UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

ECOLOGÍA

ESTRUCTURA DE COMUNIDADES DE ABEJAS (HYMENOPTERA: APOIDEA) Y MOSCAS MIMÉTICAS DE ABEJAS (DIPTERA: BOMBYLIIDAE, SYRPHIDAE) POLINIZADORAS EN EL VALLE DE CUATRO CIÉNEGAS, COAHUILA, MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

OMAR ÁVALOS HERNÁNDEZ

TUTOR PRINCIPAL DE TESIS: DR. ZENÓN CANO SANTANA, FACULTAD DE CIENCIAS, UNAM
COMITÉ TUTOR: DRA. ROSA GABRIELA CASTAÑO MENESES, FACULTAD DE CIENCIAS, UNAM
DR. EFRAÍN TOVAR SÁNCHEZ, CENTRO DE INVESTIGACIÓN EN BIODIVERSIDAD Y CONSERVACIÓN, UAEM

CIUDAD DE MÉXICO **JUNIO 2016**

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UNAM POSGRADO
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DIVISIÓN DE ESTUDIOS DE POSGRADO

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ASUNTO: Oficio de Jurado

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **11 de abril de 2016**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **ÁVALOS HERNÁNDEZ OMAR** con número de cuenta **400047742** con la tesis titulada: **"Estructura de comunidades de abejas (Hymenoptera: Apoidea) y moscas miméticas de abejas (Diptera: Bombyliidae, Syrphidae) polinizadoras en el Valle de Cuatro Ciénegas, Coahuila, México"**, realizada bajo la dirección del (la) **DR. ZENÓN CANO SANTANA:**

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Ciudad Universitaria, Cd. Mx., a 25 de mayo de 2016

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

MCAA/MJFM/ASR/ipp

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Índice

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RESUMEN

El estudio de las comunidades de insectos polinizadores es relevante por la importancia de éstos en el mantenimiento de las comunidades de plantas. Los estudios de insectos polinizadores se han centrado en abejas, pues se consideran los polinizadores más importantes. Sin embargo, las moscas también participan de forma relevante en la polinización. Syrphidae y Bombyliidae son dos familias de moscas que visitan flores y, además, presentan mimetismo con abejas. Esta relación imitador-modelo sumada al uso del mismo recurso por ambos grupos de insectos, genera una interacción compleja, en la que las moscas deben coexistir con sus modelos para recibir un beneficio del parecido, pero la coexistencia aumenta el solapamiento de uso de recursos y, por lo tanto, la competencia. Este trabajo busca conocer las especies de Bombyliidae de la zona de Cuatro Ciénegas, Coahuila; determinar los patrones espacio-temporales de diversidad y uso de recursos de las moscas Bombyliidae y Syrphidae y seis familias de abejas visitadoras de flores; y analizar el efecto del mimetismo en las comunidades de moscas miméticas. Se recolectaron abejas y moscas de las familias Syrphidae y Bombyliidae en nueve localidades del Valle de Cuatro Ciénegas y la Sierra de La Madera durante 2012 y 2013 y se registró la especie de planta de la que se alimentaba cada ejemplar. El material se determinó taxonómicamente y a partir de estos datos se estimaron la riqueza de especies, la diversidad y el número de especies de plantas que visita cada grupo. Se separaron los datos por dos regiones: sierra y valle; y por dos temporadas: lluvias y secas. Se definieron los miméticos y modelos con un método objetivo que aplica morfometría geométrica y funciones de análisis discriminante, que permite tener una medida cuantitativa de la distancia morfológica entre miméticos y modelos. Ya con los miméticos y modelos definidos se pusieron a prueba dos supuestos de la teoría de mimetismo batesiano. El primero es que a mayor abundancia de modelos habrá mayor abundancia de miméticos, el segundo es que una mayor similitud con su modelo da una mayor protección a los miméticos. Se encontraron 100 especies de Bombyliidae, 41 de las cuales son nuevos registros para el estado de Coahuila, a pesar de que el 30 % del material no pudo ser identificado debido a que la determinación taxonómica del grupo es complicada, así como por la falta de claves y revisiones taxonómicas. Esto sugiere que la región alberga una gran diversidad de dípteros de esta familia y que hay un gran desconocimiento de los grupos taxonómicos encontrados en Cuatro Ciénegas y, en general, en todo el norte del país. Al describir los patrones espacio-temporales de diversidad, de composición de especies y de

uso de recursos de estos grupos, se encontró que analizar los datos de cada familia por separado es adecuado para comparar los patrones, contrario a tratar a todas las familias de abejas o de moscas como una unidad. Se encontró que algunas familias de abejas visitaban más especies de plantas, en áreas o temporadas donde el número de especies de plantas era mayor, mientras que otras familias seguían visitando el mismo número de especies de plantas, aun cuando el número de estas aumentara. Esta capacidad de visitar más especies de plantas si estas están disponibles pueden afectar la eficiencia de estos insectos como polinizadores. Dado que cada familia tiene respuestas diferentes a las condiciones, así como patrones espacio-temporales distintos, en los estudios de polinizadores deben de tratarse cada familia por separado e incluir a las moscas que, como en el caso de Cuatro Ciénegas, pueden presentar una gran abundancia. Por otro lado, se encontró una relación negativa entre la abundancia de miméticos y la de modelos, lo cual sugiere la posible existencia de competencia entre moscas miméticas y abejas modelo por las flores. Asimismo, hubo una relación negativa entre similitud morfológica y la proporción de abundancia de miméticos con modelos, lo que apoya la hipótesis multimodelo para explicar la existencia del mimetismo imperfecto, pues, según esta hipótesis, algunos miméticos imitan a varias especies al mismo tiempo, lo que les permite tener protección ante los depredadores en la presencia de cualquiera de sus modelos, lo que a su vez permite que sean más abundantes que sus modelos. El presente trabajo es uno de los pocos estudios que estudian el mimetismo a nivel de comunidad y con datos de campo. Para tener un punto de referencia y poder comparar los patrones es necesario incluir a todas las especies de los grupos taxonómicos de interés, es decir, incluyendo a las no-miméticas. Se establece la necesidad futura de probar si el grado de solapamiento de uso de recursos es mayor entre miméticos y modelos que entre no miméticos, así como conocer cómo afecta el mimetismo al grado de especialización existente entre miméticos y modelos.

ABSTRACT

The study of communities of pollinator insects is relevant due their role in the maintenance of plant communities. These studies have focused on bees, which are considered the most important pollinators, however, flies also visit flowers and are pollinators. Syrphidae and Bombyliidae are two families of flower-visiting flies and, also, they are mimics of bees. This mimetic-model relation between flies and bees, joined with the fact that both groups use flowers as resources, creates a complex interaction, in which the mimetic flies must coexist with their models to receive a benefit from the similarity, but this coexistence increases the resource use overlap and, therefore, the competition. This study aims first, to know the species of Bombyliidae present in the Cuatro Ciénegas, Coahuila region; then, to establish the spatial-temporal diversity and resource use patterns of Bombyliidae, Syrphidae, and six bee families; and finally, to investigate the effect of mimicry on the communities of mimetic flies. Bees and flies of Syrphidae and Bombyliidae families were collected in nine sites of the Cuatro Ciénegas Valley and the surrounding mountains Sierra La Madera, during 2012 and 2013. For each specimen collected, the plant species of which it was feeding was recorded. The material was identified and species richness, diversity and the number of plant species visited were estimated for each family. Data were divided in two locations: valley and mountains; and in two seasons: rainy and dry. Mimetics and models were defined with an objective method that applies morphometry techniques and discriminant function analysis, and provides a quantitative measurement of the morphologic distance between mimics and models. Once the mimics and models were defined, two assumptions of the batesian mimicry theory were tested. The first assumption posits that a higher abundance of the models is related with a higher abundance of their mimics. The second assumption proposes that a higher similarity with their models provides a better protection to the mimics. We found 100 species of Bombyliidae, 41 of which are new records for the state of Coahuila, although 30% of the material could not be identified to the species level because of the lack of determination keys and taxonomic studies for this family. This suggests that the region contains great diversity of this Diptera family and shows the lack of knowledge of these taxa in Cuatro Ciénegas and in the north of the country. The analysis of the spatial-temporal patterns of diversity, species composition and resource use of these groups showed that it is appropriate separating the data of each family for the analysis, instead of treating all bee families as a single unit. Some bee families visit more plant species in areas or seasons where species richness of plants is higher, whereas other families keep visiting the same number of plant species, even if the number of plant species is higher. This potential for increasing the number of plant species visited if available, could affect the efficiency of these insects as pollinators. As each family has different responses to the environmental conditions, as well as different spatial-temporal patterns, the studies on pollinators must treat each family independently and include flies that, as in Cuatro Ciénegas, could present great abundance.

Also, a negative relation between the abundance of mimics and models was found. This suggests a competition interaction between mimetic flies and model bees, due the use of the same resource, the flowers. Likewise, there was a negative relation between the morphological similarity of the mimics with their models and the abundance of mimics relative to their models, which supports the multi-model hypothesis that explains the existence of imperfect mimicry. According to this hypothesis some mimics imitate more than one species at the same time, this allows them to be protected from the predators in the presence of any of their models, and to be more abundant than any of their models. This is one of the few studies that analyzes mimetism at a community level and with field data. In order to be able to compare the patterns of the mimics and their models, is necessary to have a reference point, for this the non-mimetic species of close taxonomic groups must be included in the analysis. The next step in this research field could be to test if the degree of resource use overlap is higher between mimics and models than between non-mimics, and knowing how mimetic interactions affects the specialization degree as pollinators of mimics and models.

INTRODUCCIÓN GENERAL

Comunidades biológicas y su estructura

Una comunidad biológica es el conjunto de especies que están en un mismo espacio y tiempo, y que interactúan entre sí (Morin, 1999; Begon *et al*., 2006). Si la comunidad incluye a todas las especies que interactúan en un lugar, entonces estudiar una comunidad completa es complicado o prácticamente imposible. Por eso se elige arbitrariamente una parte de la comunidad, generalmente delimitada por la taxonomía o por los gremios (Samuels y Drake, 1997; Underwood, 2008). La delimitación espacial de una comunidad también es arbitraria. Los límites entre comunidades son difusos y éstas se entrelazan. Los métodos de ordenación, como el análisis de componentes, permiten representar a las comunidades en un diagrama de acuerdo a la composición de especies y sus abundancias relativas (Begon *et al*., 2006), para ello se construye un diagrama en el que dos comunidades con las mismas especies y en proporciones similares aparecerán cercanos entre sí (Leaps y Smilauer, 2003). Por ello, estos métodos estadísticos constituyen una alternativa objetiva para la delimitación y clasificación de las comunidades.

La estructura de la comunidad es el arreglo de las propiedades de la comunidad, este arreglo puede presentar patrones ordenados o puede ser azaroso sin patrones distinguibles. No existe una medida única, una propiedad o un sólo número que describa toda la estructura de una comunidad, sino que hay varios parámetros que se usan para comparar comunidades y describir su estructura (Morin, 1999). La estructura de una comunidad se puede describir de distintas formas, pero los estudios se han concentrado en la riqueza de especies, abundancia, biomasa, diversidad y tipos de forma de vida. Se debe considerar que una comunidad puede presentar una estructura más o menos ordenada, simplemente por azar. Por puro azar se esperaría una cierta distribución de las especies y de sus abundancias (Morin, 1999). Para saber si la estructura se generó por azar es necesario comparar la comunidad con modelos nulos, que son comunidades generadas al azar (Wilson, 1987; Gotelli, 2000). Un modelo nulo no implica que la comunidad no tiene estructura, sino que la estructura se generó azarosamente y no por las interacciones. En este sentido, si la comunidad difiere de un modelo nulo, la ecología de comunidades intenta explicar la causa de los patrones.

La ecología de comunidades es criticada por ser una ciencia descriptiva más que predictiva (Keddy, 1992). Pero si la estructura de la comunidad está generada por las interacciones biológicas y abióticas, entonces la estructura no es azarosa, sino predecible a partir de estas interacciones (Caswell, 1976). Por ejemplo, la teoría de nicho y la exclusión competitiva explican que una especie debe encontrar un lugar o un hueco en el espacio del nicho para entrar a una comunidad (Hardin, 1960; Begon *et al*., 2006). Este espacio es determinado por factores abióticos y por las interacciones con otras especies de tal forma que las interacciones afectan la composición y abundancia de las especies de una comunidad. Así como las interacciones generan la estructura, de la misma forma las interacciones pueden inferirse a partir de los cambios en los parámetros de la comunidad (Morin, 1999), por lo cual la estructura de una comunidad no sólo es una descripción de los patrones sino que implica la existencia de interacciones subyacentes. La importancia relativa de cada tipo de interacción sobre la estructura de una comunidad cambia de una comunidad a otra, pero históricamente se considera a la competencia como una de las principales (Hardin, 1960; Pianka, 1974; Inouye, 1978; Gilbert y Owen, 1990; Kelt *et al.*, 1995; Goulson y Darvill, 2004), aunque también se estudia el efecto del mutualismo, como es el caso de la polinización, sobre la estructura de las comunidades de los grupos de organismos interactuantes (Bascompte *et al.*, 2003; Bascompte, 2009a; Campbell *et al.*, 2011).

En esta tesis se analiza el efecto del mimetismo sobre la estructura de las comunidades de moscas y abejas. Se postula por primera vez la idea de que, la necesidad que tienen las moscas miméticas de coexistir con las abejas modelo, para recibir un beneficio de la similitud, está en conflicto con la competencia potencial debida a que ambos grupos usan las flores como un recurso. Esto implica que los miméticos y sus modelos tendrán un mayor solapamiento de uso de recursos que los no miméticos, o que habrán evolucionado mecanismos para evitar este solapamiento, como diferente grado de especialización. Además sugiere que la relación entre las abundancias de miméticos y modelos será negativa, aun cuando tengan que coexistir.

