1			
		Morpho 57					1	
		Morpho 58						1
		Morpho 59				1		
		Morpho 60						1
		Morpho 63	1					
		Morpho 64				1		
		Morpho 70		1				
		Morpho 71		1				
		Morpho 8				1		
Parasitoid	**Braconidae**	*Aleiodes sp*	3			3		
		Apanteles sp		1				
		Diolcogaster sp	2					
		Prasmodon sp.				1		
		Unknown sp			1			
	Ichneumonidae	*Enicospilus sp*			1			
		Unknown sp						1
	Chalcididae	*Brachymeria sp.*				1		
		Conura sp 1				1		
		Conura sp 2				1		
	Eulophidae	*Unknow sp.*	1					
	Eupelmidae	*Unknow sp.*					1	
	Eurytomidae	*Aximopsis sp.*	75					
	Pteromalidae	*Unknow sp.*					1	
	Scelionidae	*Unknow sp 1*			1			
		Unknow sp 2					2	1
	Tachinidae	*Erytrhomelana sp.nr woodi*				8		
		Hyphantrophaga sp.	1			1	1	
		Siphosturmia sp.	1					
		Winthemia sp.	1					

Table S2 Overall interaction abundance of *Piper*-caterpillar and *Piper*-caterpillar-parasitoids for sites by season in surveys in the Yucatan Peninsula, México. Trophic levels are separated by an underscore. (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos (R) Rain; (RD) Rain-Dry Transition.

Interaction	***ET***		***NBB***		***TPM***	
	R	**RD**	**R**	**RD**	**R**	**RD**
P. amalago_Argyogrammana sp.				2		
P. amalago_Consul electra			1	1		
P. amalago_Consul fabius				1		
P. amalago_Dysschema gaumeri	1		2			
P. amalago_Dysschema sp.	1				1	
P. amalago_Eois sp.	3	1	2	67	3	1
P. amalago_Eudesmia sp.	2			1	3	
P. amalago_Gonodonta nitidimacula	23	4	3	4	1	
P. amalago_Gonodonta sp.			1			
P. amalago_MORPHO 1				1		
P. amalago_MORPHO 11						1
P. amalago_MORPHO 13		1				
P. amalago_MORPHO 14		1				
P. amalago_MORPHO 17				1		
P. amalago_MORPHO 20						1
P. amalago_MORPHO 21				1		
P. amalago_MORPHO 22				1		
P. amalago_MORPHO 23				1		
P. amalago_MORPHO 25	1					
P. amalago_MORPHO 27			1			
P. amalago_MORPHO 29	1					
P. amalago_MORPHO 3					1	
P. amalago_MORPHO 30	1					
P. amalago_MORPHO 33				1		
P. amalago_MORPHO 34				1		
P. amalago_MORPHO 35	1					
P. amalago_MORPHO 36	1					
P. amalago_MORPHO 37				1		
P. amalago_MORPHO 38				1		
P. amalago_MORPHO 39			1			
P. amalago_MORPHO 4				2		
P. amalago_MORPHO 40	1					
P. amalago_MORPHO 41				1		
P. amalago_MORPHO 45				1		

P. amalago_MORPHO 46						1
P. amalago_MORPHO 47				2		
P. amalago_MORPHO 48			1			
P. amalago_MORPHO 51					1	
P. amalago_MORPHO 54					1	
P. amalago_MORPHO 55						1
P. amalago_MORPHO 57					1	
P. amalago_MORPHO 58						1
P. amalago_MORPHO 6				1		
P. amalago_MORPHO 60						1
P. amalago_MORPHO 61						1
P. amalago_MORPHO 62				1		
P. amalago_MORPHO 7				1		
P. amalago_MORPHO 9				1		
P. amalago_Papilio thoas		2	2			
P. amalago_Quadrus cerialis	8	1	2	3		
P. amalago_Quadrus sp.				1		
P. amalago_Robinsonia sabata	9		1	2		
P. Jacquemontianum_Eudesmia sp.				1		
P. Jacquemontianum_MORPHO 62				1		
P. Jacquemontianum_MORPHO 64				1		
P. jacquemontianum_Quadrus cerialis				3		
P. neesianum_Apatelodes torrefacta	1		2			
P. neesianum_Eois sp.				6		
P. neesianum_Eudesmia sp.	2					
P. neesianum_Gonodonta nitidimacula	2					
P. neesianum_MORPHO 10				1		
P. neesianum_MORPHO 18			1			
P. neesianum_MORPHO 19	1					
P. neesianum_MORPHO 26				1		
P. neesianum_MORPHO 28				1		
P. neesianum_MORPHO 31	1					
P. neesianum_MORPHO 32			1			
P. neesianum_MORPHO 42				1		
P. neesianum_MORPHO 44				1		
P. neesianum_MORPHO 45				2		
P. neesianum_MORPHO 47				3		
P. neesianum_MORPHO 5				1		
P. neesianum_MORPHO 50	1					
P. neesianum_MORPHO 52						1
P. neesianum_MORPHO 53			1			

P. neesianum_MORPHO 59				1		
P. neesianum_MORPHO 63	1					
P. neesianum_MORPHO 69			1			
P. neesianum_MORPHO 70		1				
P. neesianum_MORPHO 71		1				
P. neesianum_Quadrus cerialis			1			
P. neesianum_Robinsonia sabata	2			2	1	
P. neesianum_Zanola verago			1			
P. psilorhachis_MORPHO 56			1			
P. psilorhachis_Quadrus cerialis				1		
P. yucatanense_Eois sp.		1		4		1
P. yucatanense_Gonodonta nitidimacula	1				1	
P. yucatanense_MORPHO 12						1
P. yucatanense_MORPHO 15						1
P. yucatanense_MORPHO 16				1		
P. yucatanense_MORPHO 2	1					
P. yucatanense_MORPHO 20			1			
P. yucatanense_MORPHO 8				1		
P. yucatanense_Robinsonia sabata						1
P. amalago_Consul fabius_Tachinidae sp.				1		
P. amalago_Dysschema gaumeri_Eulophidae sp.	1					
P. amalago_Dysschema sp._Pteromalidae sp.					1	
P. amalago_Eois sp._Erytrhomelana sp.				6		
P. amalago_Eois sp._Glyptapanteles sp.				1		
P. amalago_Eois sp._Hyphantrophaga sp.				1		
P. amalago_Eois sp._Tachinidae sp.				1		
P. amalago_Gonodonta nitidimacula_Aleiodes sp.	3			3		
P. amalago_Gonodonta nitidimacula_Diolcogaster sp.	2					
P. amalago_Gonodonta nitidimacula_Tachinidae sp 1	5					
P. amalago_MORPHO 57_Eupelmidae sp.					1	
P. amalago_MORPHO 58_Ichneumonidae sp.						1
P. amalago_Quadrus cerialis_Apanteles sp.		1				
P. amalago_Quadrus cerialis_Aximopsis sp.	1					
P. amalago_Quadrus cerialis_Tachinidae sp 2	1					
P. Jacquemontianum_MORPHO 62_Conura sp 2				1		
P. Jacquemontianum_MORPHO 64_Brachymeria sp.				1		
P. Jacquemontianum_Quadrus cerialis_Siphosturmia sp.				1		
P. neesianum_Zanola verago_Enicospilus sp.			1			
P. yucatanense_Gonodonta nitidimacula_Tachinidae sp 1					1	
P. yucatanense_MORPHO 20_unknown sp.			1			

Table S3. Total caterpillar species and interaction richness summarized for each site by season. Plot means and standard deviations are included in parentheses (mean+/-SD). (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos; (R) Rain; (RD) Rain-Dry Transition

Site -Season combination	Caterpillar	*Piper*-Caterpillar interactions	Caterpillar-parasitoids interactions	*Piper*-caterpillar-parasitoid interactions
ET- R	20 (13+/-4.4)	23 (7+/-4.4)	6 (3+/-1)	6 (3+/-1)
ET- RD	7 (3+/-1.5)	9 (3+/-1.5)	1	1
NBB - R	19 (4+/-2.2)	20 (4+/-2.2)	2 (1+/-0.6)	2 (1+/-0.6)
NBB - RD	31(14+/-14.2)	45 (14+/-14.2)	9 (3+/-2.07)	9 (3+/-2.07)
TPM - R	9 (2+/-1.4)	10 (2+/-1.4)	3 (1+/-0)	3 (1+/-0)
TPM - RD	12 (2+/-0.9)	13 (2+/-0.9)	1	1

Table S4. Exclusive species and interactions for each site and season. (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos (R) Rain; (RD) Rain-Dry Transition

Site -Season	Caterpillar spp	Parasitoid spp	*Piper* - Caterpillar interactions	Caterpillar-Parasitoid interactions	*Piper*-Caterpillar-Parasitoid interactions
ET - R	12 (16%)	3 (17%)	13 (15%)	4 (21%)	5(25%)
ET - RD	4 (5%)	1 (6%)	6 (7%)	1 (5%)	1 (5%)
NBB - R	10 (14%)	2 (12%)	14 (15%)	2 (10%)	2 (10%)
NBB - RD	25 (33%)	6 (35%)	36 (40%)	7 (37%)	7 (35%)
TPM - R	4 (5%)	2 (12%)	3 (3%)	2 (10%)	3 (15%)
TPM - RD	8 (11%)	1(6%)	8 (9%)	1 (5%)	1 (5%)
Total	**63 (84%)**	**15 (88%)**	**80 (90%)**	**17 (87%)**	**19 (95%)**

Table S5 Local and Regional metanetwork parameters by season. (C_{qw}) Connectance; (ID) Interaction Diversity; (H'_2) Specialization. El Tormento (ET); (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos; (YP) Yucatán Península; R= Rainy, RD =Rainy-Dry; T=Total

		ET			**NBB**			**TPM**			**YP**		
Network	Index	**R**	**R-D**	**T**	**R**	**R-D**	**T**	**R**	**R-D**	**T**	**R**	**RD**	**T**
***Piper*-caterpillar**	C_{qw}	0.4	0.4	0.4	0.3	0.2	0.25	0.4	0.4	0.4	0.29	0.24	0.25
	ID	2.4	1.9	0.62	2.9	2.5	0.52	2.2	2.6	0.73	0.61	0.51	0.56
	H'_2	0.4	0.8	0.41	0.8	0.4	0.47	0.6	0	0.44	0.5	0.41	0.35

Table S6. Observed values of seasonal beta diversity within each site compared to results of null model analysis. For each pairwise comparison between seasons for each site, a community matrix consisting of interactions or species was used to generate 1000 simulated null models and their associated dissimilarity matrices. Dissimilarity was calculated using the Jaccard index. Null matrices were created by preserving marginal totals and shuffling individuals among cells of the matrix. Observed values of beta diversity were compared with those predicted by null models. *P* values are shown for a two-tailed test. El Tormento (ET); (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos.

Species Turnover	**Site**	β_{obs}	**0.025**	**0.5**	**0.975**	***P*-value**
	ET	0.59	0.46	0.53	0.59	>0.001
	NBB	0.99	0.55	0.62	0.69	>0.001
	TPM	0.77	0.73	0.82	0.89	>0.001
Interactions Turnover	**ET**	0.94	0.65	0.73	0.82	>0.001
	NBB	0.93	0.73	0.83	0.89	>0.01
	TPM	0.95	0.82	0.92	1	0.99

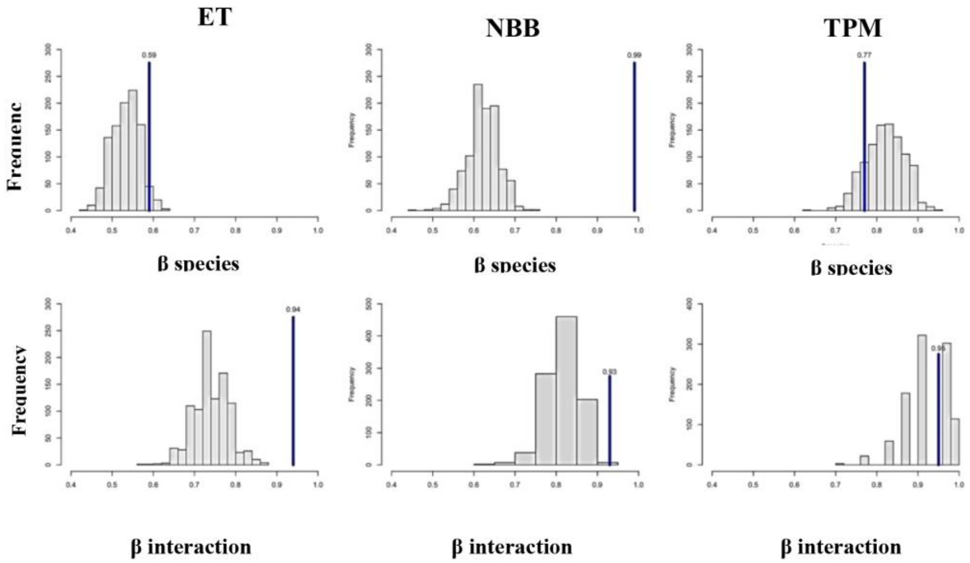

Figure S3. **Histogram of null model results of beta diversity across seasons within each site** (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos; the blue line indicates observed value. Top panel represents species beta-diversity and bottom panel the beta diversity of interactions.