Interacciones y la estructura de las comunidades

La competencia puede afectar la composición de una comunidad al evitar la coexistencia de dos especies o al modificar sus abundancias. Esto se fundamenta en la teoría de nicho que dice que la composición de especies de una comunidad depende de los nichos disponibles y el solapamiento entre éstos (Polechova y Storch, 2008). Por lo tanto, bajo esta teoría, si se tienen definidos los nichos y su amplitud se podría predecir la composición y la diversidad de una comunidad. Contrastante a esta teoría de nicho, se encuentra la teoría neutral que predice que los patrones de diversidad, composición de especies y abundancia relativa no dependen de los nichos o sus diferencias sino de procesos estocásticos neutrales (Tilman, 2004; Chase, 2011). Estas dos teorías son extremos en un continuo de escenarios en los que intervienen factores determinísticos y estocásticos que actúan simultáneamente (Chase, 2011), de forma análoga a como intervienen la selección natural (determinístico) y la deriva génica (estocástico) sobre la estructura genética de una población. Las especies se establecen en una comunidad por un procesos azaroso, pero la probabilidad de que se establezcan no son iguales, sino que dependen de las características de cada especie (Tilman, 2004). Se sabe que la importancia relativa de cada factor depende del tamaño de la comunidad, pues en comunidades con pocas especies y abundancias bajas, los procesos estocásticos afectan más profundamente a la estructura. De igual forma, en ambientes con pocos recursos, las especies con capacidad de invadir serán pocas y los procesos estocásticos tendrán menos importancia (Chase, 2011). El modelaje de la estructura de las comunidades a partir de las interacciones de competencia se basa en el solapamiento y diferenciación de nicho, así como en el principio de exclusión competitiva.

El principio de exclusión competitiva postula que dos especies con el mismo nicho, en un mismo espacio y tiempo y con tasas de crecimiento diferentes ocasionará la desaparición de una de éstas por competencia (Hardin, 1960). Aun cuando es lógico, este principio no puede refutarse porque si dos especies que compiten también coexisten, entonces se argumenta que hay diferencias en el nicho o que las tasas de crecimiento son parecidas y el proceso de exclusión será largo, casi indefinido (Hardin, 1960; Hubbell, 2005), o bien, que hay recarga de individuos de esas especies desde comunidades cercanas (Polechova y Storch, 2008). La exclusión competitiva deja la interrogante de qué tanto deben ser diferentes los nichos para que dos especies puedan coexistir.

La teoría de diferenciación de nicho dice que la coexistencia de dos especies que usan el mismo recurso sólo puede darse si sus nichos son diferentes, es decir, hay poco solapamiento entre las curvas del uso de recurso (Polechova y Storch, 2008; Begon *et al.*, 2006). El solapamiento de nicho sería inversamente proporcional a la intensidad de la competencia, de manera que dos especies con mucha competencia presentarían bajo solapamiento (Pianka, 1974; Polechova y Storch, 2008). Sin embargo, estas diferencias y similitudes entre nichos no siempre se producen por competencia, pues pueden deberse a la adaptación de las especies a las mismas condiciones (Hubbell, 2005). Al igual que con la exclusión competitiva, las predicciones de la teoría de diferenciación de nicho no pueden ponerse a prueba. Por un lado, todas las especies diferirán al menos un poco en su nicho (Pianka, 1974) de tal forma que no se observarían nunca dos especies con nichos idénticos coexistiendo. Por otro lado, en caso de que se diera la coexistencia de dos especies con nichos casi idénticos, se puede aludir a un mecanismo que permita esta coexistencia, como la distribución heterogénea espacio-temporal de recursos o condiciones o la existencia de dos recursos limitantes, cada uno aprovechado de manera eficiente por distinta especie (Hubbell, 2005; Chase, 2011). Estas diferencias en el uso de los recursos pueden reflejarse en la morfología de las especies, a lo que se conoce como desplazamiento de caracteres (Gilbert y Owen, 1990; Polechova y Storch, 2008). En este sentido, cuando se encuentran diferencias morfológicas y entre los nichos de dos especies similares que coexisten se pueden explicar por la competencia entre estas especies.

La exclusión competitiva y la diferenciación de nicho no pueden probarse tal cual como se postularon. Debido a que, si se encuentra evidencia contraria a sus predicciones, como la coexistencia de especies con un nicho muy similar, ésta evidencia puede explicarse por otros factores, como la heterogeneidad espacial de los recursos. Sin embargo, sí hay evidencia de que la competencia moldea la estructura de las comunidades. Ésta evidencia se obtiene mediante la comparación de modelos nulos con comunidades reales o mediante la experimentación. Por ejemplo, Kelt *et al.* (1995) encontraron que la composición de las comunidades de mamíferos pequeños de la Patagonia se ve afectada por la competencia, y que especies similares que compiten, coexisten menos frecuentemente de lo esperado por azar. Por otro lado, Gilbert y Owen (1990), al estudiar comunidades de Syrphidae, pusieron a prueba las hipótesis de que la competencia y exclusión es mayor entre especies del mismo gremio, que si las flores son escasas la competencia entre polinizadores afecta la composición y la abundancia relativa, y que la abundancia de cada especie es inversamente proporcional a la competencia que experimenta. Contrario a Kelt *et al.* (1995), estos autores llegaron a la conclusión de que en su sistema la competencia no estructura a la comunidad. Según sus resultados, cada especie responde por su cuenta a la distribución de los recursos. Sin embargo los autores solo compararon los patrones de coexistencia observados con modelos nulos sin probar la cantidad de recursos. Por lo que no se sabe si realmente hay competencia en ese sistema. Por otra parte, Inouye (1978) desarrolló un experimento en un sistema de dos especies de abejas y dos especies de plantas en el que midió el uso de recursos de las abejas con y sin la presencia de la otra especie. Encontró que, sin la presencia de la otra especie, las abejas visitan ambas especies de plantas con la misma frecuencia, pero en la presencia de la otra especie de abeja, cada especie visita con más frecuencia alguna de las dos especies de plantas. Esto prueba que la competencia por interferencia modifica la repartición de recurso y la amplitud de nicho.

El efecto de la competencia sobre la estructura de la comunidad es algo muy complicado de probar. Esto es porque la competencia y su intensidad se reconocen y se mide precisamente por el efecto que tiene sobre las abundancias o distribuciones de las especies. Entonces, si hay dos especies similares que coexisten, ambas con abundancias altas, se puede concluir, como lo hicieron Gilbert y Owen (1990), que la competencia no afecta a la comunidad o, por otro lado, se puede concluir que no hay competencia entre esas especies. El efecto de la competencia se puede medir adecuadamente de forma experimental, aunque esto es complicado logísticamente a nivel de comunidades. Otra aproximación es comparar los patrones de coexistencia y abundancia entre especies similares con los patrones entre especies no similares. Las diferencias podrían indicar un efecto de la competencia, aunque no es concluyente.

Otra interacción que afecta la estructura de las comunidades es el mutualismo. Para el caso particular de los insectos polinizadores, la interacción mutualista con las plantas modifica principalmente la diversidad y el grado de especialización al interior de las comunidades. La diversidad de una comunidad involucra, además del número de especies, el número de interacciones (Rico-Gray, 2007; Bascompte, 2009b). Campbell *et al.* (2011) generaron modelos y simulaciones para ver cómo se organiza una red trófica mutualista. Según su modelo, la comunidad se forma con especies de comunidades vecinas que están tienen la capacidad de invadir la comunidad. El establecimiento de la especie depende de las relaciones mutualistas que ya están en la comunidad, lo que afecta la diversidad máxima de la comunidad.

Se ha registrado que las interacciones mutualistas entre polinizadores y plantas forman redes con características constantes y predecibles (Bascompte, 2009a) y que la distribución de los especialistas y generalistas en la red no es azarosa (Rico-Gray, 2007; Bascompte *et al.*, 2003; Bascompte 2009b). Estas características de las redes forman patrones generales que se presentan independientemente de la composición de especies (Bascompte, 2009b). Esto sugiere que, a diferencia de lo que ocurre con la competencia, en las interacciones mutualistas no es tan relevante la identidad de las especies involucradas en la interacción. Uno de estos patrones es que la gran mayoría de las redes mutualistas son anidadas, es decir, presentan un núcleo de generalistas que interactúan con otros generalistas, después especialistas interactúan con generalistas y no hay interacciones de especialistas con especialistas (Bascompte *et al.,* 2003; Guimaraes *et al.*, 2006; Bascompte, 2009b). Bascompte *et al.* (2003) analizaron 52 redes mutualistas y encontraron que estos patrones de anidamiento son más claros entre más compleja sea la red (esto es, entre más elementos y conexiones tenga). Por lo tanto, la diversidad afecta la estructura de la red de interacciones.

Una tercera interacción que puede afectar la estructura de las comunidades de polinizadores es la depredación, aunque sea con un efecto indirecto. Aunque la depredación no se considera una interacción importante para la estructura de las comunidades de los polinizadores, sí puede afectarla. En primer lugar, los depredadores pueden reducir el efecto de la competencia al atacar a un competidor dominante, o si las especies deben de invertir recursos en defenderse y con eso bajar su capacidad competitiva (Begon *et al.*, 2006). Por otro lado, la depredación es una presión selectiva para las especies miméticas. A su vez, el mimetismo es también una interacción que puede tener efecto sobre la estructura de estas comunidades.

Mimetismo y estructura de las comunidades de abejas y moscas polinizadoras

El mimetismo involucra a un organismo (mimético) que simula una señal propia de un segundo organismo (modelo) que es de interés para un tercer organismo (receptor), de tal forma que, el mimético aumenta su adecuación como resultado de que el receptor lo identifica como el modelo (Vane-Wright, 1980). En específico, el mimetismo batesiano es aquel en el que el mimético sin defensas engaña a los depredadores al imitar a un modelo con defensas (Bates, 1981). Algunas especies de dípteros de las familias Bombyliidae y Syrphidae son miméticos batesianos de abejas. Estas especies miméticas deben de coexistir con sus modelos para obtener un beneficio del mimetismo, ya sea evitar la depredación (Ries y Mullen, 2008; Savage y Mullen, 2009; Skelhorn *et al*., 2010; Beatty y Franks, 2012), o reducir la competencia con otros nectarívoros (Rainey y Grether, 2007).

La teoría de mimetismo batesiano expone que las condiciones necesarias para que el mimetismo funcione son: 1) el depredador tiene capacidad de aprender la señal de alerta y evitar a los modelos y, por tanto, a los miméticos (Rettenmeyer, 1970); 2) la abundancia del mimético debe ser menor a la del modelo para que el depredador asocie la señal con el estímulo desagradable y no con alimento (Wallace, 1867); y 3) el mimético y el modelo deben coexistir en espacio y tiempo, porque sin modelo no hay beneficio para el mimético (Wallace, 1867). Otra condición implícita y que frecuentemente es ignorada es que la similitud entre las especies debe ser suficiente para considerarlas miméticas. Por otro lado, la predicción básica del mimetismo es que los miméticos recibirán un beneficio (menos depredación) que no reciben sus congéneres no miméticos (Rettenmeyer, 1970; Ruxton *et al*., 2004). Además, se espera que el beneficio para el mimético sea mayor al aumentar la similitud (Franks y Noble, 2004), al mejorar el mecanismo de defensa del modelo (*v. gr.*, más tóxico) (Lindström *et al*., 2006) y al aumentar el número de presas alternativas (Ruxton *et al*., 2004). Aquí nos enfocaremos en la abundancia de los miméticos en relación a la abundancia de los modelos, en la necesidad de coexistencia de miméticos y modelos y en la relación entre parecido y beneficio.

Los modelos de mimetismo suponen que para que haya un beneficio para los miméticos la proporción de éstos respecto a los modelos debe ser baja (Ruxton *et al*., 2004; Joron y Mallet, 1998). La evidencia con moscas miméticas indica que no siempre los modelos son más abundantes (Howarth *et al*., 2004; Azmeh *et al*., 1998), pero esto se puede explicar si el modelo es muy tóxico y los depredadores no se arriesgan a equivocarse (Brower, 1960), si hay presas alternativas que reducen la presión sobre los miméticos, o si las moscas imitan a varios depredadores y no dependen directamente de la abundancia de un sólo modelo (Gilbert, 2005).

Todas las teorías de mimetismo sostienen que el mimético obtiene más beneficio entre mayor sea su similitud con su modelo (Rettenmeyer, 1970; Franks y Noble, 2004). Esto implica que hay una presión selectiva sobre los miméticos para aumentar la similitud; sin embargo, hay miméticos llamados imperfectos que son apenas similares a sus modelos. El mimetismo imperfecto está particularmente extendido en los Syrphidae más que en ningún otro grupo de insectos (Pfennig y Kikuchi, 2012b). Se han propuesto 11 hipótesis del mantenimiento del mimetismo imperfecto revisadas por Kikuchi y Pfennig (2013). Por ejemplo, la hipótesis multi-modelo plantea que algunos Syrphidae imitan a más de un modelo (Edmunds, 2000; Howarth *et al.*, 2004) y tienen una morfología intermedia. Estos miméticos imperfectos podrán tener más abundancia que cualquiera de sus modelos. Si esta hipótesis es correcta, la similitud y la proporción entre la abundancia de miméticos y modelos estarán negativamente correlacionadas, ya que los buenos miméticos dependerán de la abundancia de sus modelos, mientras que los imperfectos no dependen de la abundancia de un modelo en específico.