Table S7. Observed values of spatial beta diversity compared to results of null model analysis. For each pairwise comparison between sites, a community matrix consisting of interactions or species was used to generate 1000 simulated null models and their associated dissimilarity matrices. Dissimilarity was calculated using the Jaccard index to obtain a null value of beta diversity for each site. Null matrices were created by preserving marginal totals and shuffling individuals among cells of the matrix. Observed values of beta diversity were compared with those predicted by null models. *P* values are shown for a two-tailed test. El Tormento (ET); (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos.

Species Turnover	**Sites**	β_{obs}	**0.025**	**0.5**	**0.975**	***P*-value**
	ET–NBB	0.77	0.39	0.44	0.50	>0.0001
	ET-TPM	0.86	0.50	0.57	0.64	>0.01
	NBB-TPM	0.95	0.43	0.50	0.56	>0.001
Interaction Turnover	**ET–NBB**	0.87	0.58	0.66	0.72	>0.0001
	ET-TPM	0.90	0.69	0.78	0.86	>0.01
	NBB-TPM	0.91	0.62	0.71	0.78	>0.001

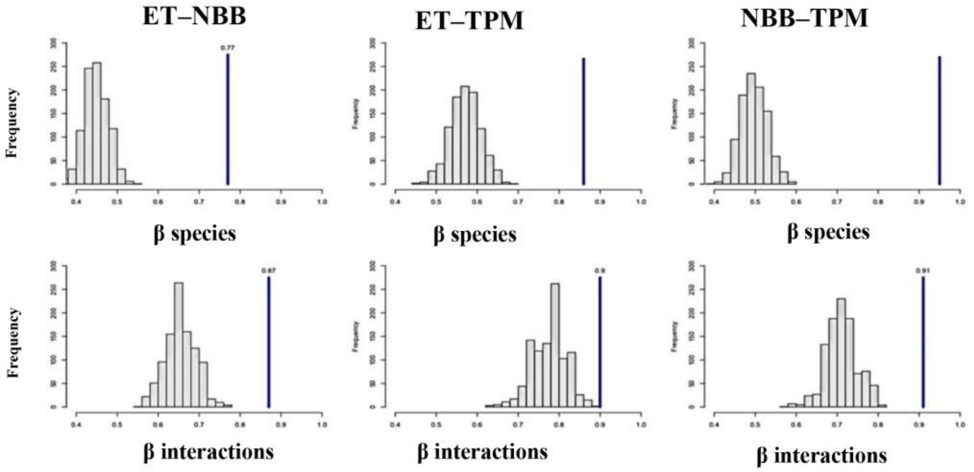

Figure S4. **Histogram of null model results of beta diversity between sites** (ET) El Tormento; (NBB) Nuevo Becal-Bacalar; (TPM) Tulum-Puerto Morelos; the blue line indicates observed value. Top panel represents species beta-diversity and bottom panel the beta diversity of interactions.

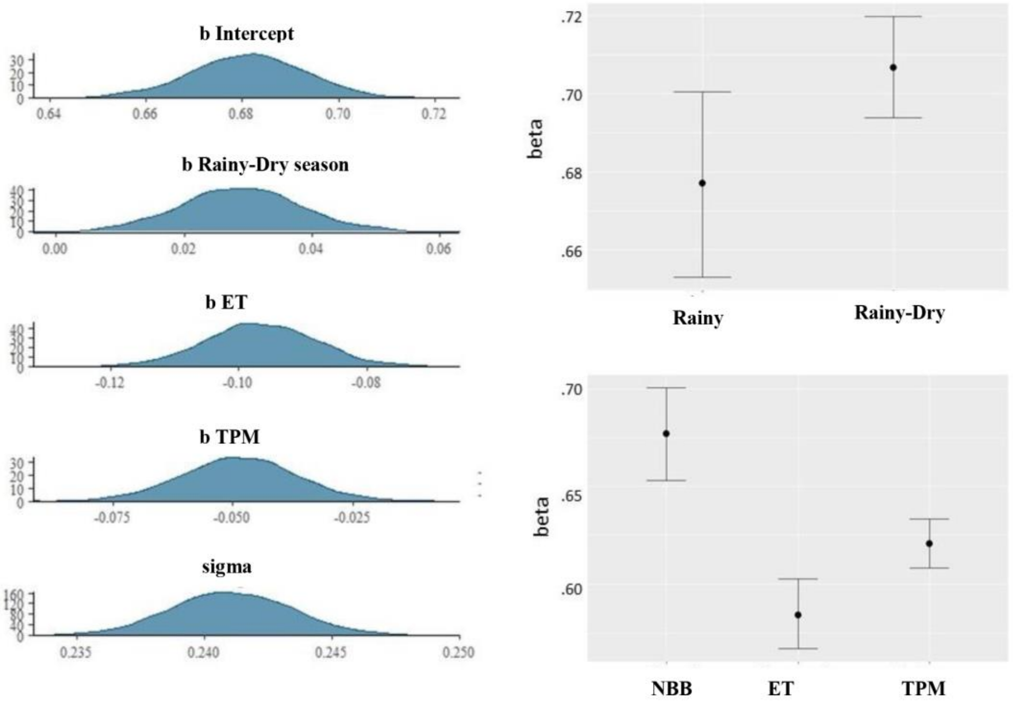

Figure S5. Posterior distributions of simple Bayesian regression comparing beta diversity across seasons and sites. The posterior distributions (left) depict raw differences between beta diversity of the indicated level of site or season and the other levels. None of the posteriors cross zero, indicating clear differences between beta diversity. Conditional effects of treatment level combinations are depicted on the right, showing the 95% credibility intervals for beta diversity of each treatment level combination. b_Intercept = y-intercept for the model; b_Rainy-Dry = difference in beta diversity between seasons; b_ET = difference in beta diversity between ET and other sites; b_TPM = difference in beta diversity between TPM and other sites; sigma = residual standard deviation for the model.

2.2 Campos-Moreno DF, Gates MW, Zhang M, Pérez-Lachaud G, Dyer LA, Whitfield JB and Pozo C. *Aximopsis gabrielae* sp. nov. A new gregarious parasitoid (Hymenoptera: Eurytomidae) of the skipper *Quadrus cerialis* Stoll (Lepidoptera: Hesperiidae) feeding on *Piper amalago* L. in southern Mexico Journal of Natural History. (En revisión).

Aximopsis gabrielae sp. nov.: A new gregarious parasitoid (Hymenoptera: Eurytomidae) of the skipper *Quadrus cerialis* Stoll (Lepidoptera: Hesperiidae) feeding on *Piper amalago* L in southern Mexico.

Diego F. Campos-Moreno[1], Michael W. Gates[2], Y. Miles Zhang[2], Gabriela Pérez-Lachaud[1], Lee A. Dyer[3], James B. Whitfield[4], Carmen Pozo[1]

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Abstract

Aximopsis gabrielae Zhang, Gates, & Campos sp. nov**.** is described from southern Mexico in the Yucatan Peninsula, Mexico. This species is a koinobiont gregarious larval-pupal endoparasitoid of the caterpillar of *Quadrus cerialis* (Stoll, 1782) (Lepidoptera: Hesperiidae) feeding on the shrub *Piper amalago* L. (Piperaceae) in the semi-evergreen forest. This is the first record of *Aximopsis* parasitoids on Hesperiidae (Lepidoptera). Morphological, biological, ecological, and geographical data are integrated to delineate the new species.

Keywords

Endoparasitoid, koinobiont, natural history, tritrophic interaction, Yucatan Peninsula.

INTRODUCTION

Discovery of species and interactions is essential to develop a deeper understanding of biodiversity (Wilson 2017). Around seventy-five percent of described species involve interactions between plants, herbivores, and natural enemies (Price 2002). The study of these trophic interactions contributes to understanding natural history, ecology and evolution (Thompson 2014; Travis 2020), specialization (Dyer et al. 2007; Forister et al. 2012), and species distributions (Giannini et al. 2013).

The pantropical and megadiverse genus *Piper* L. is made up of more than 1300 species in the Neotropics (Quijano-Abril et al. 2006), is abundant and locally diverse (Gentry 1982), and supports complex communities of arthropods (Marquis 1991; Vanin et al. 2008). Recent studies have shown that the chemical diversity of *Piper* can decrease caterpillar host immune responses and increase the recruitment of parasitoids (Richards et al. 2010, 2015; Glassmire et al. 2016; Salazar et al. 2016; Slinn et al. 2018). *Piper amalago* L., is a common species in the American tropics and frequently found on the banks of rivers and secondary roadside formations (Guimarães and Giordano 2004). *Quadrus cerialis* (Stoll, 1782) is a *Piper* generalist species distributed throughout the neotropics (Beccaloni et al. 2008; Warren et al. 2012). Long-term rearing programs in Costa Rica reported caterpillars of *Q. cerialis* feeding on leaves of more than 25 *Piper* species and parasitized by braconid, ichneumonid, eulophid, and bethylid wasps, as well as tachinid flies (Janzen and Hallwachs 2012; Dyer and Gentry 2021). In an extensive survey along Yucatan Peninsula (YP), Mexico (Campos et al. 2021), we found 14 individuals of *Q.*

cerialis feeding on *P. amalago*, and one of these caterpillars yielded parasitoids belonging to *Aximopsis* Ashmead (Hymenoptera: Eurytomidae).

The genus *Aximopsis sensu lato* was recently redefined by Lotfalizadeh et al. (2007) to include *Conoaxima* Brues, *Eurytomaria* Masi, *Mesoeurytoma* Cameron, *Aximogastroma*, and the *nodularis* species group of *Eurytoma* Illiger, based on the morphological character of having a superficial, or absent, posterior tentorial sulci. The 41 described species of *Aximopsis s.l.* are found in all continents except for Australia and Antarctica (Delvare et al. 2019; Noyes 2021), and the genus includes many undescribed species in tropical regions. *Aximopsis* species are parasitoids of endophytic insects, living in branches, stems or leafmines; most known species are parasitoids of Coleoptera and Hymenoptera (Zerova 1995, 2010; Gates et al. 2006; Gates 2009; Delvare et al. 2019; Naghizadeh et al. 2019; Noyes 2021), but also of caterpillars of several lepidopteran families (e.g., Gates and Delvare 2008; Lotfalizadeh and Hosseini 2014; Tavares et al. 2015).

A new interaction involving *P. amalago* (Piperaceae), *Q. cerialis* (Lepidoptera: Hesperiidae) and a new species of *Aximopsis* (Eurytomidae) is reported and described in this paper.

MATERIALS AND METHODS

We collected a caterpillar of *Q. cerialis* feeding on *P. amalago* (Figure 1A) in a patch of semi evergreen forest in southwestern YP (19.288º N - 88.62ºW) within the Campeche State, in a forest reserve of CONAFOR, established in 1971 (SARH 1981), with an upper canopy dominated by *Spondias mombin* L. (Anacardiaceae), *Pouteria campechiana* (L.) (Sapotaceae) and *Brosimum alicastrum* Sw. (Moraceae). The caterpillar collected was reared in the laboratory at ECOSUR in a plastic cup covered with mesh, under ambient conditions until adult parasitoids emerged; the pupa remains from which the parasitoids emerged were preserved in ethanol. The caterpillar was photographed in the laboratory using a Leica DMLB optical stereo microscope with a Nikon digital camera D850, and identified by LD and CP (Figure 1B). The caterpillar pupated after seven days, and 12 days later adults of *Aximopsis* (Eurytomidae) emerged (Figure 2).

Ethanol-preserved specimens were dehydrated by increasing concentrations of ethanol and transferred to hexamethyldisilazane (HMDS) (Heraty and Hawks 1998) before point-mounting. The specimens were identified using a Leica M205C stereomicroscope with 10X oculars and a Leica LED ring light source for point-mounted specimen observation. We took scanning electron microscope (SEM) images with a Hitachi TM3000 (Tungsten source). Body parts of disarticulated specimens were adhered to a 12.7 × 3.2 mm Leica/Cambridge aluminum SEM stub by a carbon adhesive tab (Electron Microscopy Sciences, #77825-12). Stub-mounted specimens were sputter coated with gold-palladium using a Cressington Scientific 108 Auto from multiple angles to ensure complete coverage (~20–30 nm coating). Colored images were obtained with a Canon 60D DSLR, with a Canon MP-E 65mm F/2.8 Macro photo lens or a Mitutoyo M Plan Apo 10× objective mounted on to the Canon EF Telephoto 70–200 mm zoom lens, and the Canon MT–24EX Macro Twin Lite Flash (Tokyo, Japan) with custom-made diffusers to minimize hot spots. Images saved as TIF, and focus stacked using Zerene Stacker v1.04. Image editing was done in Adobe Photoshop and plate layout in Inkscape.

Terminologies used for surface sculptures follow Harris (1979), while the morphology follows Gibson (1997), Lotfalizadeh et al. (2007), and Cruaud et al. (2021). The following measurements and abbreviations were used: F1–Fn, the first and the following flagellomeres;

POL (post-ocellar distance), the distance between the inner margins of posterior ocelli; OOL (ocellar-ocular distance), the distance from the outer margin of lateral ocellus to the inner margin of compound eye; LOL (lateral-ocular distance), the distance between lateral and frontal ocellus. St1–Stn, the first and the following gasteral sternites, Gt1–Gtn, the first and the following gasteral tergites. Voucher specimens were deposited at ECOSUR Arthropod Collection (ECO-CH-AR) and National Museum of Natural History (NMNH). Partial mtDNA *COI* for *A. gabrielae* (559bp) was acquired as a byproduct of an ongoing phylogenomic study of Eurytomidae using Ultraconserved Elements (Zhang et al *unpublished data*), with GenBank accession number MZ644991.