Por su parte, Pfennig y Kikuchi (2012a) proponen para explicar el mimetismo imperfecto que, dado que mayor parecido implica más competencia, el desplazamiento de caracteres que reduce la competencia es lo que evita una mayor similitud entre miméticos y modelos. Esto se puede probar estudiando la relación entre el uso de recursos y la similitud, pues de existir competencia se esperaría que especies más parecidas utilizaran los mismos recursos. La competencia potencial entre moscas y abejas por las flores nos lleva al tercer punto de interés, que es la coexistencia entre miméticos y modelos.

La interacción mimética entre moscas polinizadoras y abejas es compleja porque las moscas miméticas, al coexistir con abejas modelo, reciben el beneficio de la reducción de la depredación. Sin embargo, pueden presentar interacciones de parasitismo de miméticos a modelos (Gabritschevsky, 1926; Edmunds y Readers, 2013), competencia entre miméticos (Rainey y Grether, 2007; Rashed y Sherratt, 2007) y competencia entre miméticos con sus modelos (Pfennig y Kikuchi, 2012a). Estas fuerzas ecológicas no sólo ejercen presión sobre la similitud de los miméticos sino también modifican la estructura de ambas comunidades, sobre todo los patrones de abundancia, diversidad y uso de recursos. El efecto de estas fuerzas y los patrones que genera sólo se pueden reconocer con estudios a nivel de comunidad y con estudios que incluyan además de los miméticos y modelos a las especies no miméticas que usan el mismo recurso.

Factores que actúan sobre las comunidades de polinizadores

Las flores son el recurso más importante para los insectos polinizadores y la riqueza de especies de plantas con flores está asociada positivamente con la frecuencia (Ebeling *et al.*, 2008; Kearns y Oliveras, 2009) y con la diversidad de abejas (Steffan-Dewenter y Tscharntke, 2001; Potts *et al.*, 2003; Ramírez, 2004; Fründ *et al.*, 2010). Sin embargo, esta relación positiva no se da en todos los grupos o en todos los ambientes. Por ejemplo, Hegland y Boeke (2006) no encontraron relación entre la riqueza de plantas y la de polinizadores en un pastizal con clima templado. La riqueza de plantas con flores se ve afectada por factores como el suelo, los fertilizantes, el disturbio y los rasgos de la comunidad vegetal en general, lo cual puede confundir el efecto de los polinizadores sobre ésta y viceversa (Ebeling *et al.*, 2008). A su vez, los insectos no dependen sólo de las flores sino de otros recursos cuya disponibilidad varía independiente de las plantas. Si se incluye en los análisis a todos los insectos, la relación con la comunidad de plantas con flores se diluye. También hay que considerar que no todas las plantas con flores son igualmente importante para todos los polinizadores, una planta polinizada por aves o con néctar accesible a sólo un grupo de insectos, no es un recurso para todas las abejas o moscas. De tal forma que, para ver el efecto de la riqueza de plantas con flores sobre la comunidad de polinizadores se debe reconocer las plantas que realmente constituyen un recurso y dividir en gremios o en grupos taxonómicos a los insectos.

El efecto de la riqueza de especies de plantas con flores sobre la abundancia de polinizadores puede ser por dos causas, revisadas por Ghazoul (2006): 1) por atracción complementaria, esto es que la combinación de flores distintas atrae a más polinizadores; o 2) por continuidad del recurso, la diversidad de plantas provee un suministro constante de flores para los polinizadores. Esto provoca que al aumentar la riqueza de especies de plantas con flores y la cobertura vegetal aumente la riqueza de polinizadores, la frecuencia de visitas y con esto la estabilidad de ambas comunidades (MacArthur, 1955). Al aumentar las especies de insectos también aumenta la probabilidad de una planta de ser polinizada, y lo mismo ocurre para los insectos, pues si una flor desaparece hay otras para sustituirla. Esta complementariedad es mayor si la comunidad de insectos es diversa, por ejemplo, las moscas pequeñas polinizan flores pequeñas que las abejas ignoran (Ssymank *et al.*, 2008).

La relación entre plantas con flores y polinizadores no es unidireccional. La diversidad funcional de polinizadores afecta positivamente a la riqueza de especies de plantas (Fontaine *et al.*, 2006). Los polinizadores son un recurso para las plantas y funcionan como un filtro para plantas especialistas que en la ausencia de un tipo de polinizador no pueden establecerse (Sargent y Ackerly, 2008). La competencia por polinizadores puede resultar en la extinción local de especies de plantas o en el desplazamiento de los periodos de floración (Heithaus, 1979). Además, la cantidad y calidad de polinizadores determinan patrones de especialización y autocruzamiento de las plantas (Gómez y Zamora, 2006). En conclusión, las comunidades de insectos polinizadores y plantas con flores están correlacionadas.

Se debe considerar que la cantidad o calidad de los recursos flores varía temporalmente y, por lo tanto, también su efecto sobre la comunidad de polinizadores. Scriven *et al.* (2013) reportan que la diversidad de polinizadores aumenta con la densidad de flores, y aunque esta densidad no varía entre meses, sí varía dentro de cada mes. En una escala temporal menor, los horarios de forrajeo difieren entre grupos taxonómicos de acuerdo a la calidad del néctar y las capacidades fisiológicas de cada grupo de insectos (Herrera, 1990). Por otro lado, en una escala mayor, se sabe que la fenología influye en el efecto de las plantas sobre los polinizadores. Potts *et al.* (2003) encontraron que la diversidad de abejas está asociada positivamente sólo a la riqueza de plantas anuales y no a la de plantas perenes. Mientras que Steffan-Dewenter y Tscharntke (2001) reportan una tendencia de Halictidae y Syrphidae a visitar plantas anuales, contrario a Apidae y Megachilidae que prefieren plantas perennes. El componente temporal a diferentes escalas debe considerarse al evaluar los efectos de las plantas con flores en las comunidades de insectos polinizadores.

Además de las plantas, los insectos utilizan otros recursos para completar su desarrollo. Para las abejas los sitios de anidamiento o lugares para formar sus colmenas son un recurso importante que afecta la composición de las comunidades (Steffan-Dewenter *et al.*, 2001; Potts *et al.*, 2005). Las moscas depredadoras o parasitoides dependen de la disponibilidad de presas. Algunos géneros de las Syrphidae (*v. gr.*, *Eristalis*) presentan larvas acuáticas (Vockeroth y Thompson, 1981) y necesitan de cuerpos de agua para completar su ciclo de vida. Estas necesidades de cada grupo modifican la composición, diversidad y abundancia de las comunidades de insectos polinizadores independiente de las plantas con flores.

A una escala espacial más amplia se ha encontrado que la estructura de las comunidades de polinizadores es afectada por la complejidad de paisaje y la fragmentación (Steffan-Dewenter y Tscharntke, 1999; Steffan-Dewenter *et al.*, 2001, 2002; Aizen y Feinsinger, 2003; Steffan-Dewenter y Kuhn, 2003), así como por la latitud y la altitud (Motten, 1986; Eiberling y Oiesen, 1999). En términos generales, la abundancia y diversidad de abejas se incrementan al incrementarse la proporción de hábitats seminaturales y la heterogeneidad del paisaje (Steffan-Dewenter *et al.*, 2001, 2002); en cambio, disminuyen al aumentar la fragmentación (Steffan-Dewenter y Tscharntke, 1999; Aizen y Feinsinger, 2003). Por su parte, la latitud y altitud tienen un efecto similar entre sí sobre las comunidades de polinizadores. A latitudes y altitudes altas las moscas polinizadoras aumentan su abundancia e importancia y las abejas disminuyen (Motten, 1986).

Se puede afirmar que la estructura de las comunidades de insectos polinizadores está determinada principalmente por la comunidad de plantas con flores. Este efecto es recíproco y tiene un componente espacial a nivel de paisaje y altitudinal, así como un componente temporal a distintas escalas, desde diaria hasta anual e incluso más amplia.

Importancia de los polinizadores

Los insectos polinizadores tienen un papel importante en los ecosistemas naturales y agrícolas (Kearns, 2001). Se sabe que aproximadamente el 80% de los cultivos requieren ser polinizados por insectos (Klein *et al.*, 2007). Por ello, se ha estimulado la realización de estudios que cuantifican la importancia económica de los polinizadores, así como el efecto de las alteraciones al ambiente sobre sus comunidades (Morandin y Winston, 2006; Kremen *et al.*, 2007; Gallai *et al.*, 2009). Morandin y Winston (2006) observaron que los cultivos cercanos a áreas naturales producen 30% más frutos que los cultivos más alejados de este tipo de zonas, debido a la influencia positiva de las abejas nativas que allí viven. Las abejas se consideran como el grupo principal de polinizadores, sin embargo, en algunos ambientes las moscas polinizan de manera igual o más efectiva (Motten *et al.*, 1981; Motten, 1986; Pellmyr y Thompson, 1996; Kearns, 2001). Las moscas polinizadoras, aun cuando en su mayoría no visitan plantas de cultivos, son importantes porque mantienen la diversidad de plantas nativas en el ecosistema (Kremen *et al.*, 2007).

Actualmente se reconoce que existe una crisis por la pérdida de diversidad y abundancia de polinizadores nativos (Kearns *et al.*, 1998; Kevan, 1999), lo cual puede acarrear consecuencias económicas adversas, entre las que se encuentra el aumento de precio de los productos agrícolas (Kevan y Phillips, 2001), así como consecuencias ecológicas indeseables, como la reducción de plantas polinizadas por insectos, tal como se ha observado en el Reino Unido y Holanda (Biesmeijer *et al.*, 2006). Entre las causas que han provocado la reducción de polinizadores se encuentran el uso de insecticidas, la urbanización, la proliferación de parásitos transmisores de enfermedades, como el ácaro *Varroa destructor* Anderson & Trueman, la presencia de especies invasoras (Butz Huryn, 1997; Morales, 2007) y la agricultura intensiva (Cane y Tepedino, 2001; Kremen *et al.*, 2007). Asimismo, se ha registrado que el cultivo de plantas que no ofrecen néctar (como el maíz o el trigo) reduce la diversidad de los polinizadores locales (Cane y Tepedino, 2001); incluso el monocultivo de sandías (*Citrullus lanatus* (Thunb.) Matsumura & Nakai), una planta que requiere de polinizadores y sus flores sí producen néctar, provoca la reducción de la diversidad y abundancia de abejas nativas (Kremen *et al.*, 2002).

Otra práctica negativa es que, para compensar la pérdida de polinizadores nativos que hagan este servicio en los cultivos, se recurre a la introducción artificial de abejas, principalmente *Apis mellifera* L. (Cane y Tepedino, 2001; Kremen *et al.*, 2002). En lugares donde esta especie no es nativa puede afectar a las comunidades de plantas y de otros polinizadores mediante la competencia con otras abejas y alterando el mutualismo entre plantas y abejas ya establecidas (Kremen *et al.*, 2007). En este sentido, se sabe que los polinizadores introducidos pueden desplazar a los polinizadores naturales locales (Motten, 1986; Ollerton *et al.*, 2012).

Dado todo lo anterior, es clara la enorme relevancia que tiene el estudio de las comunidades de polinizadores y de los factores que las afectan.

Área de estudio

El municipio de Cuatro Ciénegas

Este estudio se llevó a cabo en el el Valle de Cuatro Ciénegas y en la Sierra de la Madera dentro del municipio de Cuatro Ciénegas, Coah. (26° 59' N y 102° 03' O), que se localiza al noreste de México (Fig. 1). En el municipio se encuentra el humedal del Valle de Cuatro Ciénegas (150,000 ha, 730 m s.n.m.) y el área natural protegida del mismo nombre (84,347 ha) (INE, 1999), dentro del cual destacan tres cuerpos de agua: el río Mezquites y las lagunas Churince y Playitas (INE, 1999). Una fracción de la Sierra de La Madera pertenece en parte al municipio, y corre de sureste a noroeste y está ubicada al noroeste del Valle y se eleva desde los 700 hasta los 3000 m s.n.m.

La región de Cuatro Ciénegas es única a nivel mundial por su ubicación y características ambientales y biológicas. Se considera de importancia biológica por su grado de aislamiento y su antigüedad como ecosistema (Arriaga *et al.*, 2000). Aun con una precipitación de sólo 200 mm al año, la presencia de agua subterránea que aflora en pozas y ríos le provee características ambientales muy distintas a las regiones desérticas aledañas, que son más secas. La región ha llamado la atención de la Agencia Aeroespacial nacional de Estados Unidos (NASA, por sus siglas en inglés), ya que presenta comunidades microbianas características del Precámbrico, por lo que se considera un laboratorio natural para estudiar la evolución de la vida en la Tierra (Souza *et al.*, 2012). A partir de la separación de Pangea, Cuatro Ciénegas formó parte de un océano poco profundo, y la región quedó aislada del océano Atlántico al elevarse la Sierra Madre Oriental en el Eoceno medio hace 40 ma. Las bacterias en Cuatro Ciénegas tienen características fisiológicas de organismos marinos, además de relaciones filogenéticas cercanas con especies marinas, lo que indica que al retirarse el océano parte del agua se quedó atrapada en el Valle (Moreno-Letelier *et al.*, 2012).