RESULTS

A caterpillar of *Quadrus cerialis* was collected, and later about 80 adults of an Eurytomidae wasp emerged from the pupae. A study of these wasps revealed that this species belongs to the genus *Aximopsis* and is new to science. Its description is given below.

Taxonomy

Family: Eurytomidae Walker, 1832

Subfamily: Eurytominae

Genus: *Aximopsis* Ashmead 1904

Description

Aximopsis gabrielae Zhang, Gates, & Campos

Figures 2–8

Female. Holotype body length 2.4mm.

Diagnosis**.** *Aximopsis gabrielae* can be distinguished from other members of *Aximopsis s.l.* by the absence of horns on the vertex and mesodorsal pronotum (Figures 2A-B, 3A), *sensu* Gates et al. (2006), the clypeus ventrally protruding, the protuberant supraclypeal area forming a bump (Figures 3A, 4B) and the very short, cup-like funiculars in the female. The male has four funiculars very shortly tapering basally and not at all tapering apically and a two-segmented clava, with a slight division near the tip (Figure 8A), while all other known species have strongly tapering F1–F4, giving the appearance of a peduncle for the following segment.

Type material. Holotype ♀ ECO-CH-AR. Mexico, Campeche, Escarcega Forestal Reserve CONAFOR, 15. VIII.2018 19.288ºN, 88.62ºW (D. Campos - C. Pozo Leg.) Ex. pupa *Q. cerialis*. USNMENT01558247. Paratypes Same locality as holotype (8♂8♀) (USNMENT01558218, 01558221, 1558290, 01558326, 01558422, 01558427, 01558433, 01558523, 01558547, 01558557, 01558586, 01558603, 01558609, 01558654, 01558659) (6 ♂♂50♀♀) (ECO-CH-AR 0597-0653).

Color. Black except for the following: flagellomeres, tegula, wing veins brown; scape, pedicel, apices of femora, tibiae, tarsi, ovipositor sheaths testaceous (Figure 2A).

Head. Rectangular and 1.25✕ as wide as long in dorsal view, with umbilicate sculpture and bearing filiform, adpressed and sparse setae, those on lower face longer and directed downwards, the others shorter and directed upwards. Lower face strigose, the carinulae converging towards edge of oral fossa and extending above to antennal toruli, clypeus distinctly protruding, its surface forming a bump, mandible weakly tridentate (Figure 3A). Malar space 0.62× eye height. Genal carina present as wrinkles projected to the center of malar space. Malar sulcus form a small strip of asetose, imbricate band below eyes. Toruli positioned above lower ocular line, intertorular space 1.5× that of the diameter of torulus. Scrobal depression carinate laterally, with parallel edges, ventromedially carinate. Vertex imbricate, ratios of POL: OOL: LOL equal to 2.5:1.4:1. Head posteriorly with postgenal lamina, postgenal groove straight, fading about at level with upper edge of hypostomal carina, and slightly converging ventrally, ending far from genal carina. Subforaminal bridge transversely strigulose and with broad median strip of ornamentation. Posterior tentorial sulci present and deep (Figure 4A).

Antenna. Ratio of scape (minus radicle): pedicel: anellus: F1:F2:F3:F4:F5:club as 12:4:1:4.2:4:4:3.8:3:8.8; pedicel chalice-shaped; funiculars very short with F2-F4 transverse and cupuliform; funiculars thus bearing a single row of longitudinal sensilla and two whorls of setae, shorter than relevant segment; clava clearly two-segmented (Figure 3B).

Forewing. Ratio of marginal: postmarginal: stigmal veins as 1.8:1.2:1. Costal, basal cells, and speculum bare except for basal and cubital folds with a line of setae, short setation on the distal parts of the wing (Figure 6A).

Mesosoma. Mesosoma 1.33× as long as broad; pro- and mesonotum umbilicate, notauli complete, shallow (Figure 6B); lateral prepectus triangular, smooth, sublateral prepectus with deep pit; ventral surface of prepectus with median tooth (Figure 5B, arrow). Adscrobal area with three long and erect setae. Mesopleuron strigose, epicnemium flat, entirely carinately delimited

(Figure 5A), anterior projection of ventral shelf elevated, narrowly projecting anteriorly (Figure 5B). Ventral part of the femoral depression with a large areola (Figure 5B). Metepimeron regularly umbilicate and bearing long, hair-like setae. Postscutellum with inverted V-like raised strip forming a very obtuse angle. Propodeum flattened medially, the relevant surface carinately delimited laterally, reticulate anteriorly and transversely strigulose laterally, followed by subquadrate adpetiolar areola; propodeum coarsely umbilicate laterally and bearing filiform, erect setae. (Figure 7B).

Leg. Oblique carina on procoxa forming a shelf for reception of lower head (Figure 4B, arrow), imbricate. Mesocoxa without lamella; metacoxa bare dorsally, metatibia with a row of adpressed setae, subequal to the width of the metatibia.

Metasoma. Petiole longer than metacoxa, cylindrical, rugose to alveolate, 0.4 × as long as gaster in lateral view; dorsally with median carina leading to anterior teeth above the “can-opener” shaped articular area; no ventral transverse carina delimiting petiole from petiolar part of St1. Gaster elliptical in lateral view, narrowly tapering posteriorly (Figure 7A), smooth, setose from Gt4. Gt4 much longer than other tergites, emarginate posteriorly in dorsal view.

Male. 2.2mm. Color largely similar to females, except antennae wholly black, and tibiae dark brown; sculpture as described for females (Figure 2B). Antenna with four funiculars longer than wide, cupuliform, funiculars with single row of longitudinal sensilla and two or more rows of filiform, erect setae longer than its bearing segment. Clava two-segmented, tip of clava tapering

(Figure 8A). Gastral petiole in lateral view 0.65× as long as metasoma, cylindrical, weakly reticulate to smooth. Metasoma triangular in shape (Figure 8B).

Variation. Female body length ranges from 2.2–2.5mm, male from 2–2.3mm.

Biology. This is a gregarious larval-pupal endoparasitoid of *Quadrus cerialis* (Lepidoptera: Hesperiidae) feeding on *Piper amalago* (Piperaceae). Caterpillars of *Q. cerialis* are abundant in August (unpublished data), the month when *A. gabrielae* parasitized one of the caterpillars collected.

Distribution. Southern Mexico, in the Yucatan peninsula, in a forest reserve of semi-evergreen tropical forest. This species is probably widely spread through the Neotropical Region, where *Q. cerialis* and *P. amalago* are distributed.

Etymology**.** *Aximopsis gabrielae* is named in honor of Gabriela Pérez-Lachaud, who has dedicated most of her life to the study of the ecology and behavior of parasitoids in southeastern Mexico.

DISCUSSION

This is the first report of *Aximopsis* parasitizing larvae of Hesperiidae; our study contributes to know a group of species within the genus *Aximopsis* parasitizing Lepidoptera. Several species formerly included in *Eurytoma* but that conform to the generic concept of *Aximopsis* of Lotfalizadeh et al. (2007) parasitize pyralid moth larvae. For example, *Aximopsis oryzivora* (Delvare) attack the rice borer (Gates and Delvare 2008), and *Aximopsis augasmae* (Zerova) and *Aximopsis* sp. near *ghazvini* (Zerova) parasitize *Etiella zinckenella* (Treitschke) (Pyralidae) (Lotfalizadeh and Hosseini 2014). Another undescribed *Aximopsis* species was reared from the pupae of *Thyrinteina arnobia arnobia* Stoll (Geometridae) and *Thagona tibialis* Walker (Erebidae: Lymantriinae) (Tavares et al. 2015).

As already stated, *Aximopsis* species are parasitoids of endophytic insects. Interestingly, this is the first time a member of the *Aximopsis* is recorded attacking caterpillars that built shelters. *Quadrus* is a concealed feeder, and according to Gentry and Dyer (2002), concealed feeders experience very high levels of parasitism. *Quadrus cerialis* has been recorded as host to *Apanteles* Foerster (Braconidae), *Goniozus* Foerster (Bethylidae), *Hyposoter* Foerster (Ichneumonidae) and *Siphosturmia* Coquillett (Tachinidae) (Janzen and Hallwachs 2012; Dyer and Gentry 2021). Our finding of a new species of eurytomid attacking *Q. cerialis* adds to the diversity of parasitoids of this species. Baer and Marquis (2020) studying a community of caterpillars that built shelters, found a negative correlation between parasitism and predation of the herbivore, which was modulated by shelter traits. Their results provide support for the parasitoid enemy-free space hypothesis (Murphy et al. 2014), which proposes that parasitoids prefer hosts that are less likely to be killed by predators.

In addition to the ecological differences, *A. gabrielae* differs from other known *Aximopsis s.l.* morphologically in via the presence of deep posterior tentorial sulci, which are absent or superficial in other species. Other outstanding characters include the protruding clypeus, very short funiculars in females, and the segmentation of the flagellum in the males. Based on preliminary phylogenomic data (Zhang *et al unpublished data*), *A. gabrielae* groups with other Neotropical *Aximopsis* species, but the genus itself is paraphyletic.

Given the neotropical region's undescribed diversity, additional taxonomic, ecological, and phylogenetic studies of *Aximopsis* are needed to understand its host range and generic limits fully. Nevertheless, knowing the interaction with *Q. cerialis/P.amalago* species gives us some idea about the potential distribution of *A. gabrielae* and expands our knowledge of the biology of the genus *Aximopsis* brings us one step closer to that goal.

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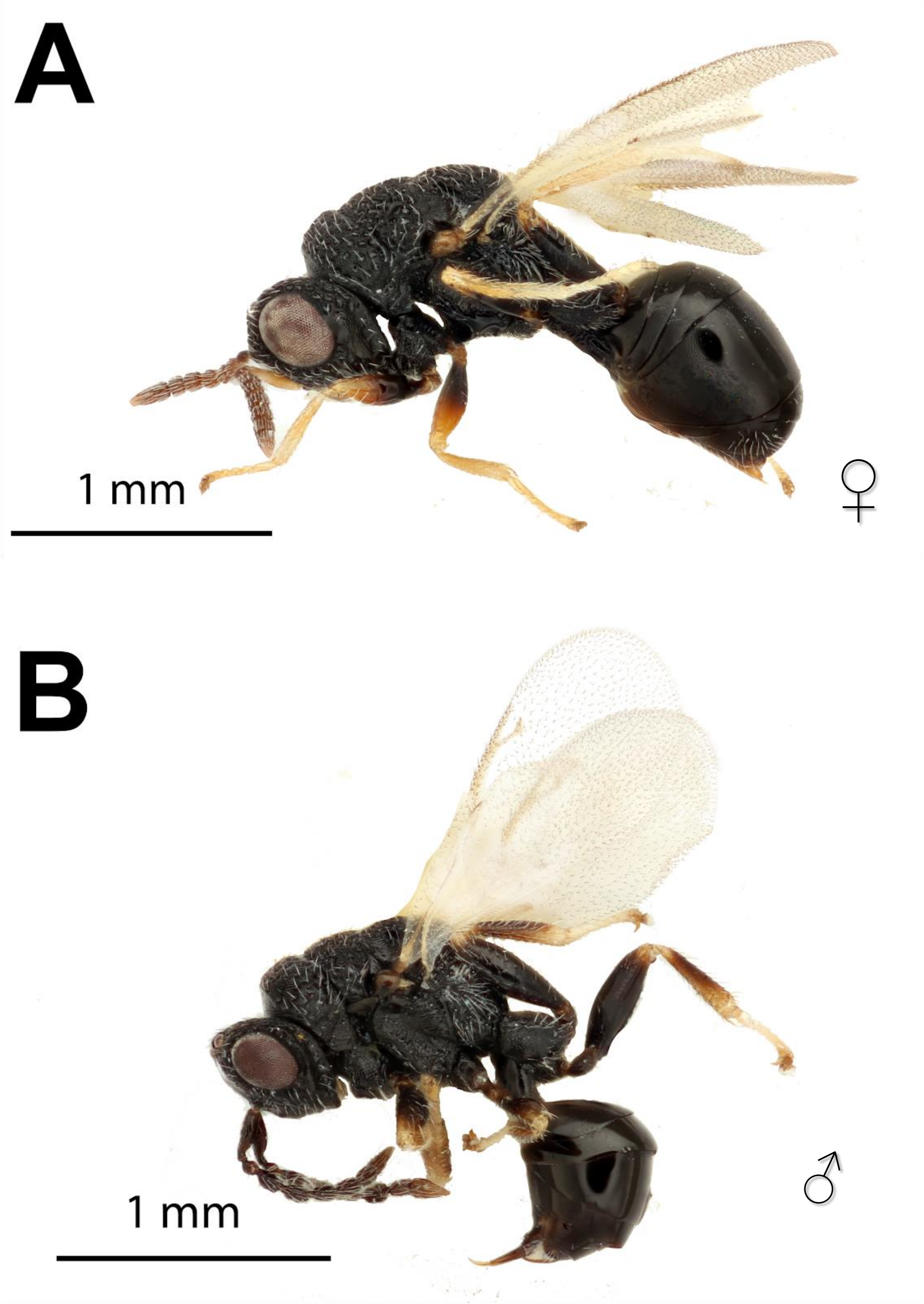
Figure 1.