La historia de aislamiento del área se ve reflejada también en los eucariontes. La región presenta un grado de endemismo alto, similar al de las islas Galápagos (Souza *et al.*, 2012). En plantas vasculares es la zona con más endemismos del estado, con 58 taxones endémicos (Villarreal-Quintanilla y Encina-Domínguez, 2005). Además de estar aislada, el ambiente en la región ha sido estable. La evidencia palinológica indica que la vegetación actual es básicamente idéntica a la de hace 30,000 a 40,000 años (Pinkava, 1979). Otros endemismos incluyen dos géneros y seis especies de crustáceos (Cole, 1984) y seis especies de reptiles (McCoy, 1984). Todas estas características hacen de esta región importante e interesante biológicamente. Hasta ahora no se han realizado estudios sobre comunidades de insectos en esta región.

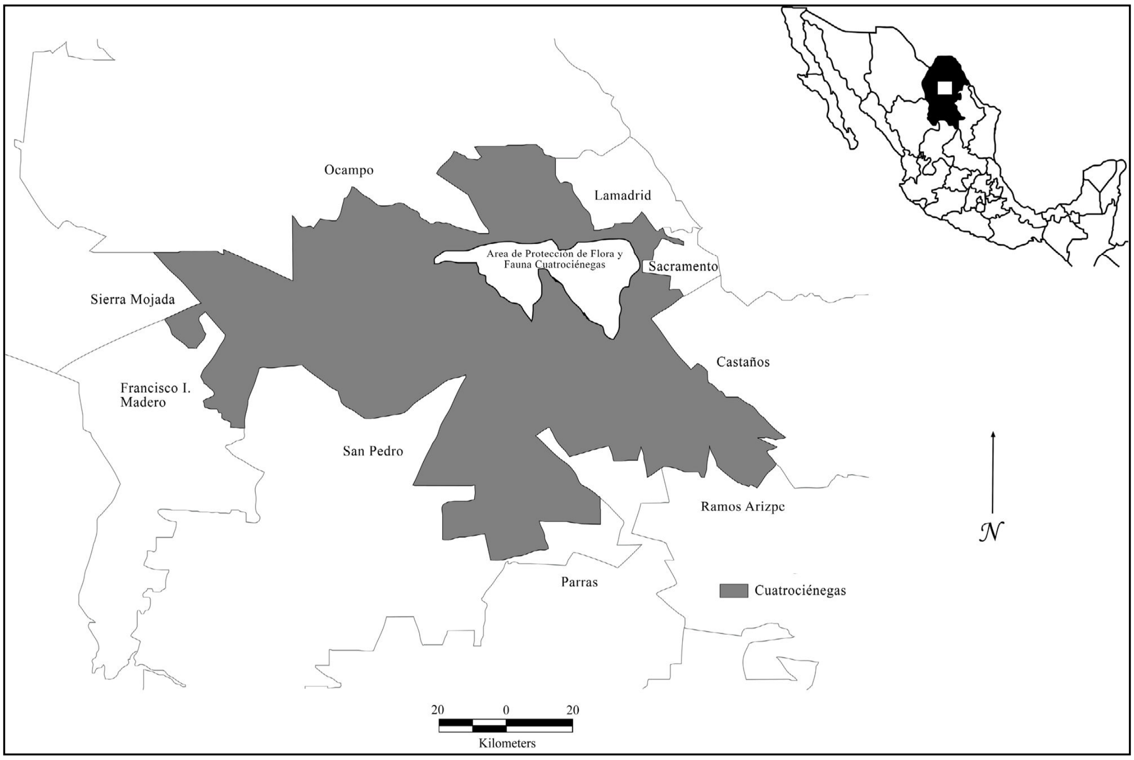

Figura 1. Ubicación del municipio de Cuatro Ciénegas en México.

En Cuatro Ciénegas se encuentran ocho tipos de vegetación (Pinkava 1979, 1984; INE, 1999). Las especies vegetales de cada uno de éstos están asociadas a condiciones de suelo y humedad específicas, según se expone a continuación.

1) Vegetación halófita. Se localiza en el valle en suelos salinos, dominado por pastos y zacates. En algunas áreas estos pastos son reemplazados por cultivos o usados para pastoreo. Los pastos predominantes son *Distichlis spicata* (L.) Greene, *Sporobolus airoides* (Torr.) Torr. y *Monanthochloe littoralis* Engelm., pero en las áreas menos salinas se encuentran *S. spiciformis* Swallen y *S. wrightii* Scribn.; en las áreas perturbadas domina la forbia *Suaeda* sp. y el arbusto *Prosopis glandulosa* Torr.

2) Vegetación acuática y semiacuática. Se encuentra alrededor y dentro de las pozas. Las especies cambian según el estado de sucesión que tenga cada poza. En pozas recién formadas las especies son las mismas que la vegetación que la rodean. Las especies de las primeras etapas de sucesión permanecen aunque en menor abundancia en etapas subsecuentes. Los pastos típicos de las pozas recién formadas son *Funastrum angustifolium* (Pers.) Liede & Meve, *Phragmites australis* (Cav.) Trin. ex Steud., *Setaria parviflora* (Poir.) M.Kerguelen y *Spartina spartinae* (Trin.) Merr.; los que están en pozas maduras son *Fimbristylis thermalis* S.Watson, *Fuirena simplex* Vahl y *Schoenus nigricans* L. Las forbias características de las pozas recién formadas son: *Eustoma exaltatum* (L.) Salisb. ex G.Don, *Flaveria chlorifolia*

A.Gray y *Polygala turgida* Rose, en tanto que las de pozas maduras son: *Anemopsis californica* (Nutt.) Hook. & Arn., *Bacopa monnieri* (L.) Pennell, *Conoclinium betonicifolium* (Mill.) R.M.King & H.Rob., *Heliotropium curassavicum* L., *Ipomoea sagittata* Poir., *Ludwigia octovalvis* (Jacq.) Raven. y *Mentha rotundifolia* (L.) Huds. Entre las plantas acuáticas de las pozas recién formadas están: *Carex pringlei* L.H.Bailey, *Eleocharis caribaea* (Rottb.) S.F.Blake, *E. cellulosa* Torr. y *E. rostellata* (Torr.) Torr.; mientras que las de las pozas maduras son: *Chara* spp., *Nymphaea ampla* (Salisb.) DC. y *Utricularia gibba* L. En las pozas maduras también se registran los arbustos *Senegalia greggii* (A.Gray) Britton & Rose, *Prosopis glandulosa* Torr. y *Salix nigra* Marsh. y árboles de *Fraxinus berlandieriana* A.DC.

3) Vegetación gipsófila. Está presente en dunas de yeso formadas por evaporación ubicadas en la parte noroeste del valle donde el viento, mueve las dunas y entierra a las plantas, aunque algunas especies funcionan como anclaje de las dunas y evitan que se desplacen. En esta zona se registran plantas estabilizadoras de dunas, como la hierba *Varilla mexicana* A.Gray, la rosetófila *Yucca treculeana* Carriere y los arbustos *Senegalia greggii* y *Prosopis glandulosa*. En esta zona también se hallan las hierbas gipsófilas *Thymophylla gypsophila* (B.L.Turner) Strother, *Gaillardia gypsophila* B.L.Turner, *Haploesthes robusta* I.M.Johnst., *Xanthisma gypsophilum* (B.L.Turner) D.R.Morgan & R.L.Hartm. y *M. restiformis* B.L.Turner. Otras plantas típicas de este tipo de vegetación son las hierbas *Euphorbia astyla* Engelm. ex Boiss., *Nerisyrenia incana* Rollins, *Petalonyx crenatus* A. Gray ex S. Wats., *Acleisanthes purpusiana* (Heimerl) R.A.Levin y *Tiquilia hispidissima* (T. & G.) A.Richardson, así como los arbustos *Fouquieria splendens* Engelm. y *Cylindropuntia leptocaulis* (DC.) F.M. Knuth.

4) Vegetación de transición. Esta vegetación forma una banda de arbustos alrededor del valle, a las faldas de las montañas. Es la transición entre la vegetación del valle y el matorral desértico de la parte baja de las montañas. Se pueden encontrar los arbustos *Senegalia greggii*, *Vachellia vernicosa* (Britton & Rose), Seigler & Ebinger, *Allenrolfea occidentalis* (S. Watson) Kuntze, *Atriplex canescens* (Pursh) Nutt., *Condalia warnockii* M.C.Johnst., *Proposis glandulosa* y *Suaeda* sp..

5) Matorral desértico. Está presente en cañadas y partes bajas de las sierras. Las plantas que componen el matorral son características del desierto Chihuahuense. La forma de vida dominante es la rosetófila donde tenemos a *Agave falcata* Engelm., *A. lechuguilla* Torr., *Hechtia texensis* S.Watson y *Yucca rostrata* Engelm. ex Trel.. Aunque el arbusto *Larrea tridentata* (DC.) Coville es muy abundante en algunas zonas, otros arbustos menos abundantes en esta vegetación son *Cordia parvifolia* A. DC., *Euphorbia antisyphilitica* Zucc., *Jatropha dioica* Sessé y *Parthenium incanum* Kunth. También se pueden encontrar forbias como *Thymophylla pentachaeta* var. *belenidium* (DC.) Strother, *Selaginella lepidophylla* (Hook. & Grev.) Spring o suculentas como *Ariocarpus fissuratus* (Engelm.) K. Schum., *Echinocactus horizonthalonius* Lem., *E. enneacanthus* Engelm., *Epithelantha bokei* L.D.Benson, *E. micromeris* (Engelm.) A. Weber ex Britton & Rose, *Ferocactus hamatacanthus* (Muehlenpf.) Britton & Rose, *Lophophora williamsii* (Lem. ex Salm-Dyck) J.M. Coult. y *Grusonia bradtiana* (J.M. Coult.) Britton & Rose.

6) Chaparral. Está presenta principalmente en las laderas norte y este de las montañas, en las cañadas y arroyos protegidos, por debajo del bosque montano. Los encinos en esta vegetación no superan los dos metros de altura. Las especies que se pueden encontrar son *Quercus hypoxantha* Trel., *Q. intricata* Trel., *Q. invaginata* Trel. y *Q. pringlei* Seemen ex Loes. Otros árboles también presentes son *Arbutus xalapensis* var. *texana* (S.F.Buckley) A.Gray, *Arctostaphylos pungens* Kunth y *Pinus cembroides* Newb. En este ambiente se pueden ver diferencias entre las zonas secas y húmedas. Las zonas secas se caracterizan por la presencia del pasto *Bouteloua curtipendula* (Michx.) Torr., hierbas del género *Salvia* y rosetófilas como *Agave*, *Dasylirion* y *Nolina cespitifera* Trel. También en zonas secas encontramos arbustos como *Senegalia berlandieri* (Benth.) Britton & Rose, *Chrysactinia mexicana* A.Gray, *Eysenhardtia texana* Scheele, *Parthenium incanum* Kunth y *Sophora secundiflora* (Ortega)DC. Mientras que los arbustos presentes en zonas húmedas son *Amelanchier denticulata* (Kunth) W.D.J. Koch., *Ceanothus greggii* A.Gray, *Cercocarpus mojadensis* Schneid., *C. montanus* Raf., *Forestiera angustifolia Torr.*, *Fraxinus greggii* A.Gray, *Rhus aromatica* Ait. y *R. virens* Lindheimer ex Gray.

7) Bosque de pino-encino. El chaparral da paso al bosque de pino-encino que se encuentra en las partes altas y húmedas, por encima de los 2000 msnm. La hierba dominante es *Vitis arizonica* Engelm., también se pueden encontrar los arbustos *Cecocarpus* spp., *Garrya ovata* Benth., *Prunus serotina* Ehrh., *Frangula betulifolia* (Greene) Grubov y *Salvia regla* Cav. y árboles de *Arbutus xalapensis* var. *texana*, *Juniperus pinchotii* Sudw., *Juniperus flaccida* Schltdl., *Pinus cembroides*, *Ptelea trifoliata* L., *Quercus glaucoides* M.Martens & Galeotti, *Q. gravesii* Sudw.y *Q. pringlei* Seemen ex Loes.

8) Bosque montano. Localizado en la parte más alta de la sierras por encima del bosque de pino-encino. Se distingue el bosque de las laderas norte y sur, estas últimas con menos humedad y más expuestas. En las laderas sur abundan las rosetófilas de los géneros *Agave* y *Dasylirion* y suculentas del género *Opuntia*. También en la ladera sur se pueden encontrar los arbustos *Linnaea coriacea* (Hemsl.) Christenh., *Arctostaphylos pungens* Kunth, *Garrya ovata* y *Spiraea northcraftii* I.M.Johnst., y los árboles *Pinus arizonica* Engelm., *P. cembroides*, *Quercus greggii* (A.DC.) Trel., *Q. hypoxantha Q. intricata.* Por su parte en las laderas norte dominan el arbusto *Cornus sericea* subsp. *sericea* Michx. y los árboles *Abies durangensis* var. *coahuilensis* (I. M. Johnst.) Martínez, *Arbutus xalapensis* var. *texana*, *Cupressus arizonica* Greene, *Acer grandidentatum* Nutt. ex Torr. & Gray, *Pinus arizonica*, *P. strobiformis* Engelm., *Pseudotsuga menziesii* (Mirb.) Franco y *Quercus greggii*.

Destaca la presencia de *P. glandulosa* y *Senegalia greggii* en todos los tipos de vegetación del valle. El matorral desértico tiene especies únicas en el área que no comparte con otros tipos de vegetación. En las montañas, los tipos de vegetación prevalecientes incluyen algunas especies de pinos y encinos. En el valle y dentro de áreas relativamente pequeñas alrededor de las pozas se pueden encontrar varios parches de distintos tipos de vegetación intercalados por lo que es difícil definir una zona amplia con algún tipo de vegetación exclusivo.