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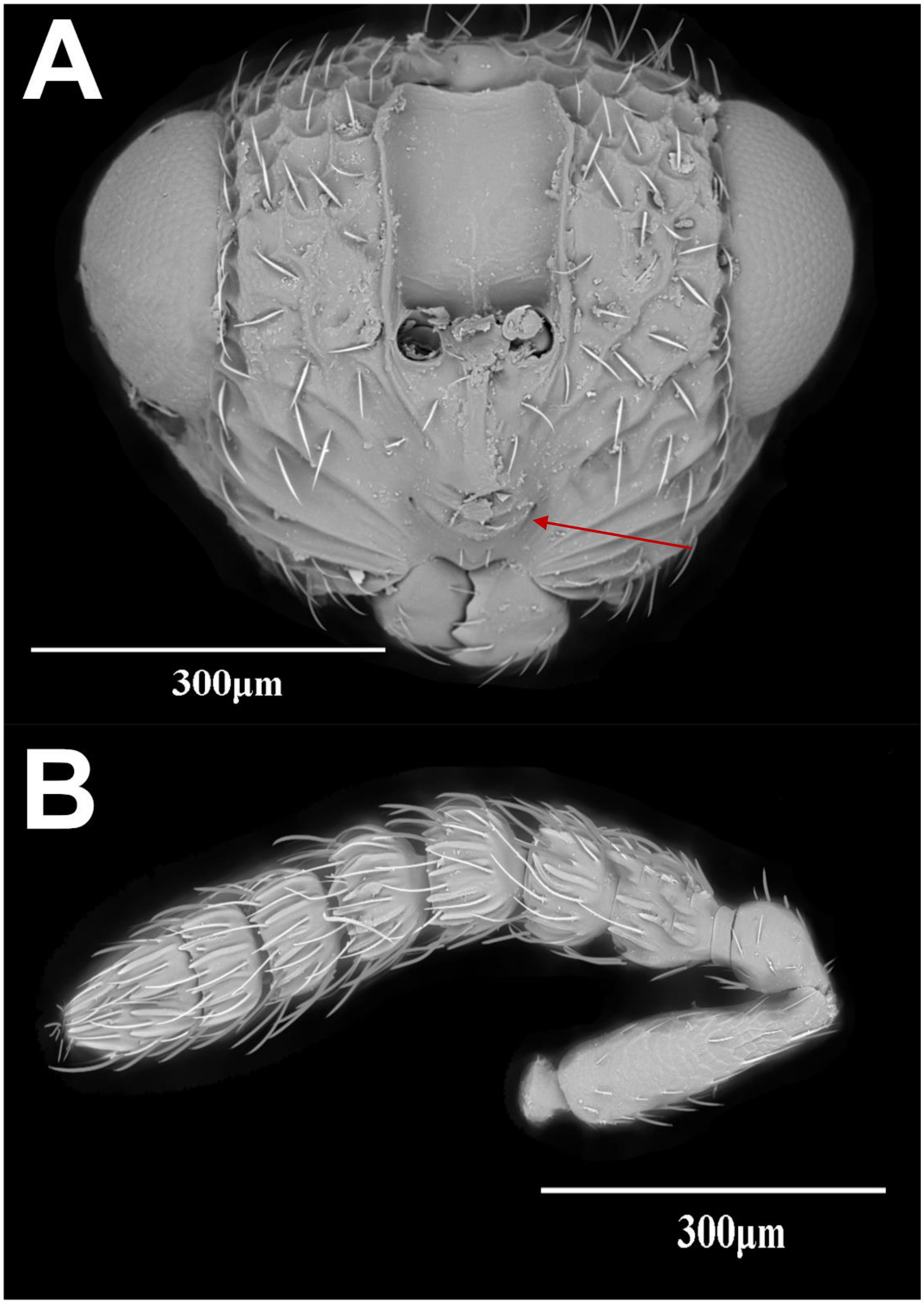

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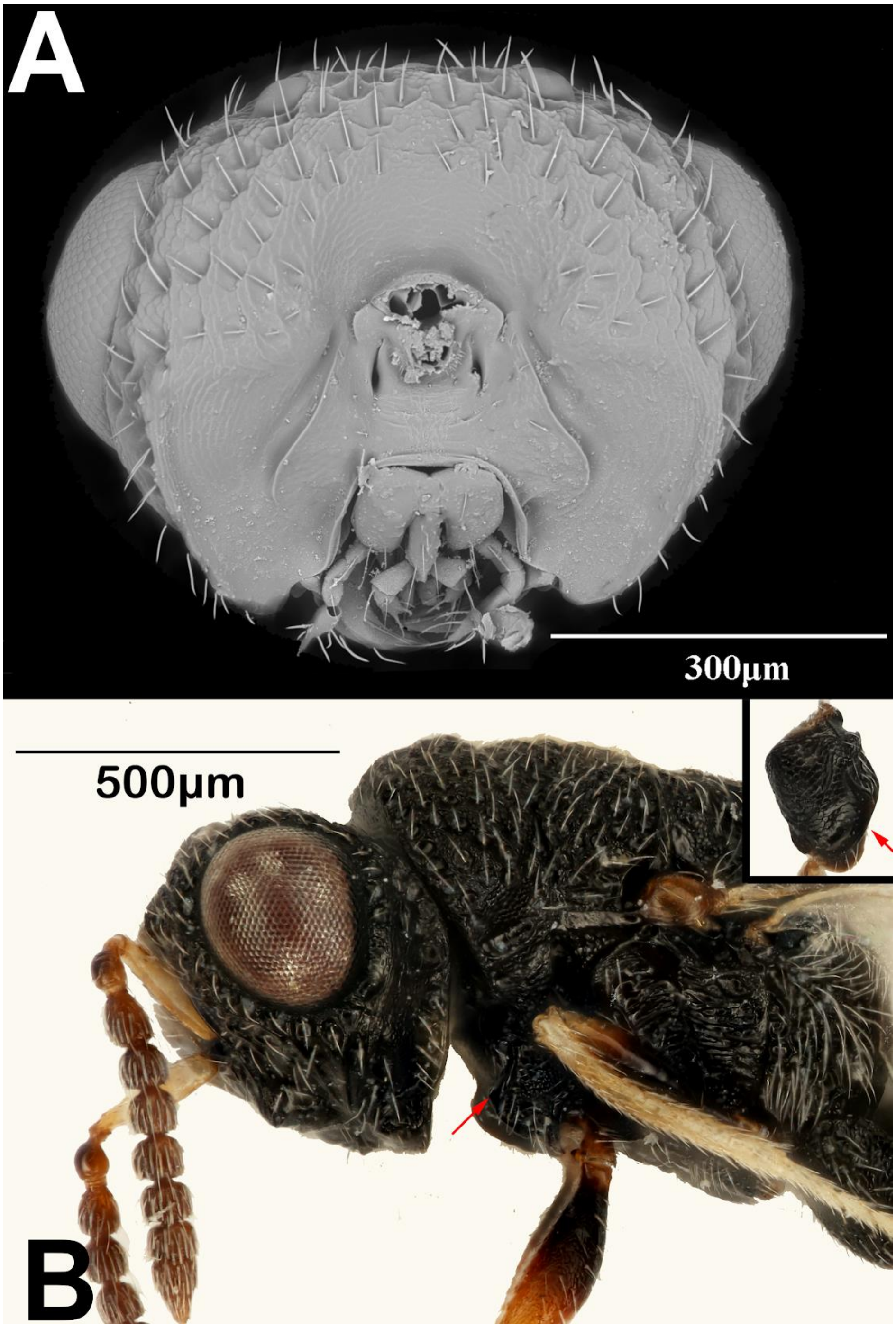

Figure 4

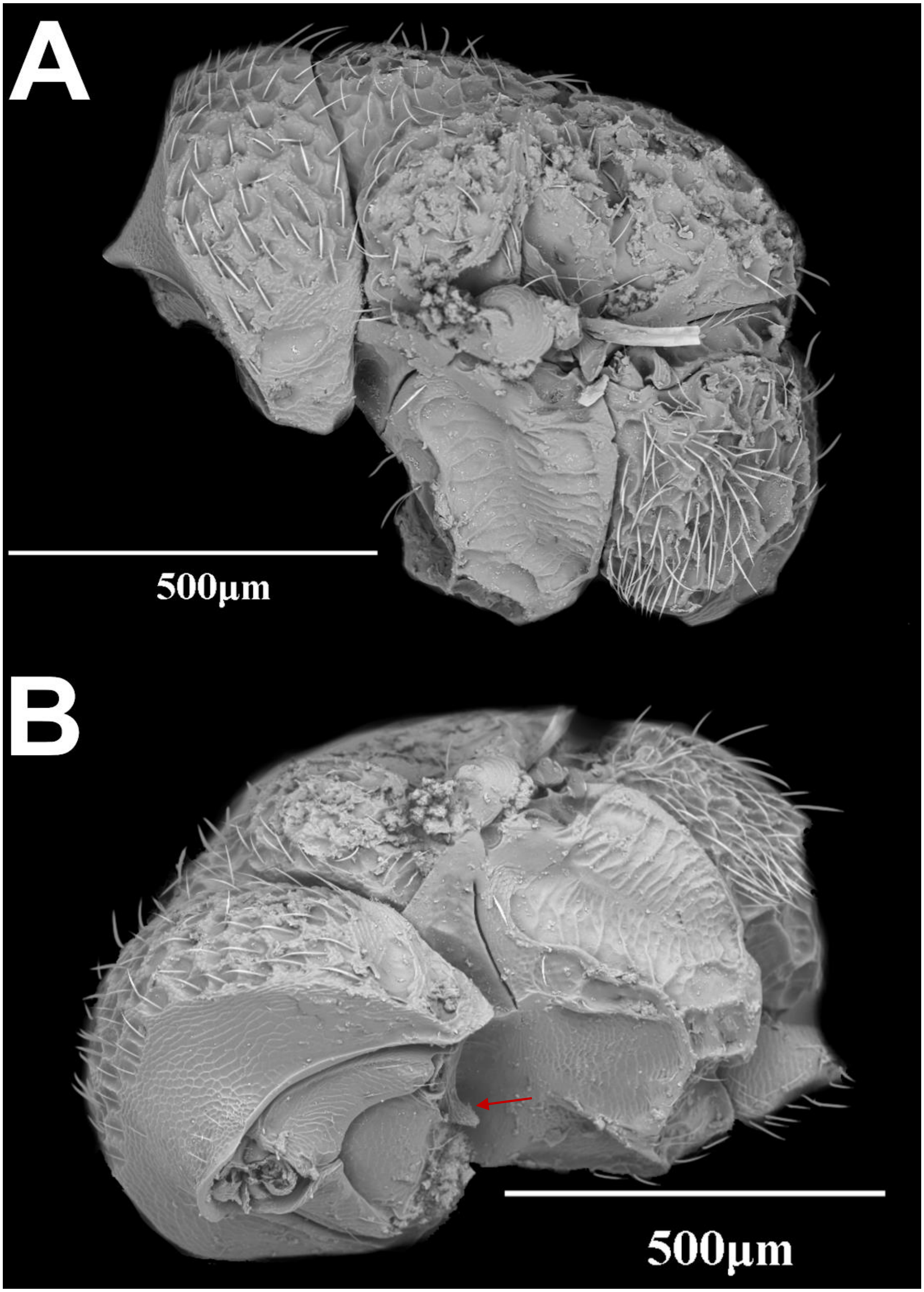

Figure 5.

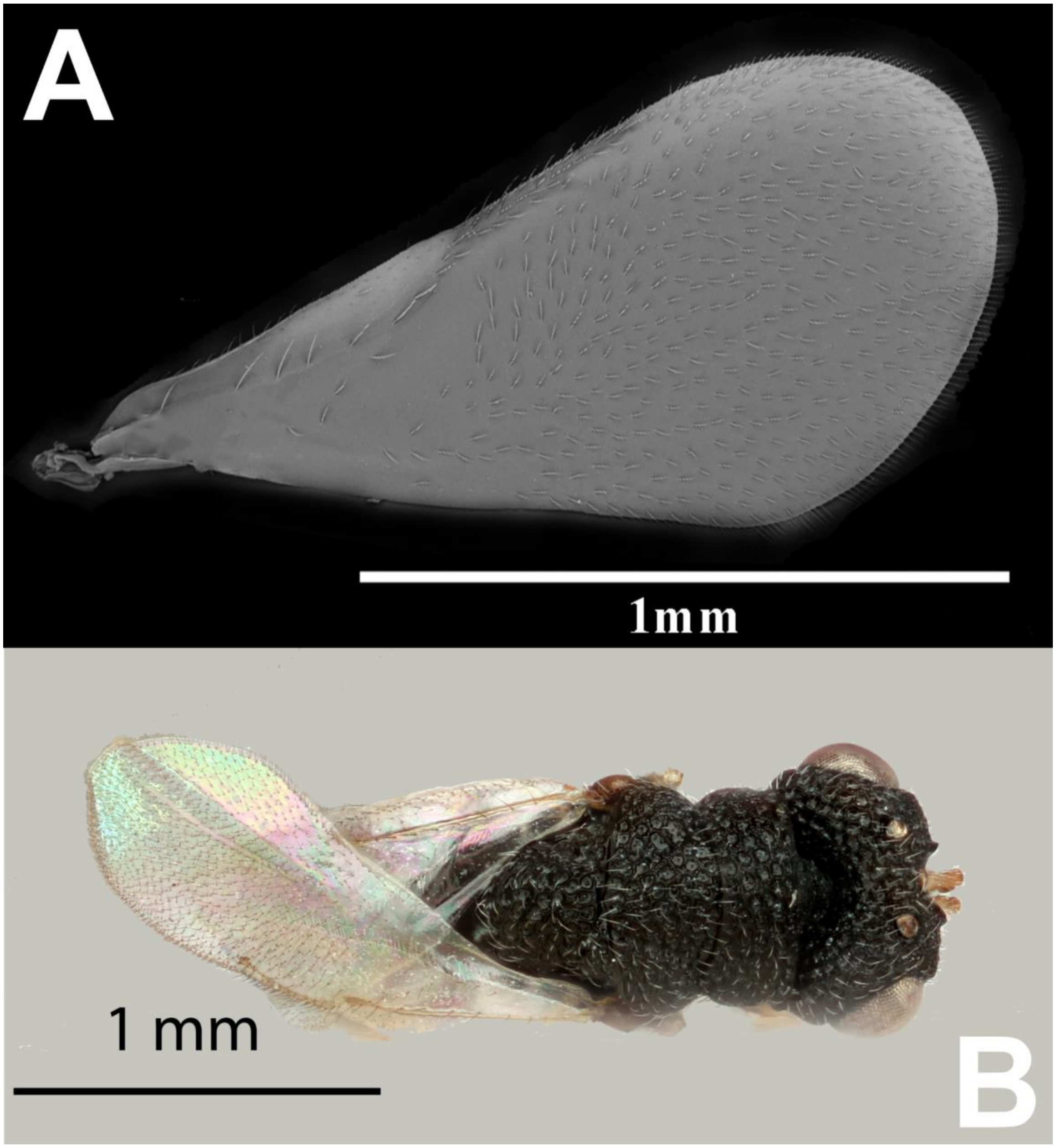

Figure 6

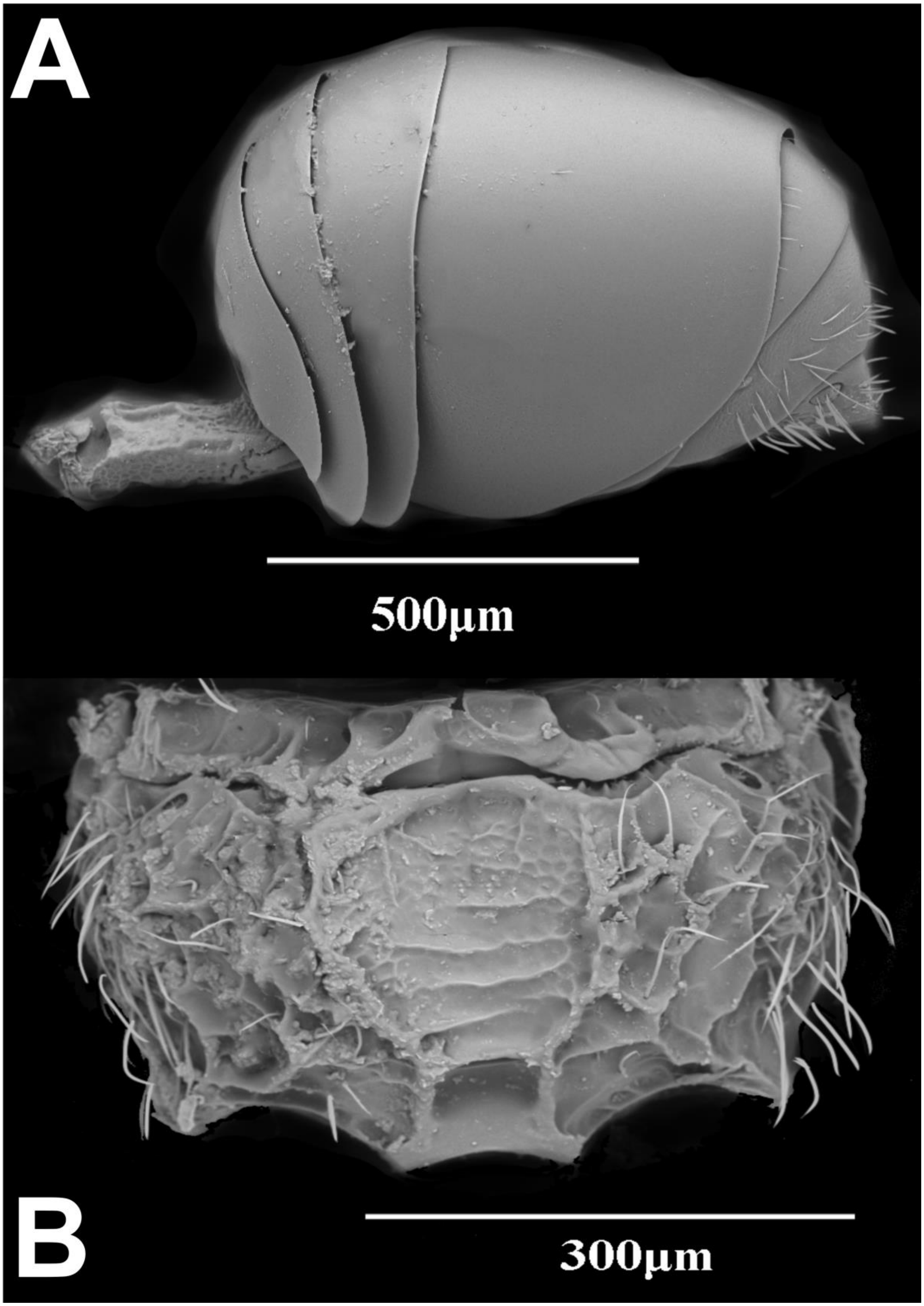

Figure 7.

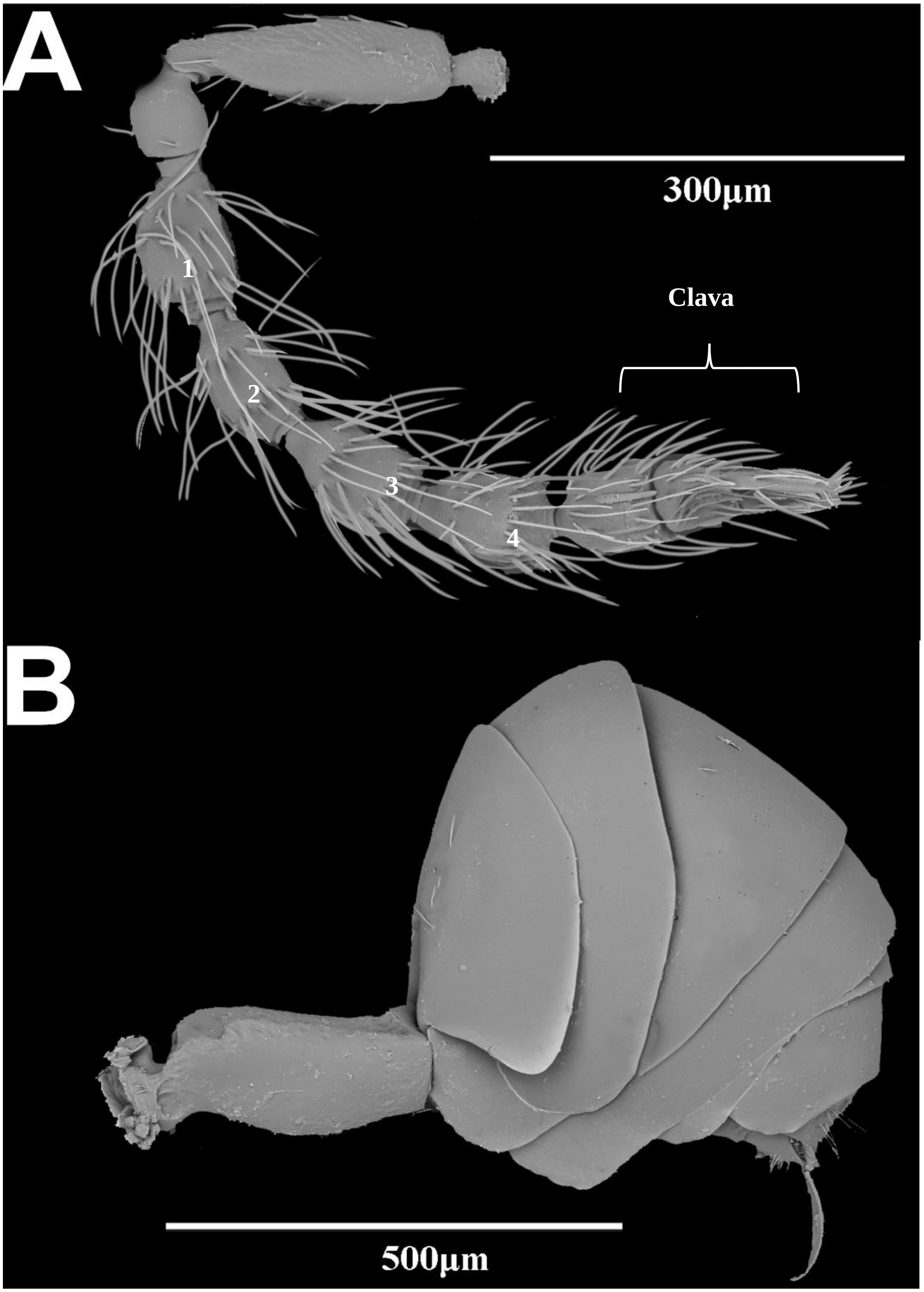

Figure 8

2.3 Campos-Moreno DF, Palacio E, Lara-Pérez LA, Dyer LA, Whitfield JB and Pozo C. (En preparación). A new species of *Enicospilus* Stephens (Ichneumonidae, Ophioninae) from Mexico, parasitoid of *Zanola verago* Cramer (Lepidoptera: Apatelodidae) on *Piper neesianum* C.D C. (Piperaceae).

A new species of *Enicospilus* Stephens (Ichneumonidae, Ophioninae) from Mexico, parasitoid of *Zanola verago* Cramer (Lepidoptera: Apatelodidae) on *Piper neesianum* C.D C. (Piperaceae)

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Abstract

A new tritrophic interaction involving the shrub *Piper neesianum* C.DC. (Piperaceae), a caterpillar belonging to *Zanola verago* Cramer (Lepidoptera: Apatelodidae), and a new species of parasitic wasp belonging to *Enicospilus* Stephens (Ichneumonidae: Ophioninae) are described.

Key words

Endoparasitoid, koinobiont, natural history, tritrophic interaction, Yucatán Península

INTRODUCTION

The study of interactions between plants, herbivores, and natural enemies contributes to understand evolutionary and ecological outcomes of interactions, such as host specificity (Dyer et al. 2007; Forister et al. 2012). Despite the importance of plant-insect relationships, natural history studies describing plant-caterpillar-parasitoid interactions are still relatively uncommon (Dyer et al. 2010).

The genus *Piper*, with a pantropical distribution, is one of the most diverse within the angiosperms, with more than 1,300 species in the Neotropics (Quijano-Abril et al. 2006). *Piper neesianum* C. D. C. is native to the "ramonales" forests of the Yucatán Península, in semi evergreen forest on calcareous soils dominated by *Brosimum alicastrum* Sw. (Borstein 1989). Currently, their distribution is known in southern Mexico, Guatemala and Belice (Ulloa et al. 2018), and there are no reports of herbivores associated with this species (Robinson et al. 2010; Janzen and Hallwachs 2012).

The genus *Zanola* Walker was created for a single species, *Z. diffisilis* (*Z. verago*) from Venezuela, and currently the genus contains eight valid species placed in the family Apatelodidae (GBIF 2021). *Zanola verago* (Cramer) is distributed through neotropical region (Walker and Gray, 1855; Dyar 1912); found in understory shrubs of semi-deciduous forest (Ricardo-Molina et al. 2019). The larva is gray-black with orange and characterized by two subdorsal lines (Fig. 1B). The head and tail have tufts of long black hairs with the tips widened into flag triangular scales (Dyar 1912). The species *Z. verago* is polyphagous, feeding on at least 12 plant species in 11 families across its range of distribution (Dyar 1912; Janzen and Hallwash 2012; Rabelo 2016; Ricardo-Molina et al. 2019). *Cotesia* and *Glyptapanteles* (both Braconidae: Microgastrinae) are the only genera that have been recorded parasitizing *Z. verago* (Santos et al. 2017; Arias-Penna et al. 2019).