OBJETIVOS E HIPÓTESIS

Dado que no existen estudios sobre las diferencias en la estructura de las comunidades de abejas y moscas polinizadoras, ni cómo utilizan éstas los recursos florales y, en el mismo sentido, no se conoce el efecto del mimetismo sobre las comunidades de estos insectos, este estudio tiene como objetivo general describir la estructura de las comunidades de abejas (Apoidea) y moscas polinizadoras miméticas de abejas (Bombyliidae y Syrphidae) en términos de la riqueza de especies, diversidad y abundancia en el área de Cuatro Ciénegas.

Los objetivos particulares, derivados del anterior, son los siguientes:

1. Actualizar la lista de especies de Bombyliidae en Cuatro Ciénegas, Coahuila.

2. Estimar la riqueza y diversidad de especies de estos insectos y comparar estos parámetros espacial (valle/sierra) y temporalmente (lluvias/secas).

3. Definir los patrones espacio-temporales en el uso de recursos florales y compararlos entre las familias.

4. Determinar si los patrones espacio-temporales de diversidad y abundancia de las familias de Apoidea, bombiílidos y sírfidos son similares entre sí.

5. Determinar qué especies de Bombyliidae y Syrphidae son miméticas de abejas en esta región.

6. Conocer la relación entre la abundancia y la diversidad de las abejas modelos con la abundancia y diversidad de las moscas miméticas.

7. Conocer la relación entre el grado de parecido de los miméticos a sus modelos y la abundancia de los miméticos.

Se formulan como hipótesis de trabajo las siguientes:

1. Dado que la diversidad de insectos en México y en particular en zonas áridas del norte del país es poco estudiada, y comparado con estudios similares en otras regiones del país, se espera duplicar el número de especies registradas para el estado de Coahuila.

2. Debido a la heterogeneidad ambiental y las diferencias marcadas entre la época de lluvias y de secas en esta región se espera que haya una estructura de estas comunidades bien definida tanto en el tiempo como en el espacio. Esta estructura se verá reflejada en las

diferencias en la composición de especies y diversidades entre las ubicaciones y entre las temporadas.

3. Aun cuando estos insectos son todos polinizadores y su recurso principal son las flores, las diferencias en las historias de vida se reflejarán en diferentes patrones de diversidad y uso de recursos para cada familia.

4. El Valle de Cuatro Ciénegas tiene condiciones particulares como la presencia de cuerpos de agua durante todo el año, lo que lo hace diferente a las regiones aledañas. Esto genera un grado de aislamiento del valle que se verá reflejado en una composición de especies única, tanto de abejas como de moscas polinizadoras, diferente a la composición de Sierra La Madera.

5. Si las moscas miméticas más parecidas a las abejas modelos reciben más protección contra los depredadores, entonces la abundancia de miméticos estará positivamente relacionada con el grado de similitud con sus modelos. Pero, si como dice la hipótesis de multimodelo, los miméticos imperfectos reciben más protección que los miméticos más similares, al imitar a varios modelos, entonces la relación entre la similitud entre miméticos y modelos y la abundancia de miméticos será negativa.

6. Si una mayor abundancia de modelos provee una mayor protección a los miméticos, se espera que la abundancia de abejas modelos esta positivamente relacionada con la abundancia de moscas miméticas.

7. Una mayor diversidad de abejas representa más morfos potenciales que pueden imitar las moscas, por lo tanto la diversidad de abejas modelo estará positivamente relacionada con la diversidad de moscas miméticas.

Estructura de la tesis

En este trabajo se describe la estructura de las comunidades de abejas y moscas polinizadoras en la región de Cuatro Ciénegas, Coahuila. Se comparan los patrones de las comunidades de abejas y de moscas. También se evalúa la relación entre la diversidad y abundancia de insectos-modelo sobre la diversidad y abundancia de insectos-miméticos.

La tesis está compuesta por cinco apartados, una introducción general, tres capítulos que corresponden a artículos publicados o enviados para su publicación y una discusión general. En el primer capítulo se presentan los nuevos registros de Bombyliidae para Cuatro Ciénegas, obtenidos a partir del trabajo de campo. En el segundo capítulo se describe y compara a las comunidades de abejas y moscas en cuanto a su riqueza de especies, diversidad y fenología. Se presenta la riqueza y diversidad de cada familia. Se ordenan a las comunidades en función de su similitud en composición de especies y abundancias, para ver patrones espacio-temporales. En el tercer capítulo se analiza el efecto del mimetismo en las comunidades de moscas. Se reconocen a las especies de moscas que son miméticas de abejas mediante técnicas de morfometría y análisis multivariado para clasificar según su parecido morfológico. Se mide la relación entre la riqueza de especies y abundancia de abejas modelo y la riqueza de especies y abundancia de moscas miméticas. También se analiza la relación entre la similitud morfológica de los miméticos con sus modelos y la abundancia de los miméticos. Al final se formula una discusión general donde se interpretan y relacionan los resultados de los tres capítulos presentados y se proponen nuevas líneas de investigación a partir de este trabajo.

CAPITULO 1

ARTÍCULO PUBLICADO

Nuevos registros de moscas abeja (Diptera, Bombyliidae) de Cuatro Ciénegas, Coahuila, México.

Ávalos-Hernández, O., J. Kits, M. Trujano-Ortega, U. O. García-Vázquez y Z. Cano-Santana. 2014. New records of bee flies (Diptera, Bombyliidae) from Cuatro Ciénegas, Coahuila, Mexico. *Zookeys,* 422: 49–86.

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New records of bee flies (Diptera, Bombyliidae) from Cuatro Ciénegas, Coahuila, Mexico

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Abstract

Forty one new records of species of Bombyliidae are reported for Coahuila in northeastern Mexico. Nine of these species are reported for the first time for the country. The specimens were collected in the Cuatro Ciénegas Basin and Sierra La Madera mountains during 2007–2013. The modified distributions of species are discussed. The gaps in the distribution of many species suggest an undersampling of this group of insects in the north of Mexico.

Keywords

Biodiversity, distribution expansion, Nearctic region, desert fauna

Introduction

The bee flies (Bombyliidae) belong to the superfamily Asiloidea and are the eighth most diverse family within Diptera with 5382 described species (Pape et al. 2011). All species of Bombyliidae are parasitoids, hyperparasitoids or predators of immature stages of Coleoptera, Hymenoptera, Lepidoptera, Orthoptera, Neuroptera, and

Diptera (Yeates and Greathead 1997, Boesi et al. 2009). Unlike most other taxa, bee flies are most abundant and diverse in arid and semiarid portions of the world (Hull 1973, Evenhuis 1989). In the immature stages these insects function as a natural control for populations of other insects and as adults are efficient pollinators (Motten et al. 1981, Kearns 2001).

Some faunistic studies have been completed including Bombyliidae in Mexico (Rodríguez-Ortuño 1989, Ávalos-Hernández 2007), but the northern region of the country is poorly known for this family. Although Evenhuis and Greathead (1999) list 15 species of Bombyliidae for Coahuila, species richness in this state is probably higher as suggested by the richness of surrounding Mexican states with similar or even smaller size and similar ecosystems (e.g., Nuevo León, 37 species; Durango, 41 species) and of Texas (171 species), the nearest USA state.

Cuatro Ciénegas Basin in the northeast of Coahuila is especially interesting because of its geological history and the presence of water ponds and gypsum dunes, which create a different environment from the surrounding areas. The basin was a shallow sea from the Pangea breakup until the Eocene, 40 Ma, when the Sierra Madre Oriental in the east of Mexico rose isolating the Basin from the Atlantic Ocean (Souza et al. 2012). The physiology of Cuatro Ciénegas bacteria is similar to that of marine species, with which they are closely related (Souza et al. 2006). According to Moreno-Letelier et al. (2012) this evidence indicates that some water was kept trapped in the Basin when the ocean retreated giving the basin unique characteristics. These characteristics produced a high number endemism for vertebrates and prokaryotes in Cuatro Ciénegas (Souza et al. 2006, 2012).

The present study is the first known long-term systematic sampling of Diptera in Cuatro Ciénegas. The objective of this project is to complete the list of species of Bombyliidae in the basin and surrounding mountains. In this paper, 41 new species-level records for Coahuila from Cuatro Ciénegas are presented, including nine new records for Mexico. The modified distributions of the species are discussed.

Methods

Beeflies were collected at nine sites from Cuatro Ciénegas Basin and Sierra La Madera within the Municipality of Cuatrociénegas (Figure 1). Abbreviations for study sites (Table 1) are used throughout. Samplings were performed during 2007-2013, using aerial net and a Malaise trap. The Malaise trap had white polyester netting, was square in configuration, 210 cm tall and 120 cm wide and the collecting head located at the top. Trap was set from 9:00 to 17:00 when weather conditions allowed it. To avoid damage to the specimens no killing agent was used, insects were extracted at the end of the day. Specimens were pinned and labeled. Generic identification was carried out under a stereomicroscope according to the keys by Hall (1981b) and Kits et al. (2008). Species were identified by the first and second authors with specialized keys for each genus and comparison with museum specimens, keys used for identification of each

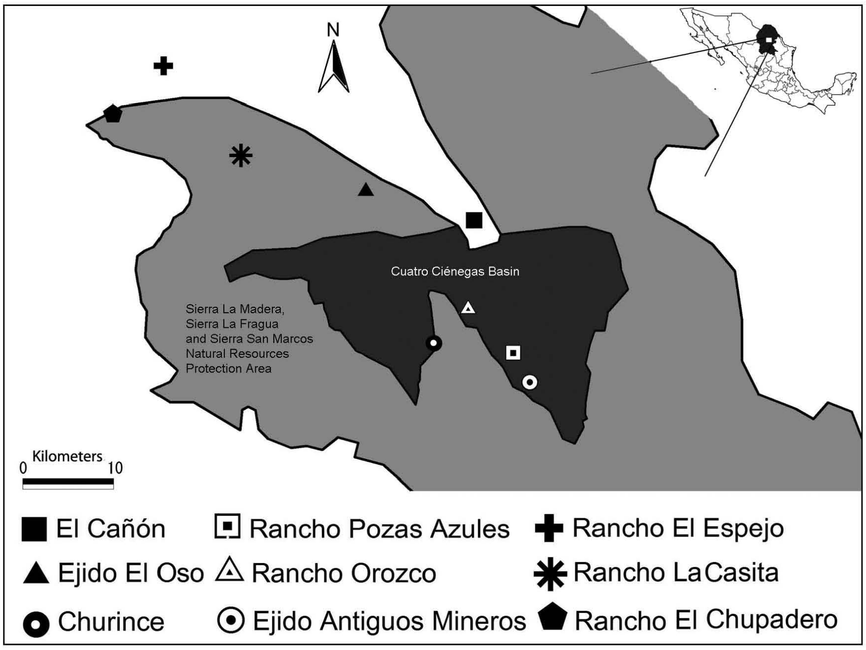

Figure 1. Field work sites. Cuatro Ciénegas basin is located in Coahuila at northeast of Mexico. Sierra La Madera is located at northwest of the basin.

genera are specified below. Taxonomic classification and distribution data are based on Evenhuis and Greathead (1999) and host data are based on Hull (1973), if not indicated otherwise. Distribution gaps are suggested as disjunct distribution patterns or the result of under sampling by comparing the location of records in Mexico with those in the southern states of the USA. All specimens are deposited in the Colección Nacional de Insectos (Instituto de Biología, Universidad Nacional Autónoma de México; CNIN-IBUNAM).

Results

A total of 41 new species-level records are presented for the state of Coahuila. Nine of these 41 species are recorded for the first time in Mexico, being their most southern records. Of the 15 species previously listed for Coahuila, two were collected during this study: *Heterostylum robustum* (Osten Sacken, 1877) (Material collected: CHU: Apr (1 M), Sep (1 M); EAM: Mar (2 M), Sep (1 F), Jun (2 F), Jul (1 F), Oct (1 F); ROR: Apr (1 F, 3 M), May (1 F, 2 M), Jul (3 F), Sep (1 F); RPA: Apr (1 F, 1 M), Jul (2 F, 2 M), Sep (1 M), Oct (2 M)); and *Anastoechus melanohalteralis* Tucker, 1907 (Material collected: EAM: Oct (1 M); ECA: Oct (1 F, 1M); ROR: Oct (7 F, 6 M); RPA: Sep (1 M)).

Table 1. Field work sites in Cuatro Ciénegas. Vegetation according to Pinkava (1979).

	Site (Code)	Location	Altitude (m)	Vegetation
1	Churince (CHU)	N26°50'30", W102°08'10”	770	Gypsum dunes; sedges and marshes; mezquital, halophile
2	Rancho Orozco (ROR)	N26°52'18", W102°05'17”	740	Sedges and marshes; mezquital; halophile
3	Rancho Pozas Azules (RPA)	N26°49'39", W102°01'24”	710	Sedges and marshes; mezquital; halophile
4	Ejido Antiguos Mineros (EAM)	N26°46'58", W102°00'20”	725	Sedges and marshes; mezquital; halophile
5	El Cañón (ECA)	N27°00'34", W102°04'42”	780	Mezquital; desert scrub
6	Ejido El Oso (EEO)	N27°03'08", W102°13'35”	1085	Desert scrub; chaparral
7	Rancho El Espejo (REE)	N27°13'19", W102°30'19”	1425	Desert scrub; chaparral
8	Rancho El Chupadero (REC)	N27°10'07", W102°34'26”	1790	Desert scrub; chaparral; Pine-Oak forest
9	Rancho La Casita (RLC)	N27°06'45", W102°23'40”	1630	Desert scrub; chaparral; Pine-Oak forest

New records of the species included in this paper are from 17 genera for which modern revisions are available. Six taxa of *Hemipenthes* (3), *Lordotus* (1), *Paravilla* (1) and *Rhynchanthrax* (1) could not be identified accurately, being probably undescribed species. Identification of species in another 10 genera found in the study (e.g. *Villa*, *Chrysanthrax*, and *Exoprosopa*) is difficult and unreliable. The number of morphospecies and specimens collected of these genera are presented in Table 2. Six species of *Tmemophlebia* (1), *Geron* (1), *Exoprosopa* (3) and *Villa* (1) previously listed for Coahuila were probably collected but specimens of these genera are still being identified. Taxonomic work will continue, updates of the species list and descriptions of the new taxa will be published in subsequent papers.