The species of the subfamily Ophioninae are large-sized nocturnally active ichneumonid wasps with slender body and orange to brown colouration. All are koinobiont solitary endoparasitoids of crepuscular and nocturnal Lepidoptera (Gauld 1988a). *Enicospilus i*s the most species-rich genus within the subfamily, with more than 150 described species in the New World (Fernández-Triana 2005; Yu et al. 2016). The genus is predominantly tropical in distribution and, in the New World is found from southern USA to Argentina and Chile, including the Caribbean (Gauld 1988b). In Mexico, *Enicospilus* encompasses 61 species (Ruíz-Cancino 2015). *Enicospilus* and related genera (the *Enicospilus* genus-group *sensu* Gauld 1985) are parasitoids of large moth caterpillars including Lasiocampidae, Erebidae, and Lymantriidae, but most are restricted to Saturniidae (Gauld 1988a; Peigler 1994; Janzen and Hallwachs 2012).

As a result of intensive survey for the project *Piper*- caterpillar-parasitoid in semi-evergreen forest of Yucatán Península (Campos-Moreno et al. 2021), a new species of *Enicospilus* was found and is described here. The new species parasitizing to *Z. verago* caterpillar feeding on *P. neesianum* documents a new trophic interaction for this forest system.

MATERIALS AND METHODS

The *Zanola verago* caterpillar was sampled feeding on *P. neesianum* (Fig. 1A) in semi-evergreen forest at southeastern of Yucatán Península (19.28ºN - 88 62 º W). This locality is part of Insitituto Nacional de Investigaciones Forestales Agropecuarias y Pecuarias (INIFAP), a forest reserve established in 1971 (SARH 1981), with an upper canopy dominated by *Spondias mombin* L. (Anacardiaceae), *Pouteria campechiana* (L.) (Sapotaceae) and *B. alicastrum* (Moraceae). The collected caterpillar (Fig. 1B) was reared in the laboratory at El Colegio de la Frontera Sur (ECOSUR-Chetumal) in a plastic cup covered with mesh, under laboratory conditions of light, temperature and humidity, feeding on leaves of *P. neesianum* until the emergency of the adult parasitoid. The caterpillar was photographed in the laboratory using a Leica DMLB optical stereo microscope with a Nikon digital camera D850, and identified by LD and CP. The caterpillar pupated after eight days, and 18 days later one female adult of *Enicospilus* (Ichneumonidae) emerged. The caterpillar remains from which the parasitoids emerged were preserved in ethanol at ECOSUR Arthropod Collection (ECO-CH-AR).

Morphological description

Morphological terminology and measurements for the species description follow Gauld (1988ab). Stacked photos were taken of *E. carmenae* sp. nov. at the Instituto Colombiano Agropecuario using a LEICA MC170 HD camera attached to a LEICA S8 APO Stereomicroscope and for the female holotype of *E. gamezi* at Natural History Museum of United Kingdom (NHMUK) using a Canon SLR EOS 5DSR with 65 mm macro lens mounted on a copy stand with an automated Z-stepper; images were aligned using Helicon Focus software version 6.6.1. The holotype specimen is deposited at ECOSUR Arthropod Collection (ECO-CH-AR).

DNA barcoding

DNA was extracted using standard protocol (Ivanova et al. 2006) from a single hind leg, and a 658 bp region of the mitochondrial cytochrome oxidase subunit I (COI) gene was sequenced using the primers and protocol described in Hebert et al. (2003). This portion of the COI gene of the mitochondrial DNA has been widely applied as molecular marker for species identification

(Hebert et al. 2003), using comparisons with libraries available in the Barcode of Life Data (BOLD) system following Ratnasinghan and Hebert (2013).

For distance calculations, we used the program MEGA10 (Kimura 1980) to performed pairwise interspecific distance matrices and neighbor-joining (NJ) tree using the Kimura-2-Parameter (K2P) distance model to display divergences (Saitou and Nei 1987) using available sequences of species closely related (blast best hit) to *Enicospilus* sp. Barcodes of the closely related species, *E. gamezi* and *E. carmenae*, were aligned to identify differences in nucleotide position in BOLD System (*E. ugaldei*, *E. robertoi*, *E. bozal*, *E. chiriquensis*, *E. glabratus*, *E. colini*, *E. hacha*). *Cryptophion inaequalis* was used as the outgroup.

RESULTS

As part of the survey of herbivores on *Piper*, one caterpillar of *Zanola verago* was collected from *P. neesianum*, and one female ichneumonid wasp emerged from the pupae. A study of this wasps revealed that this species belongs to the genus *Enicospilus* and is new to science. Its description is given below.

Taxonomy

Family: Ichneumonidae Latreille, 1802

Subfamily: Ophioninae Shuckard, 1840

Genus: *Enicospilus* Stephens, 1835

Description

Enicospilus carmenae Campos & Palacio, sp. nov.

(Figures 1C-3)

Female length of body *1.9* mm.

Diagnosis

E. carmenae can be distinguished from other species of *Enicospilus* by the combination of the following characters*:* slender mandibles with upper tooth sub-truncated at apex (Fig. 3B), 1.39x the length of the lower; clypeus 1.6x as broad as long (Fig. 3A); fore wing with vein *Rs* + 2*r* tubular and sinuous, not basally angulate below; fenestra without distinctive sclerites (Fig. 3C); apex of fenestra detached from *Rs* vein base; second discal cell 3.29x longer than high; anterior transverse carina of propodeum complete, strong; hind leg claws evenly down-curved on their apical quarters (Fig. 4C).

Head. Mandibles long, distally parallel-sided, apically twisted less than 35 degrees, upper tooth with apex sub-truncated (Fig. 3B), 1.39x the length of the lower; outer mandibular surface centrally and proximally flat. Labrum 0.278x as long as broad; malar space 0.4x as long as basal mandibular width. Clypeus in profile weakly convex, in frontal view 1.6x as broad as long, margin sub truncate (Fig.3A). Lower face as broad as long, polished, punctate. Head in dorsal view with genae rounded behind eyes; posterior ocellus very close to eye; FI = 0.651 (65%); occipital carina mediodorsally distinct, not joining hypostomal carina. Antenna with 61 flagellomeres.

Mesosoma. Mesoscutum polished, with fine shallow punctures, in profile evenly rounded, with anterior margin slightly turned forwards; notauli vestigial. Mesopleuron polished, the upper and lower part punctostriate; epicnemial carina abruptly curved towards anterior margin of pleuron. Scutellum, in profile weakly convex, laterally carinate for all of its lenght; in dorsal view 1.11x as long as anteriorly wide, virtually smooth. Metapleuron strongly convex, with fine diagonal striation; submetapleural carina broadened towards base; posterior transverse carina of mesosternum complete. Propodeum in profile more or less abruptly declivous; anterior transverse carina complete, strong (Fig. 4A); posterior transverse carina absent; anterior area coriaceous to striate; spiracular area short, slightly rugulose; posterior area strongly rugose; metapleural carina complete, not joined to spiracular margin by a short carina. Fore tibia slightly flattened, with scattered spines on outer surface. Mid leg with longer tibial spur 1.40x the length of the shorter. Hind leg with tarsomere IV 3.3x as long as broad; claws evenly down-curved on its apical quarter (Fig. 4C), with long stout pecten.

Wings. Fore wing length 16 mm; AI = 1.285; CI = 0.421; ICI = 0.633; SDI = 1.254; vein *Rs* + 2*r* strongly sinuate, not basally angulated below (Fig. 3C, arrow); fenestra without distinct sclerites, basally not extending to level of base of pterostiga, its apex clearly separated from base of vein *Rs*; *cu-a* proximal to base of *RS* and *M* by about 0.27x its own length; marginal cell proximally evenly hirsute; first subdiscal cell with anterior 0.4 sparsely hirsute; second discal cell 3.29x as long as wide. Hind wing with 8 hamuli on R1, first abscissa of *Rs* straight, second abscissa slightly curved.

Metasoma. Gaster slender, tergite 2 in profile 4.4x as long as posteriorly deep, laterotegite not pendant, thyridia oval and separated from anterior margin of tergite by about 3.9x its own length (Fig. 4B). Ovipositor slender, its sheath narrow.

Colour. Body pale yellowish brown, with basal antennomeres and metasomal segments V + darker (Fig. 2A); interocellar area with black markings bordering the ocelli. Pterostigma golden, wings hyaline.

Male. Unknown.

Remarks

E. carmenae sp. nov. is morphological close to *E. gamezi* (Fig. 2B) but differs in the more slender mandibles with sub-truncated upper tooth (Fig. 3B) (more thick mandibles, with upper tooth pointed in *E. gamezi* – Fig. 3E), clypeus 1.6x as broad as long (Fig. 3A) (1.4 – 1.5x in *E. gamezi* – Fig. 3D), vein Rs+2r of fore wing not basally angulated below (Fig. 3C) (clearly angulated below in *E. gamezi* – Fig. 3F), and hind leg tarsal claw evenly down-curved on its apical quarter (Fig. 4C) (abruptly down-curved in *C. gamezi* – Fig. 4D).

Type Material

Holotype 1 ♀ (ECO-CH-AR No. xxx), NBBRP3D5, Mexico, Quintana Roo, Bacalar, Reserva Forestal INIFAP, Sector 5. 18º 7719/ - 88º 3686, reared from *Zanola verago* (Apatelodidae). Host collected 15. viii.2018, D. Campos and C. Pozo cols. wasp eclosed 17.ix.2018.

Etymology. *Enicospilus carmenae* is named in honor of Carmen Pozo, who has dedicated most of her life to the study of the taxonomy, biogeography and ecology of Lepidoptera and the conservation of biodiversity in southeastern Mexico.

Ecological affinities. As far as we know, there are no other reports of *Enicospilus* parasitizing *Zanola*, and this is the first report of *Zanola verago* feeding on *P. neesianum*. It thus constitutes the first report of a new tritrophic association.

Distribution and Biology. Southern Mexico, in the Yucatan peninsula, in a forest reserve of semi-evergreen tropical forest. This species is probably widely spread through the Neotropical Region, in semi evergreen forest where *Z. verago* and *P. neesianum* are distributed.

DNA barcodes/Molecular diagnosis. A single 584-bp sequence was recovered from the holotype (ECO-CH-AR XXXXX, Bold no. DFCM CH752B07, NCBI SUB8369760 Enicospilus MZ960307). The closest related species was *E. gamezi* (Fig. 5) with variation p-distance of 1.5%. Interspecific variation with other related species (*E. cameronii, E. bozai, E. chiriquensis*) showed variation p-distance of 6 to 8% with differences in nucleotides position 238G, 268A, 340C, 373G, 442C, 460C, 562C, 628A.

DISCUSSION

In this work, we proposed *E. camenae* as a new species supported by host caterpillar, clear morphological differences (mandibles, vein Rs+2r fore wing, and hind leg tarsal claws) and DNA barcode that differ at eight nucleotide positions (238, 268, 340, 373, 442, 460, 562, 628). The shallow split in the cluster of barcodes between specimens of *E. gamezi* from Costa Rica and *E. camenae* is 1.5 % divergent, which sufficient to separate many morphologically and ecologically distinctive species (Burns et al. 2007; Janzen et al. 2017; Janzen and Hallwachs, 2016).

In the tropics, it appears that most species of the genus *Enicospilus* are found parasitizing Saturniidae, and some species specialized in a single genus or subfamily (Peigler 1994; Janzen and Hallwachs 2012). The clade including *E. gamezi* and *E. carmenae* seems to be unique in parasitizing Apatelodidae with an apparent parapatry distribution (Janzen and Hallwachs 2012).

E. gamezi was considered an endemic species to the open deciduous forest in the north-western Costa Rica, in Guanacaste, at 17 to 500 m (Gauld 1988a; Janzen and Hallwachs 2012) and recently, based on morphological characters, was recorded for Mexico in the state of Yucatan in dry forest (Gonzalez-Moreno and Bordera 2011). After a 40-yr of biodiversity inventory in Area de Conservación on Guanacaste (ACG), there have only been recorded *E. gamezi* parasitizing three species of the Apatelodidae family (*Apatelodes adrastia, A. firmiana, A. merlona*), and one species to the Erebidae family (Janzen and Hallwachs 2012). Until now, *E. carmenae* was only found in *Zanola verago* feeding on *P. neesianum*, a new host plant record for *Z. verago*, which is in turn a new host for a new ichneumonid wasp. *Z. verago* has only reports of parasitism by microgastrinae wasps from the genus *Cotesia* in Panama (Santos et al. 2017) and the species *Glyptapanteles iangauldi* and *Diradops* sp. in Costa Rica (Arias et al. 2019; Janzen and Hallwachs 2012).

The interaction reported here is unique to the local distribution of *P. neesianum*, without other records of herbivory before. *Zanola verago* has only one record of herbivory on *Piper*, on *P. arboreum* from Brasil (Rabelo 2016) and *Piper auritum* from Costa Rica (Janzen and Hallwachs 2012). The discovery of this new species and its interaction is the product of a single rearing event, highlighting the importance of continuing to document interactions that remain poorly documented in tropical regions.

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Figure 3. Morphologial differences between *E. carmenae* **sp. nov.** and **Holotype** ♀ *E. gamezi* . **A – C.** *E. carmenae* **sp. nov.** (photos by E. Palacio). **A.** Head in frontal view. **B.** Mandibles. **C.** Fore wing. **D – F.** *E. gamezi,* holotype ♀ (photos by G. Broad). **D.** Head in frontal view. **E.** Mandibles. **F.** Fore wing. Arrows point the basal section of vein *Rs* + 2*r*.