A total of 28 genera were found during this study, of which 21 are new records for the state. Two genera previously listed for Coahuila (*Neacreotrichus* and *Relictiphthiria*) were not found in Cuatro Ciénegas area. With the new records presented here, the list of bee fly species in Coahuila increases to 56 (Table 2).

Subfamily Toxophorinae

Genus *Toxophora* Meigen

Remarks. *Toxophora* is distributed worldwide, being more diverse in the Afrotropical and Palearctic regions. Mexico's fauna includes three Neotropical species and five Nearctic species. All Nearctic species of Mexico were distributed in the western half of

Table 2. Updated list of genera and species of Bombyliidae in Coahuila (* species not collected in this study, but recorded previously in Coahuila; ** species most likely collected in this study, but identification not yet certain).

Subfamily, genus and species name	**New record**	**Unidentifiable material**
PHTHRIINAE		
***Neacreotrichus* Cockerell**		
**Neacreotrichus consors* (Osten Sacken, 1887)		
***Poecilognathus* Jaennicke**	Coahuila	1 morphospecies, 3 specimens
***Relictiphthiria* Evenhuis**		
**Relictiphthiria psi* (Cresson, 1919)		
***Tmemophlebia* Evenhuis**		1 morphospecies, 21 specimens
** *Tmemophlebia coquilletti* (Johnson, 1902)		
TOXOPHORINAE		
***Geron* Meigen**		2 morphospecies, 194 specimens
***Geron holosericeus* Walker, 1849		
***Systropus* Wiedemann**	Coahuila	1 morphospecies, 5 specimens
***Toxophora* Meigen**	Coahuila	
Toxophora maxima Coquillett, 1886	Coahuila	
Toxophora virgata Osten Sacken, 1877	Coahuila	
BOMBYLIINAE		
***Anastoechus* Osten Sacken**		
Anastoechus melanohalteralis Tucker, 1907		
***Bombylius* Linnaeus**		
Bombylius (*Bombylius*) *frommerorum* Hall & Evenhuis, 1980	Coahuila	
* *Bombylius* (*Bombylius*) *sylphae* Evenhuis, 1984		
* *Bombylius* (*Parabombylius*) *aleophilus* (Hall & Evenhuis, 1981)		
* *Bombylius* (*Parabombylius*) *coahuilensis* (Hall & Evenhuis, 1981)		
* *Bombylius* (*Parabombylius*) *paradoxus* (Hall & Evenhuis, 1981)		
* *Bombylius* (*Parabombylius*) *syndesmus* (Coquillett, 1894)		
***Conophorus* Meigen**	Coahuila	1 morphospecies, 3 specimens
***Heterostylum* Macquart**		
Heterostylum croceum Painter, 1930	Mexico	
Heterostylum robustum (Osten Sacken, 1877)		
***Lordotus* Loew**	Coahuila	1 morphospecies, 38 specimens
Lordotus diplasus Hall, 1954	Coahuila	
Lordotus divisus Cresson, 1919	Coahuila	
Lordotus perplexus Johnson & Johnson, 1959	Coahuila	
***Triploechus* Edwards**	Coahuila	
Triploechus novus (Williston, 1893)	Coahuila	
LOMATIINAE		
***Ogcodocera* Macquart**	Coahuila	
Ogcodocera analis Williston, 1901	Coahuila	
TOMOMYZINAE		
***Paracosmus* Osten Sacken**	Coahuila	
Paracosmus (*Paracosmus*) *morrisoni* Osten Sacken, 1887	Coahuila	
ANTHRACINAE		
***Anthrax* Scopoli**	Coahuila	
Anthrax atriplex Marston, 1970	Coahuila	

Subfamily, genus and species name	**New record**	**Unidentifiable material**
Anthrax cybele (Coquillett, 1894)	Mexico	
Anthrax georgicus Macquart, 1834	Coahuila	
Anthrax irroratus Say, 1823	Coahuila	
Anthrax oedipus Fabricius, 1805	Coahuila	
Anthrax pauper (Loew, 1869)	Mexico	
Anthrax seriepunctatus (Osten Sacken, 1886b)	Coahuila	
***Aphoebantus* Loew**	Coahuila	4 morphospecies, 236 specimens
***Chrysanthrax* Osten Sacken**	Coahuila	6 morphospecies, 240 specimens
***Dipalta* Osten Sacken**	Coahuila	
Dipalta serpentina (Osten Sacken, 1877)	Coahuila	
***Exoprosopa* Macquart**		9 morphospecies, 395 specimens
***Exoprosopa aztec* Painter & Painter, 1969		
***Exoprosopa butleri* Johnson & Johnson, 1958		
***Exoprosopa dorcadion* Osten Sacken, 1877		
***Hemipenthes* Loew**	Coahuila	3 morphospecies, 146 specimens
Hemipenthes jaennickeana (Osten Sacken, 1886a)	Coahuila	
Hemipenthes lepidota (Osten Sacken, 1886b)	Coahuila	
Hemipenthes scylla (Osten Sacken, 1887)	Coahuila	
Hemipenthes sinuosa (Wiedemann, 1821)	Coahuila	
***Lepidanthrax* Osten Sacken**	Coahuila	
Lepidanthrax arizonensis Hall, 1976	Mexico	
Lepidanthrax disiunctus (Wiedemann, 1830)	Coahuila	
Lepidanthrax hesperus Hall, 1976	Coahuila	
Lepidanthrax hyposcelus Hall, 1976	Coahuila	
Lepidanthrax proboscideus (Loew, 1869)	Coahuila	
***Ligyra* Newman**	Coahuila	1 morphospecies, 2 specimens
***Neodiplocampta* Curran**	Coahuila	
Neodiplocampta (*Neodiplocampta*) *miranda* Hull & Martin, 1974	Coahuila	
***Paravilla* Painter**	Coahuila	1 morphospecies, 48 specimens
Paravilla edititoides (Painter, 1933)	Coahuila	
Paravilla flavipilosa (Cole, 1923)	Coahuila	
Paravilla parvula Hall, 1981a	Coahuila	
Paravilla separata (Walker, 1852)	Mexico	
***Poecilanthrax* Osten Sacken**	Coahuila	
Poecilanthrax effrenus (Coquillett, 1887)	Coahuila	
Poecilanthrax fasciatus Johnson & Johnson, 1957	Mexico	
Poecilanthrax hyalinipennis Painter & Hall, 1960	Mexico	
Poecilanthrax poecilogaster (Osten Sacken, 1886b)	Coahuila	
***Rhynchanthrax* Painter**	Coahuila	1 morphospecies, 70 specimens
Rhynchanthrax capreus (Coquillett, 1887)	Mexico	
Rhynachantrax texanus (Painter, 1933)	Coahuila	
***Thyridanthrax* Osten Sacken**	Coahuila	
Thyridanthrax pallidus (Coquillett, 1887)	Mexico	
Thyridanthrax selene (Osten Sacken, 1886b)	Coahuila	
***Villa* Lioy**		9 morphospecies, 115 specimens
***Villa fumicosta* Painter & Painter, 1962		
***Xenox* Evenhuis**	Coahuila	
Xenox xylocopae (Marston, 1970)	Coahuila	

the country. These two new records represent the first of this genus in Coahuila and the most eastern distribution of the Nearctic species in the country. The New World species of this genus were keyed using Cunha et al. (2011).

Toxophora maxima Coquillett, 1886

Figure 2a, b

Material examined. CHU: Jul (1 M); EEO: Jul (2 F, 2 M), Oct (1 F, 3 M).

Known Nearctic records. Mexico (Baja California, Baja California Sur, Coahuila); USA (Arizona, California, Idaho, Kansas, New Mexico, Oklahoma, Oregon, Texas).

Comments. In Mexico *T. maxima* was only known from Baja California Peninsula and now Coahuila. This apparent gap in its distribution is probably due to undersampling. Sampling of the intermediate zones is necessary to know if these populations form a continuous unit as they do in the southern states of USA.

Toxophora virgata Osten Sacken, 1877

Figure 2c, d

Material examined. EAM: Jun (1 F, 1 M), Jul (1 F); CHU: Aug (1 M), Oct (1 M); EEO: Jul (1 M), Oct (1 F, 1 M); RLC: Jun (1 M); ROR: Apr (1 F, 2 M); RPA: Oct (1 F).

Known Nearctic records. Mexico (Baja California Sur, Coahuila, Sonora); USA (Arizona, California, Colorado, Georgia, Idaho, Nevada, New Mexico, Oklahoma, Texas, Utah).

Known hosts. *Odynerus* sp. (Vespidae); *Stenodynerus toltecus* Saussure (Vespidae).

Comments. This species is present in the all southwestern states of the USA and northwest of Mexico. This is the first record in the northeast of Mexico. The species is probably also present in Chihuahua, between Sonora and Coahuila.

Subfamily Bombyliinae

Genus *Bombylius* Linnaeus

Remarks. With 278 described species, *Bombylius* is the second most diverse genus of Bombyliidae. It has a worldwide distribution being especially diverse in the Palearctic and Nearctic regions. One endemic species is present in Coahuila: *B.* (*Parabombylius*) *coahuilensis* (Hall & Evenhuis, 1981). Four other species are reported for the state: *B. sylphae* Evenhuis, 1984, *B. aleophilus* (Hall & Evenhuis, 1981), *B. paradoxus* (Hall & Evenhuis, 1981), *B. syndesmus* (Coquillett, 1894). A review with identification keys for Nearctic species is presented in Hall and Evenhuis (1980), later Evenhuis (1984) revised and present keys for the *comanche* group of America.

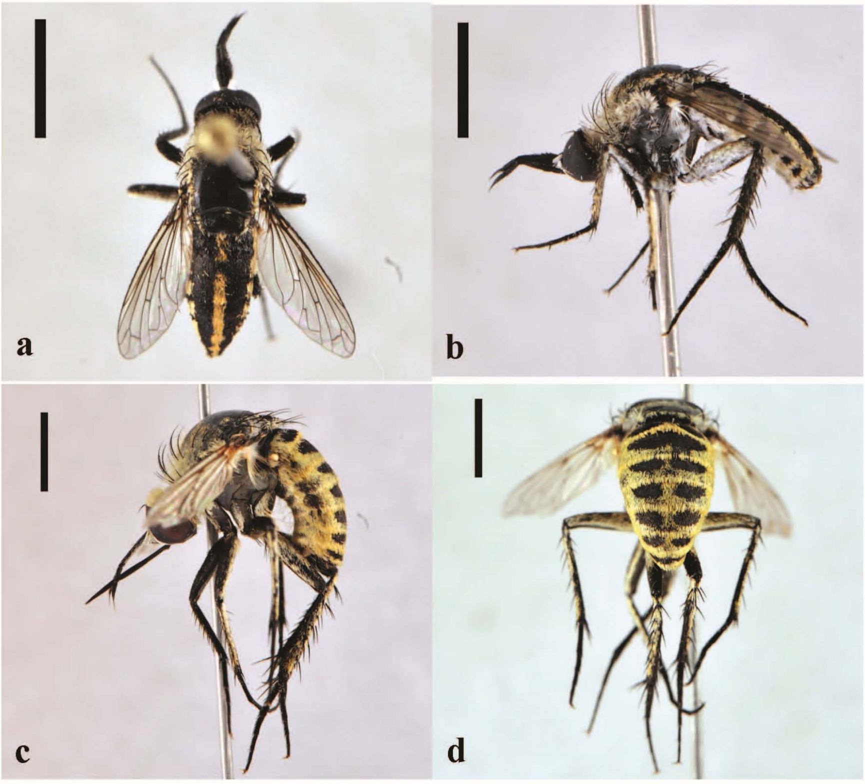

Figure 2. *Toxophora*. *T. maxima*, male (CNIN 1115) **a** dorsal view **b** lateral view; *T. virgata*, male (CNIN 1109) **c** lateral view **d** posterior view. All scale bars: 3 mm.

***Bombylius* (*Bombylius*) *frommerorum* Hall & Evenhuis, 1980**
Figure 3

Material examined. EEO: Aug (1 M), Oct (1 F).

Known Nearctic records. Mexico (Chihuahua, Coahuila); USA (Arizona, New Mexico, Texas).

Comments. This species is restricted to the southwest of the USA and north of Mexico.

Genus *Heterostylum* Macquart

Remarks. The genus is only present in Nearctic and Neotropical regions. Although not as diverse as other genera (only 12 species), specimens from some species are abun-

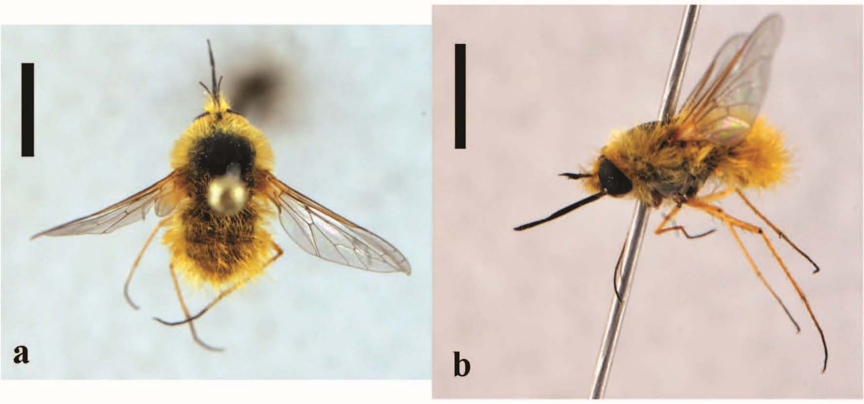

Figure 3. *Bombylius* (*B.*) *frommerorum*, female (CNIN 772) **a** dorsal view **b** lateral view. All scale bars: 3 mm.

dant in the field. *Heterostylum robustum* was previously known from Coahuila and was collected during this study. This species is distributed from Canada to central Mexico. There are two revisions for this genus that contains identification keys, one by Hall and Evenhuis (1980) and the more recent by Cunha et al. (2007).

Heterostylum croceum Painter, 1930

Figure 4

Material examined. REE: Apr (1 F).

Known Nearctic records. Mexico (Coahuila); USA (Colorado, Kansas, Missouri, New Mexico, Texas).

Comments. *Heterostylum croceum* is recorded for the first time in Mexico; previously known from the southern-central United States. Hall and Evenhuis (1980) suggest that *H. croceum* may be related to *H. engelhardti* Painter, 1930 or even be a subspecies of that taxon, *Heterostylum croceum* is the eastern form and *H. engelhardti* the western form (Arizona, California, Texas, Utah) although both species are present in Texas. Cunha et al. (2007) comment that *H. engelhardti* can be distinguished by the presence of white to very pale yellow hair and brown-tipped hairs on the abdomen compared with the darker yellow hairs in *H. croceum*.

Genus *Lordotus* Loew

Remarks. Most of the 29 species in this exclusively Nearctic genus are distributed in the southwest of the USA and north of Mexico, although eight species are present in the northwest of the USA (*L. apicula* Coquillet, 1887; *L. bipartitus* Painter, 1940; *L. diversus* Coquillett, 1891; *L. gibbus* Loew, 1863; *L. miscellus* Coquillett, 1887; *L.*

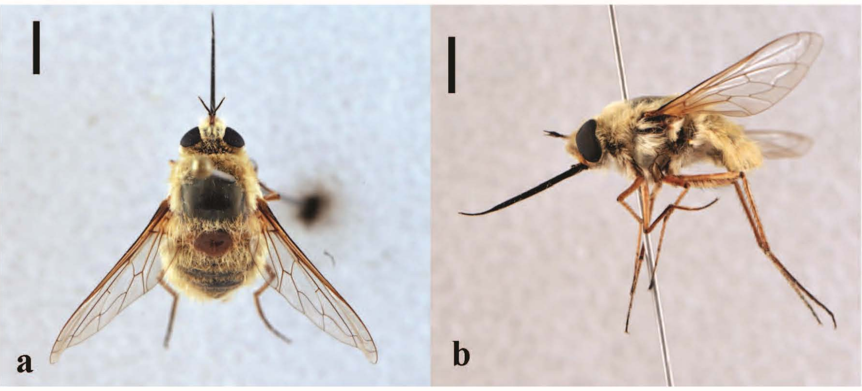

Figure 4. *Heterostylum croceum*, female (CNIN 858) **a** dorsal view **b** lateral view. All scale bars: 3 mm.

pulchrissimus Williston, 1893; *L. striatus* Painter, 1940; *L. zona* Coquillett, 1887). The three species present in Coahuila are also found in California; their distribution probably includes all northern states of Mexico. Hall (1954) and Hall and Evenhuis (1982) present reviews of the genus and keys to the species.

Lordotus diplasus Hall, 1954

Figure 5a, b

Material examined. CHU: Sep (2 M); RLC: Sep (2 M); RPA: Sep (1 F).

Known Nearctic records. Mexico (Coahuila, Zacatecas); USA (Arizona, California, New Mexico).

Lordotus divisus Cresson, 1919

Figure 5c

Material examined. ECA: Mar (1 M), Apr (2 M); EEO: Apr (16 M); REE: Apr (4 M); ROR: Apr (1 M).

Known Nearctic records. Mexico (Coahuila, Baja California); USA (Arizona, California, Nevada, New Mexico, Texas).

Lordotus perplexus Johnson & Johnson, 1959

Figure 5d, e

Material examined. CHU: Apr (1 H), ECA: Apr (1 H); EEO: Apr (4 F); REE: Apr (7 F); ROR: Apr (1 F).

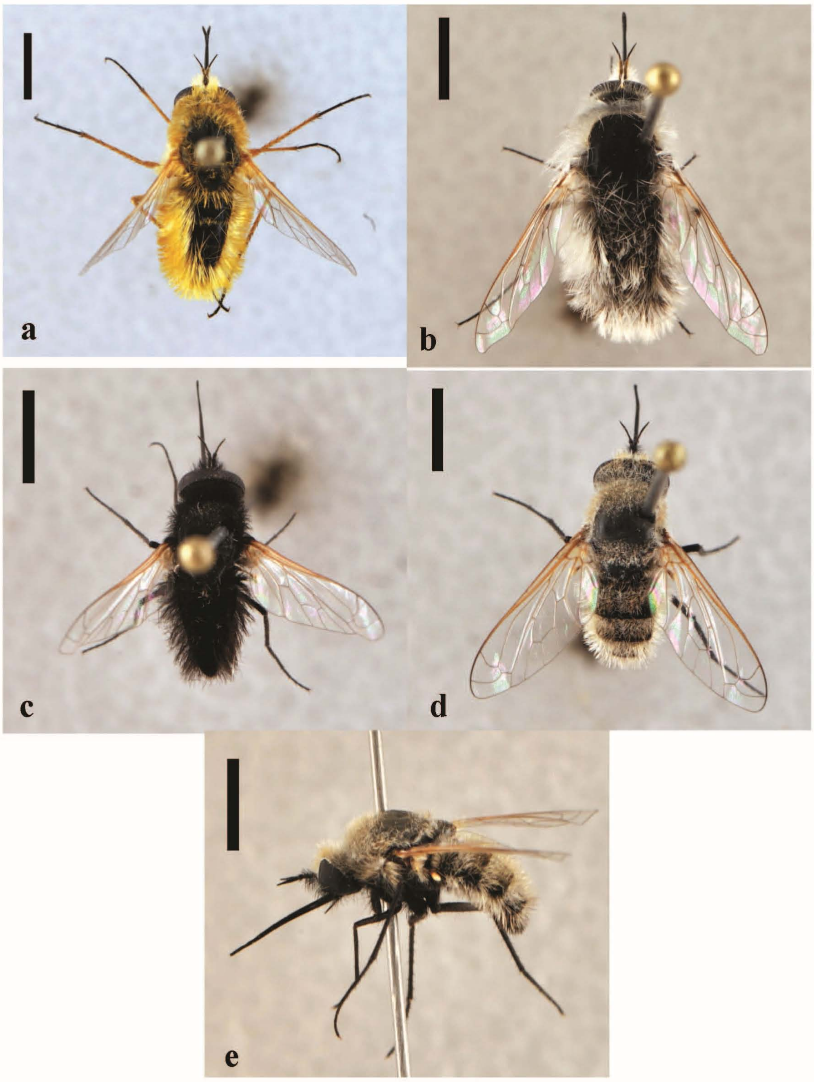

Figure 5. *Lordotus*. *L. diplasus*, **a** female (CNIN 774) dorsal view **b** male (CNIN 861) dorsal view **c** *L. divisus*, male (CNIN 777) dorsal view; *L. perplexus*, female (CNIN 801) **d** dorsal view **e** lateral view. All scale bars: 3 mm.

Known Nearctic records. Mexico (Baja California, Coahuila, Sinaloa, Sonora); USA (Arizona, California, Nevada, Texas).

Comments. *Lordotus perplexus* has the most southern distribution in the genus, reaching Sinaloa on the Pacific coast.

Genus *Triploechus* Edwards

Remarks. Four species of *Triploechus* are present in Nearctic region: *T. luridus* Hall, 1975; *T. novus* (Williston, 1893); *T. sackeni* (Bigot, 1892); *T. stagei* Hall, 1975. Of these *T. stagei* is endemic to Mexico and *T. novus* has the widest distribution of this genus, being present in the south of the USA and center of Mexico. Hall and Evenhuis (1981) present a revision and key for species for this genus.

Triploechus novus (Williston, 1893)

Figure 6

Material examined. CHU: Apr (7 F, 6 M); REE: Apr (1 M); RPA: Apr (1 M).

Known Nearctic records. Mexico (Coahuila, Durango, San Luis Potosí, Sonora); USA (Arizona, California, Nevada, New Mexico, Texas).

Comments. This is a widespread and apparently common species. All specimens were collected in April so it may have a short flight season.

Subfamily Lomatiinae

Genus *Ogcodocera* Macquart

Remarks. The only two species in this genus have been collected from the neotropical part of Mexico to north of the USA and Canada. *Ogcodocera leucoprocta* (Wiedemann, 1828), not sampled during this study, is present in the whole Nearctic region from Canada to south of Mexico.

Ogcodocera analis Williston, 1901

Figure 7

Material examined. EEO: Aug (2 M), Oct (1 M).

Known Nearctic records. Mexico (Coahuila, Guerrero, Morelos); USA (Arizona, Texas).

Comments. This record is the first of this species in the north of Mexico, but it has been previously collected in the south of Mexico and in the south of USA, and thus is probably distributed across the whole country. Unlike *O. leucoprocta*, *O. analis* has its most northern distribution in Arizona and Texas.

Figure 6. *Triploechus novus*, female (CNIN 1237) dorsal view. Scale bar: 3 mm.

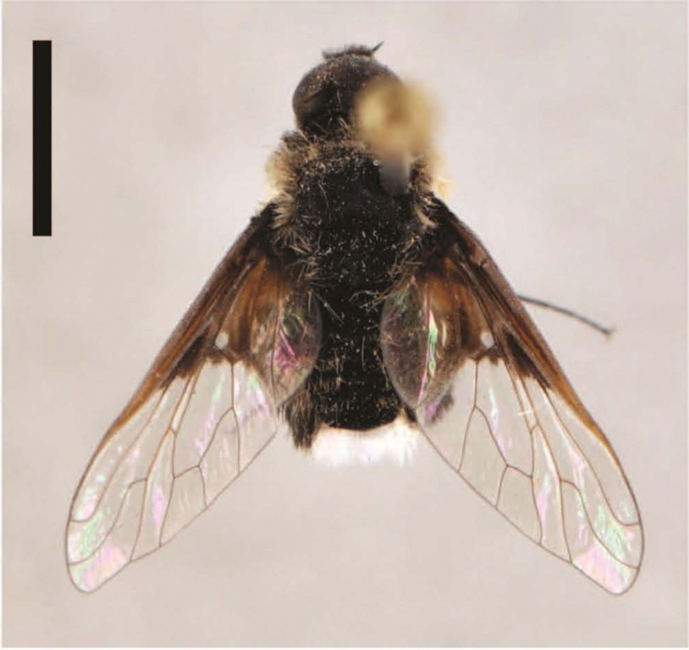

Figure 7. *Ogcodocera analis*, male (CNIN 146) dorsal view. Scale bar: 3 mm.

Subfamily Tomomyzinae

Genus *Paracosmus* Osten Sacken

Remarks. All five extant species of *Paracosmus* have Nearctic distributions, and all are present in California. Two of these species have been collected in the northwest of Mexico (*P.* (*Actherosia*) *rubicundus* Melander, 1950 and *P.* (*Paracosmus*) *morrisoni* Osten Sacken, 1887).

Paracosmus (*Paracosmus*) *morrisoni* Osten Sacken, 1887

Figure 8

Material examined. EAM: Apr (1 F, 1 M); CHU: Apr (2 M), Jul (1 F), Aug (2 F); ECA: Apr (1 M); EEO: May (1 F); REE: Apr (1 F); ROR: Apr (2 M), May (1 F, 3 M); RPA: Apr (1 F).

Known Nearctic records. Mexico (Coahuila, Sonora); USA (Arizona, California, Nevada, Texas).

Comments. *Paracosmus* (*P.*) *morrisoni* has the widest distribution within this genus, but in Mexico had previously only been recorded in Sonora. This record represent the most eastern distribution for the genus in the country.

Subfamily Anthracinae

Genus *Anthrax* Scopoli

Remarks. This is a diverse genus with 248 species worldwide. Two old but complete revisions of the genus, including distribution maps and keys, were made by Marston (1963, 1970). Thanks to these *Anthrax* species can be easily identified. Some *Anthrax* species are widely distributed occupying two biogeographic regions. From the seven *Anthrax* species collected in this study in Coahuila, just *A. cybele* (Coquillett, 1894) has a restricted distribution. The other six species are widespread across the Nearctic region. Two species of *Anthrax* are reported for the first time for Mexico.

Anthrax atriplex Marston, 1970

Figure 9a

Material examined. EAM Apr (1 F); ROR: Oct (2 M); RPA: Aug (1 M); Sep (1 M); Oct (1 F, 2 M).

Known Nearctic records. Mexico (Baja California Sur, Coahuila, Durango, Sonora, Tamaulipas); USA (Arizona, California, New Mexico, Oregon, Texas, Utah).