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Figure 5. Neighbor-joining tree based on K2P distances for COI for *E. carmenae* sp.nov. and related sequences of the genus *Enicospilus* (Downloaded from BOLD System and International Nucleotide Sequences Database). Black circle indicates holotype.

Figure 1.

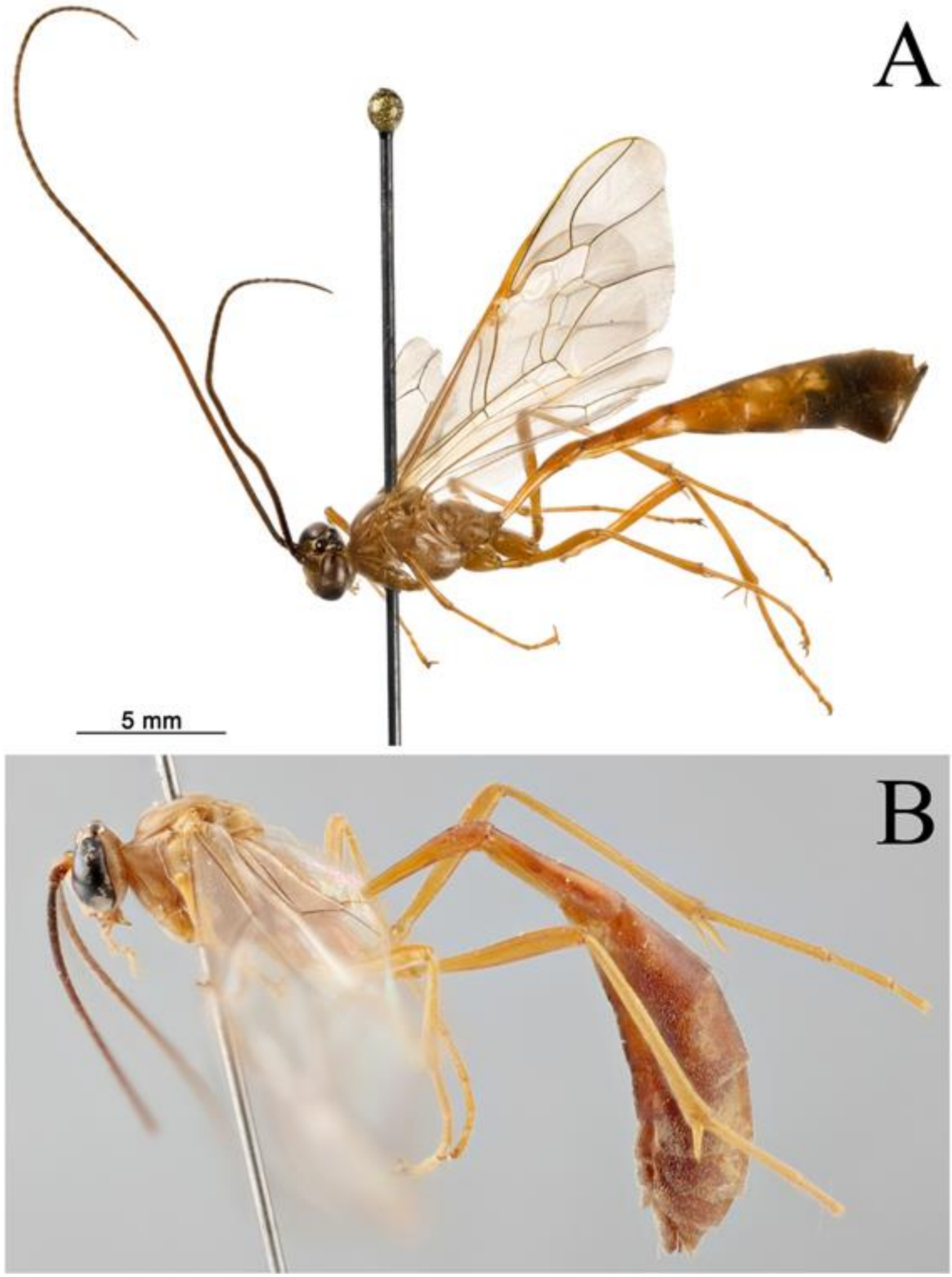

Figure 2.

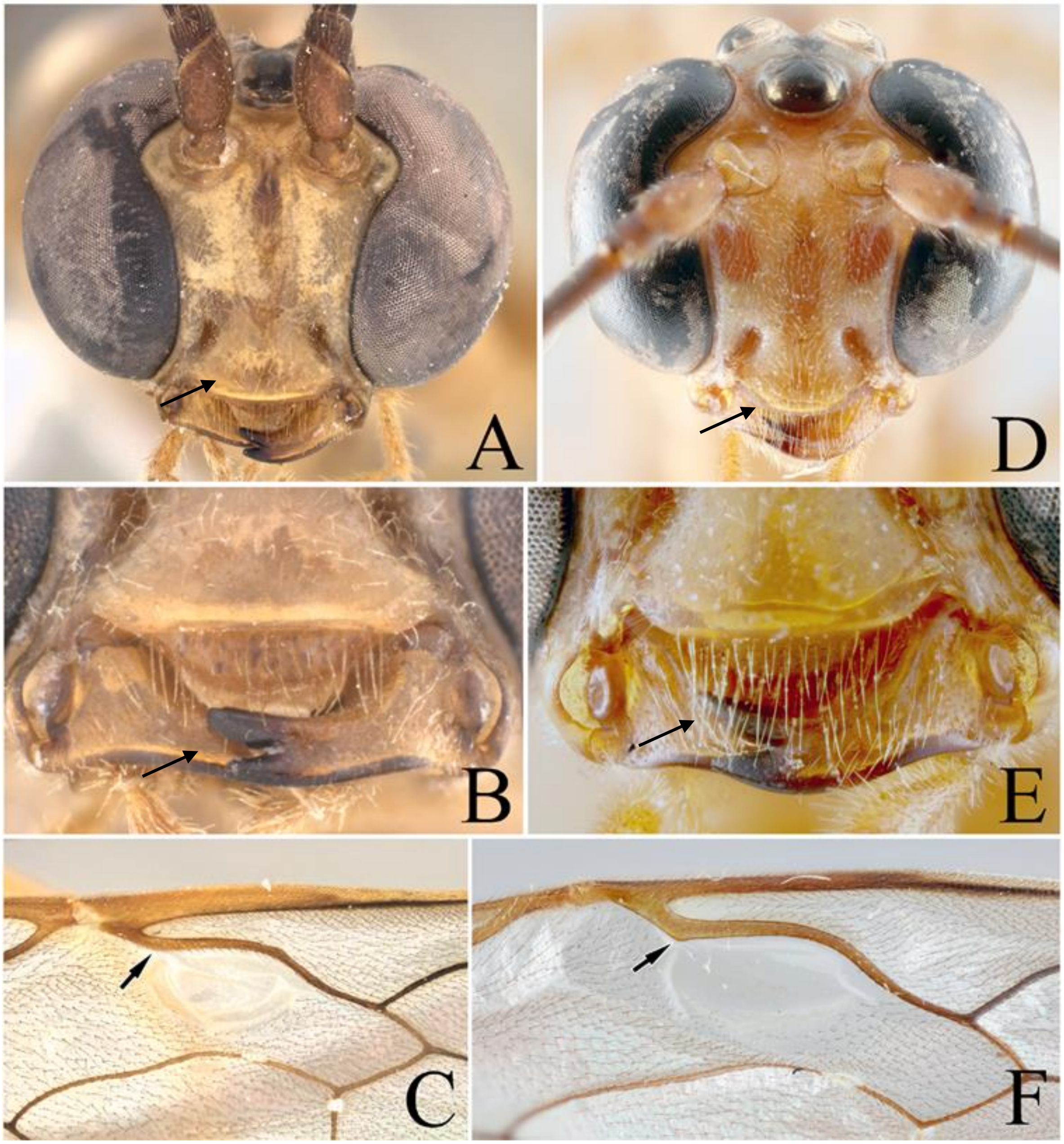

Figure 3.

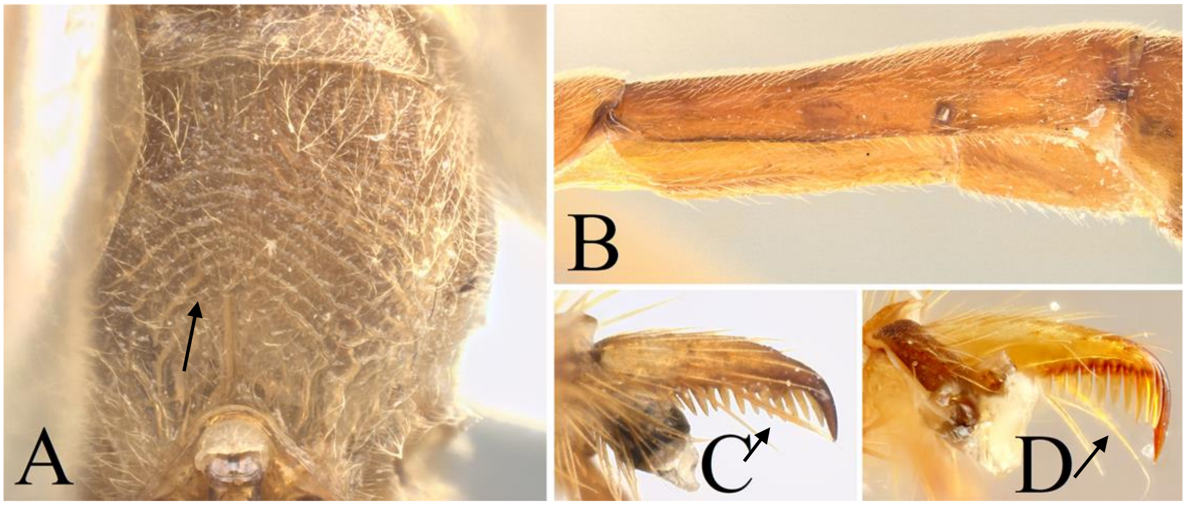

Figure 4.

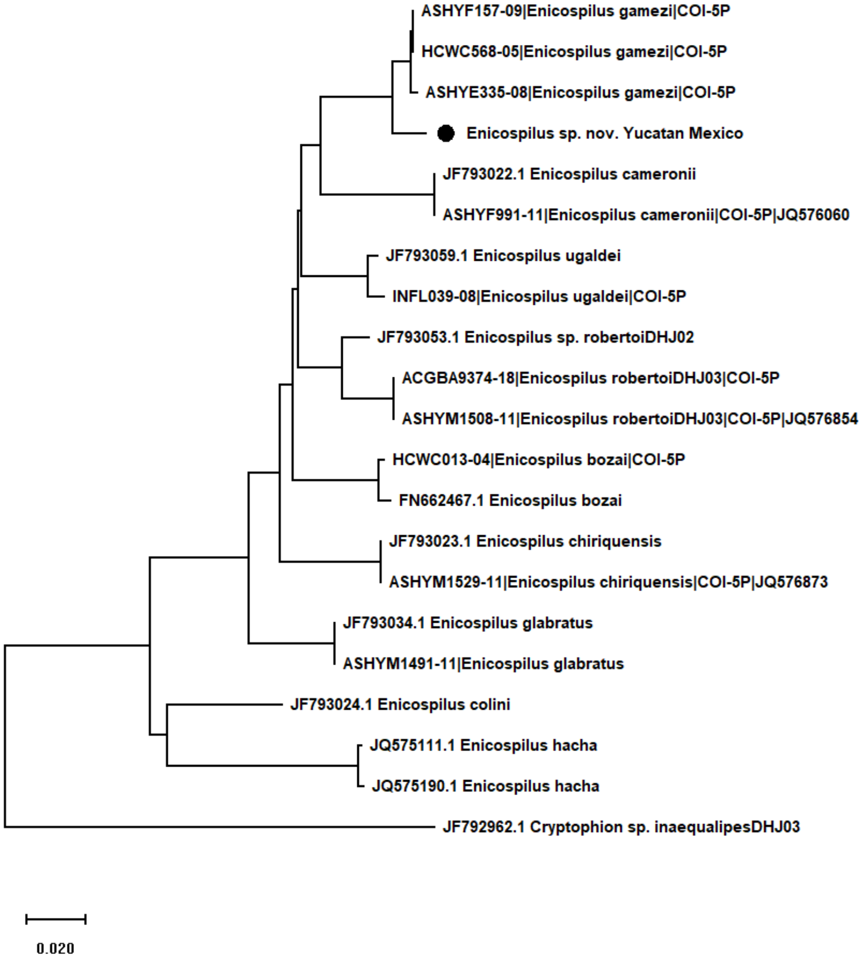

Figure 5.

CAPITULO 3. DISCUSIÓN GENERAL

Este estudio evidenció que, bajo el efecto de periodos climáticos y localidades, existe un recambio de especies e interacciones en el sistema *Piper*-orugas-parasiotoides de la PY. Describe nuevas especies e interacciones bi y tritróficas, integrando datos geográficos, ecológicos y de historia natural. De esta manera resalta la importancia de incluir las interaciones tróficas, para comprender la estructura y composición de comunidades y su variación espacial y temporal en estudios de biodiversidad.

3.1 Variación espacial y temporal de especies e interacciones

Diferencias en riqueza y abundancia de especies de *Piper* y orugas a lo largo de periodos y sitios, se reflejan en la topología y parámetros de las redes (p. ej., Cqw, H'2). Estudios similares han demostrado que la variación en la abundancia a niveles tróficos inferiores tiene efectos ascendentes en la frecuencia y fuerza de las interacciones, apoyando la hipótesis de abundancia-asimetría (Vázquez et al., 2007), como observamos en este estudio. Esta variación en la abundancia de plantas también puede afectar el tamaño, la diversidad y la robustez de las redes de interacción (Fornoff et al., 2019), la topología de la red (Oliveira et al., 2019) y la estabilidad de la comunidad.

El análisis de diversidad beta de redes de interacción *Piper*-orugas-parasitoides, demuestra que, en la escala espacial, la composición de especies tuvo mayor influencia sobre el recambio total entre sitios, lo cual puede estar influenciado por diferencias debidas a la distancia y el tamaño del área. Este es el caso de NBB con mayor número de especies e interacciones, probablemente por presentar una mayor área con respecto a las otras localidades estudiadas. Por extensión de la teoría de biogeografía de islas, una mayor área conlleva a un mayor número de especies (MacArthur y Wilson 2001), pero también a un mayor número de interacciones (Galiana et al. 2018). Adicionalmente, para esta localidad que tiene tala selectiva, se sabe que los procesos de tala abren claros de bosque y crean mayor heterogenidad, lo que podría también incidir en una mayor riqueza de especies (Richards y Coley 2007). El caso opuesto lo representa TPM, en donde el desarrollo turístico ha dado lugar a fragmentos de menor área reduciendo el número de especies e interacciones y probablemente ocasionando un empobrecimiento funcional de las comunidades, situaciones descritas anteriormente en diferentes taxa y niveles tróficos (Isbell et al. 2011, Lefcheck et al. 2015, Emer et al. 2020) y, que nuestros resultados evidencian.

Por otra parte, altos valores de diversidad beta entre periodos climáticos, debidos principalmente a la reorganización de las interacciones (especies compartidas interactuando de manera diferente), sugieren una gran capacidad de resiliencia de las especies de orugas que persisten durante periodos climáticos, lo cual evidencia ampliación de dieta de herbívoros ante los cambios fenológicos de las plantas. Este comportamiento puede representar una estrategia adaptativa a la variación que presentan las plantas entre estaciones, ya sea en cantidad, edad o composición química de sus hojas, lo cual hace que varíe su disponiblidad y calidad nutricional (Boege y Marquis 2006; Murakami et al. 2008). Se sabe que las orugas de especies univoltinas son propensas a persistir en la transición de la estación lluviosa a seca (Janzen 1993; Morais et al. 1999) lo que puede estar relacionado con una mayor disponibilidad de recursos para orugas que se alimentan de hojas, ya que la productividad del bosque subperennifolio ofrece mayor disponibilidad de material foliar al final de la temporada de lluvias cuando hay mayor evapotranspiración y precipitación (Uuh-Sonda et al. 2018). Adicionalmente, algunos estudios en la PY registran patrones de estacionalidad con respecto a la abundancia de Lepidoptera (Pozo et al. 2008; Montero-Muñoz et al. 2013; Essens et al. 2014).

Estos cambios en la fenología de las plantas pueden también generar patrones similares cuando se consideran las interacciones tritróficas planta-herbívoro-enemigo natural, en los cuales el primer nivel trófico impulsa cambios en los niveles tróficos superiores (Coley 1998; Stireman III y Singer 2002, 2003; Connahs et al. 2011; Calixto et al. 2021). Esta reorganización que presentan las interacciones puede promover la estabilidad de las comunidades (Bartley et al. 2019) y contribuir a la resiliencia y complejidad de las comunidades en entornos fluctuantes (Mougi y Kondoh 2012).

La reorganización de las interacciones, mantiene la estructura de las comunidades y plantea preguntas sobre los efectos a corto plazo en procesos fundamentales en ecología y conservación, como ensamble, estabilidad, complejidad, robustez y resiliencia de comunidades, así como procesos a largo plazo como adaptación y especialización de especies.

Los resultados de este estudio mostraron asimetría en la riqueza y abundancia entre niveles tróficos a lo largo de las estaciones, lo que dió lugar a algunas diferencias en topología y parámetros de la red; sin embargo, estas diferencias son menos evidentes en metaredes sumando toda la región, en las que pareciera mantenerse la estructura sin muchos cambios, como también se ha encontrado en otros estudios (p. ejem. Kemp et al. 2017; Dallas y Poisot 2018).

Las redes regionales pueden ser menos precisas que redes locales al estimar parámetros de red. Esto resalta la importancia del estudio de ecología de redes a escala local, en donde ocurren procesos muy importantes para comunidades y ecosistemas. Los resultados de esta investigación, confirman estudios similares en interacciones planta-oruga (Lepesqueur et al. 2018; Dell et al. 2019) y planta-hormiga (Dáttilo et al. 2019).

3.2 Composición de especies e interaciones dentro y entre niveles tróficos

Se registraron seis especies de *Piper*: *P. amalago* L., *P. jacquemontianum* L., *P. marginatum* Jacq., *P. neesianum* C. DC., *P. psilorhachis* C. DC. y *P. yucatanense* C. DC., siendo *P. neesianum* la especie mas común, con el 86% de registros, seguida de *P. amalago* y *P. yucatanense* (Cap 2.1. Figura S2A-C, Tabla S1). Aunque ninguno de estos representa un nuevo registro para la zona (ver Villaseñor 2016), estos resultados brindan elementos para entender la distribución de estas especies de *Piper* y algunas condiciones que pueden incidir en su abundancia a escala local (por ejemplo, heterogeneidad paisajística, características del suelo, grado de perturbación, etc.)

En el nivel trófico intermedio considerando los herbívoros asociados a hojas de *Piper,* se recolectaron 264 orugas de 12 familias, 25 generos, 29 especies válidas y 50 morfoespecies que no fue posible identificar (Cap 2.1, Tabla S1). Las orugas recolectadas confirman asociaciones de herbívoros en *Piper* siendo *Eois* sp. (Geometridae), la especie mas común (35% de todos los individuos), seguida de *Gonodonta nitidimacula* (Erebidae) (14%) y *Quadrus cerialis* (Hesperiidae) (7%) (Cap 2.1. Figuras S2D-F, Cuadro S1). Estos registros confirman algunas asociaciones de orugas en *Piper* (Connahs et al 2009; Salazar et al. 2016; Cosmo et al. 2019) y contribuyen a entender la dinámica de herbívoros asociados a *Piper*, incluyendo patrones de especialización a escala local, en los que se pudo confirmar que las especies de orugas dominantes pueden alimentarse de dos o máximo tres especies de *Piper*. A pesar de no ser la especie mas abundante, *P. amalago* tuvo el 40% del total de interacciones *Piper*-oruga en el muestreo. Esto puede deberse a una mayor disponibilidad de su área foliar y a diferencias en la composición y textura su hoja que se puede asociar a una mayor riqueza y abundancia de herbívoros, con respecto a otras especies de *Piper* con diferenre condición foliar. Esto podrá confirmarse una vez obtenidos algunos resultados de este estudio sobre la composición y variación espacial y temporal inter e intraespecífica de las especies de *Piper*, en relación a la riqueza y abundancia de herbívoros asociados, así como sobre el grado de herbivoría que puede tener en diferentes condiciones.

La gran proporción de morfoespecies de orugas sin identificar alimentándose de hojas de *Piper* en nuestro estudio, representadas por uno o pocos indivíduos, da una idea de la riqueza de especies raras, lo que puede explicarse por la diversidad que aún falta por conocer, y por el pequeño tamaño poblacional de herbívoros en el trópico, como se ha encontrado en otros estudios (Price et al. 1995; Novotný y Basset 2000; Novotný et al. 2006).

En el nivel trófico superior, representado por parasitoides, se encontraron 20 especies de parasitoides que emergieron de 14 especies de lepidópteros (Cap 2.1,

Cuadro S2). Los parasitoides encontrados, del orden Diptera comprenden cuatro morfoespecies, cuatro géneros de la familia y del orden Hymenoptera comprenden 16 morfoespecies, ocho géneros de ocho familias, principalmente Braconidae, Ichneumonidae, Eurytomidae y Chalcididae (Cap. 2.1, Tabla S1).

Los parasitoides encontrados representan en su mayoría especies aún sin describir o en proceso de descripción, dando una idea de la diversidad por descubrir en las asociaciones *Piper*-orugas-parasitoides. También amplia el conocimiento sobre historia natural, ecología y taxonomía de las especies que participan en estas asociaciones, evidenciando la importancia de seguir documentando las interacciones planta-herbívoro-parasitoide que siguen estando poco documentadas en el trópico,

De acuerdo con la cantidad de orugas parasitadas, puede considerarse un parasitismo de 13%. Los parasitoides encontrados, tienen en su mayoría, biología de endoparasitoides koinobiontes, reresentando un patrón de especialización que requiere confirmarse con mas estudios y abriendo nuevas posibilidades de investigación sobre la dinámica y variación de interacciones tritróficas en respuesta a factores bióticos y abióticos en diferentes escalas espaciales y temporales.

En nuestros resultados describimos dos nuevas especies de parasitoides en herbívoros associados a especies de *Piper*: *Aximopsis gabrielae* sp nov. (Eurytomidae) y *Enicospilus carmenae* sp nov. (Ichneumonidae: Ophioninae), estas descripciones integran datos de historia natural, morfología, biologia molecular y ecología.

Las interacciones descritas amplían el conocimiento sobre la biología de los géneros *Aximopsis* y *Enicospilus* y, representan un avance en el conocimiento de las relaciones entre plantas, herbívoros y parasitoides, y los factores que pueden incidir en la distribuición de herbívoros y parasitoides asociados a especies de *Piper*.

3.3 Recomendaciones y perspectivas

El estudio del sistema tritrófico *Piper*-orugas-parasitoides representa una gran oportunidad para probar hipótesis ecológicas y evolutivas que relacionan heterogeneidad ambiental en escalas espaciales y temporales con diversidad de recursos y consumidores, así como con procesos de herbivoría, parasitismo, especialización, etc.; por ejemplo la Hipótesis de mosaico geográfico de coevolución (Thompson 1999, 2005), el Paisaje fitoquímico (Hunter 2016); el nicho tritrófico (Singer y Stireman 2005), enemigos (Letorneau 1987; Russell 1989; Staab y Schuldt 2020), la asimetría (Vázquez et al. 2007), la provisión (Yachi y Loreau 1999; Moreira et al. 2016; Tyson y Adams 2019), entre otras.

Dada la diversidad que aún está sin describir en la región neotropical, se necesitan estudios taxonómicos y ecológicos adicionales para el conocimiento y comprension de patrones de distribución y especialización de herbívoros y parasitoides.

La continuidad de estas investigaciones basadas en datos empíricos obtenidos a través de métodos estandarizados es fundamental en el trópico para un mayor conocimiento y comprensión de la biodiversidad. Para lograrlo se recomienda seguir implementando métodos de observación y experimentación estandarizados, incluyendo monitoreo de factores bióticos y abióticos. En este sentido, resulta fundamental establecer parcelas de experimentación en ambiente natural a mediano y largo plazo, que permitan comparar el efecto de los factores bióticos y abióticos en la estructura y dinámica de comunidades en el trópico, en escalas de tiempo y espacio. Esto nos brindará la oportunidad de entender la dinámica de poblaciones, comunidades y ecosistemas.

Por otra parte, dada la sensiblidad que demuestran tener las interacciones ecológicas al cambio climático, heterogenidad espacial, cambio de cobertura, especies invasoras entre otros factores, su inclusión es no solo necesaria, sino urgente en programas de inventario y monitoreo de la diversidad. En particular, en las interacciones tróficas mediadas químicamente como es el caso de *Piper,* es muy recomendado incluir la variación fitoquímica y genética de las especies que participan en las redes de interacción, ya que estas variaciones debida pueden tener un gran poder de explicación y predicción sobre la participación de herbívoros y parasitoides, como lo demuestran algunas investigaciones (Glassmire et al 2016; Richards et al. 2015; Salazar et al. 2016). Por este motivo es recomendable hacer experimentación en ambiente natural, eligiendo especies y controlando factores abióticos que permitan inferencias sobre el efecto de la diversidad taxonómica, funcional y filogenética en el sistema.

Una perspectiva de investigación en este sistema, es su potencial para evidenciar cambios de interacciones en escalas biogeográficas. Es muy probable que, si los rasgos de defensa contra herbívoros varían en escalas biogeográficas, dicha variación potencialmente brinde elementos de explicación a patrones de distribución de especies e interacciones en regiones biogeográficas (Giannini et al. 2013; Violle et al. 2014; Galiana et al. 2018; Gravel et al. 2019).

Desde la perspectiva de investigación, estudios centrados en sistemas planta-herbívoro-enemigo natural, como es el caso del modelo *Piper*-orugas-parasitoides brindan un marco de referencia para plantear preguntas de investigación básica en ecologia, evolución o comportamento sobre los efectos de factores bióticos y abióticos en herbivoría, parasitismo o especialización en escalas espaciales y temporales tanto, en ecosistemas naturales como intervenidos, lo cual tiene gran aplicación en estrategias de control de insectos plaga en agroecología con prácticas de cultivos sustentables, o sobre funciones ecosistémicas en el campo de la biologia de la conservación.

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