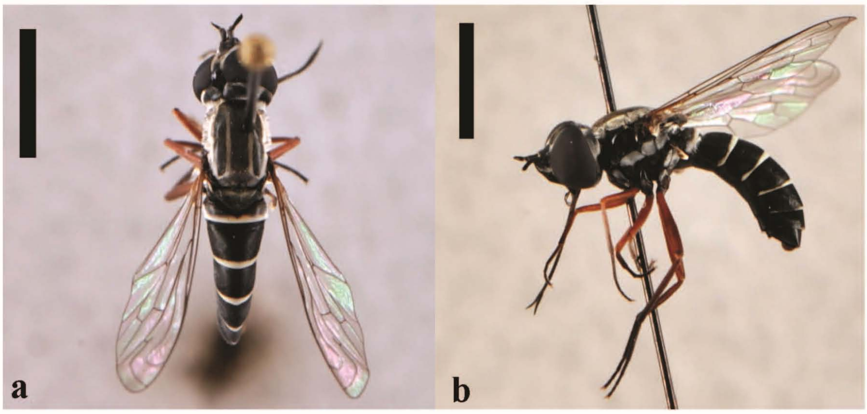

Figure 8. *Paracosmus* (*P.*) *morrisoni*, male (CNIN 832) **a** dorsal view **b** lateral view. All scale bars: 3 mm.

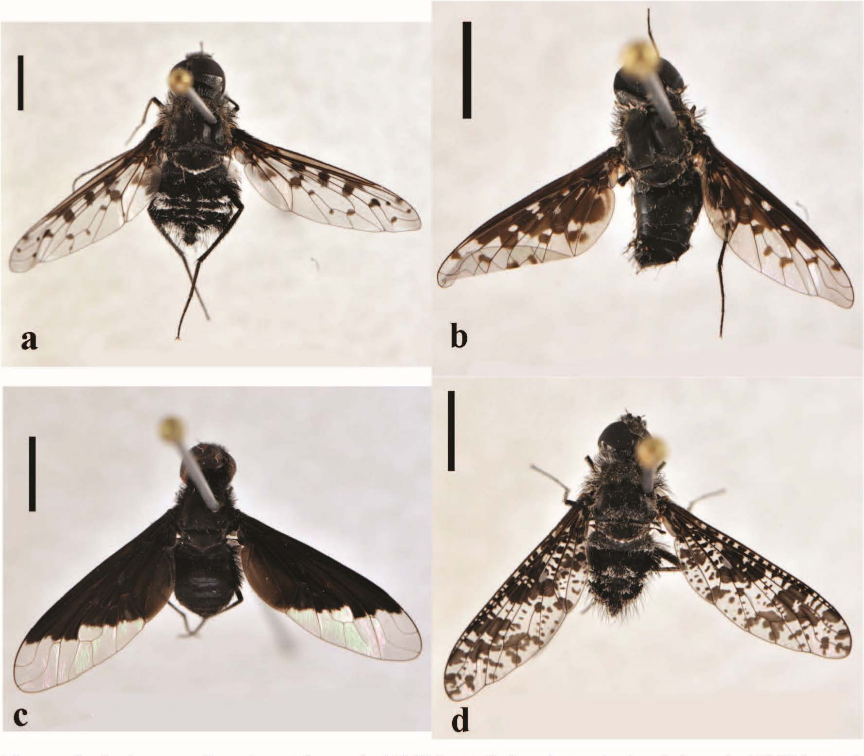

Figure 9. *Anthrax* part I. **a** *A. atriplex*, male (CNIN 1098) dorsal view **b** *A. cybele*, male (CNIN 1087) dorsal view **c** *A. georgicus*, female (CNIN 1071) dorsal view **d** *A. irroratus*, male (CNIN 1027) dorsal view. All scale bars: 3 mm.

Known host. *Megachile gentilis* Cresson (Megachilidae).

Comments. This species may be present in all the north of Mexico, including Chihuahua, Nuevo León and possibly Sinaloa.

Anthrax cybele (Coquillett, 1894)

Figure 9b

Material examined. ECA: Apr (2 F); EEO: Apr (1 M).

Known Nearctic records. Mexico (Coahuila); USA (Arizona, California).

Comments. This is a rare species flying in April. Its distribution is disjunct so far, present in the southwest of the USA and northeast of Mexico. It is probably also found in New Mexico and Texas in the USA and Sonora and Chihuahua in Mexico.

Anthrax georgicus Macquart, 1834

Figure 9c

Material examined. EAM: Mar (1 F), Apr (1 M), Jun (1 F, 2 M), Jul (2 F), Sep (2 M); ROR: Apr (1 F), Sep (1 M); RPA: Mar (1 M), Apr (1 F, 1 M), Jul (2 F, 1 M), Sep (6 F, 3 M), Oct (6 F, 3 M).

Known Nearctic records. Canada (Alberta, British Columbia, Manitoba, Northwest Territory, Ontario, Quebec, Saskatchewan); Mexico (Coahuila, Guerrero, Michoacán de Ocampo, Morelos, Nuevo León, Puebla, Sonora, Veracruz); USA (Arizona, Arkansas, California, Colorado, Connecticut, Delaware, District of Columbia, Florida, Georgia, Idaho, Illinois, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming).

Comments. The range of *A. georgicus* includes all North America and Central America (Nicaragua, Costa Rica) covering a wide diversity of habitats and environmental conditions. Common in the rainy season and present in the dry season (March), this species is probably present in most if not all states of Mexico, but has only been collected in eight of them.

Anthrax irroratus Say, 1823

Figure 9d

Material examined. EAM: Apr (1 M), Aug (2 M), Oct (1 M); ECA: Apr (1 F), May (1 F, 1 M); EEO: Apr (2 F), Jul (4 F), Aug (1 M); REC: Apr (3 F, 10 M), Aug (1 M); REE: Aug (1 M); RLC: Jul (6 F, 10 M); ROR: Feb (1 M), Aug (5 M), Sep (1 M); RPA: Apr (1 M), Aug (2 M).

Known Nearctic records. Canada (Alberta, British Columbia, Manitoba, Northwest Territory, Nova Scotia, Ontario, Quebec, Saskatchewan); Mexico (Baja California, Baja California Sur, Coahuila, Colima, Guerrero, Michoacán, Morelos, Nayarit, Puebla, San Luis Potosí, Sinaloa, Sonora, Veracruz, Zacatecas); USA (Alaska, Arizona, Arkansas, California, Colorado, Connecticut, Idaho, Illinois, Indiana, Kansas, Maryland, Massachusetts, Michigan, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, Oregon, Pennsylvania, Tennessee, Texas, Utah, Virginia, West Virginia, Wyoming).

Known hosts. *Megachile gentilis* Cresson (Megachilidae); *M. mendica* Cresson (Megachilidae); *Dianthidium heterulkei fraternum* Timberlake (Megachilidae); *Aschmendiella bucconis denticulata* Cresson (Megachilidae); *Hylaeus asininus* Cockrell and Casad (Colletidae). Scott and Strickler (1992) also reared *A. irroratus* from *Megachile relativa* Cresson (Megachilidae) and *M. inermis* Provancher (Megachilidae).

Comments. *Anthrax irroratus*, like *A. georgicus* (above), is present in all of North America and reaches Central America and Caribbean islands (Honduras, Puerto Rico). More abundant than its congener, this species has been collected in 15 states in Mexico (including Oaxaca of the Neotropical region not listed above) and all regions of the USA. *A. irroratus* should be collected in any systematic, long term Bombyliidae sample in Mexico and the USA.

Anthrax oedipus Fabricius, 1805

Figure 10a

Material examined. ECA: Apr (1 F, 1 M), Jul (1 F); EEO: Apr (2 F, 1 M), May (1 F, 4 M), Jul (1 M); REC: Apr (1 F); REE: Apr (2 M); RLC: Jul (2 F, 4 M), Sep (1 F); RPA: Apr (1 M), Aug (1 M).

Known Nearctic records. Mexico (Baja California, Coahuila, Nayarit, Morelos, Sinaloa, Sonora); USA (Nevada, Texas).

Comments. Apparently closely related to *A. irroratus*, *A. oedipus* has a narrow distribution in the Nearctic region but is widely distributed in all South America. In the USA it has been collected only in two southern states, while it occurs in most of the northern states of Mexico and one central state (Morelos); it may be present in most areas from Texas to Argentina.

Anthrax pauper (Loew, 1869)

Figure 10b

Material examined. CHU: Apr (1 F, 1 M).

Known Nearctic records. Canada (Ontario); Mexico (Coahuila); USA (Alabama, Colorado, Illinois, Indiana, Kansas, Maryland, Massachusetts, Michigan, Nebraska, New Jersey, New Mexico, New York, Oklahoma, Pennsylvania, Texas, Utah, Vermont, Virginia, Wisconsin).

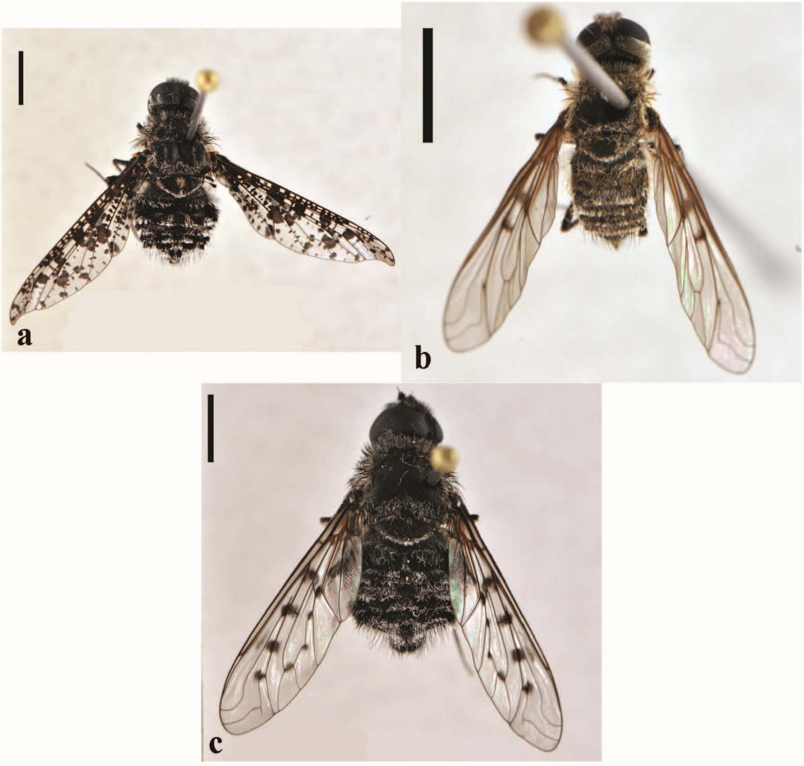

Figure 10. *Anthrax* part II. **a** *A. oedipus*, female (CNIN 1055) dorsal view **b** *A. pauper*, female (CNIN 1085) dorsal view **c** *A. seriepunctatus*, female (CNIN 1089) dorsal view. All scale bars: 3 mm.

Comments. With just two specimens collected, *A. pauper* appears to be a rare species in this region. This population is the most southern recorded of this species, mostly present in the center and east of the USA. Presumably adapted to colder climates, it is no coincidence that it was collected in the most elevated site sampled.

Anthrax seriepunctatus (Osten Sacken, 1886b)

Figure 10c

Material examined. EAM: Jun (1 M); CHU: Apr (1 F), Aug (1 F), Sep (1 F); ECA: Jun (1 M); REE: Aug (1 F); RLC: Jun (1 F), Jul (1 F, 2 M).

Known Nearctic records. Mexico (Baja California Sur, Coahuila, Sonora, Puebla); USA (Arizona, Nevada, New Mexico, Texas).

Comments. This species is recorded mostly from the south of the USA and north of Mexico, but its presence in Puebla in central Mexico suggests a wider distribution within the country, at least in all northern states.

Genus *Dipalta* Osten Sacken

Remarks. *Dipalta* is a small genus with just two species. *Dipalta banksi* Johnson, 1921 is only present in eastern Canada and USA, while *D. serpentina* is distributed from Central America to the northern USA.

Dipalta serpentina (Osten Sacken, 1877)

Figure 11

Material examined. REC: Aug (1 M); RLC: Jul (1 M).

Known Nearctic records. Mexico (Coahuila, Guerrero, Hidalgo, México, Morelos, Puebla, San Luis Potosí, Sinaloa); USA (Arizona, Arkansas, California, Colorado, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nebraska, Nevada, New Mexico, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, South Dakota, Tennessee, Texas, Utah, Washington, Wisconsin, Wyoming).

Known host. *Myrmeleon immaculatus* De Geer (Myrmeleontidae).

Comments. This species is probably present in all of Mexico, but this is the only record in the north of Mexico.

Genus *Hemipenthes* Loew

Remarks. *Hemipenthes* is equally diverse in the Nearctic (29 species), Neotropical (26 species) and Palearctic (37 species) regions, with just six species in the Oriental region and one in the Afrotropical region. Four species of this genus were collected in Coahuila. All of these have broad distributions but apparently from poor sampling because records are not continuous, especially in Mexico. Ávalos-Hernández (2009) recently published a revision of *Hemipenthes*, with a key for Nearctic species.

Hemipenthes jaennickeana (Osten Sacken, 1886a)

Figure 12a

Material examined. REC: Apr (18 F), Aug (4 F); REE: Feb (3 F); RLC: Mar (7 F), Jul (23 F, 3 M), Sep (3 F).

Known Nearctic records. Mexico (Coahuila, Morelos, Sonora); USA (Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Utah).

Comments. Present mainly in the Pacific coast states of the USA and Mexico, from Oregon as far as Morelos in the center of Mexico. This record is the most eastern record in Mexico.

Figure 11. *Dipalta serpentina*, male (CNIN 215) dorsal view. Scale bar: 3 mm.

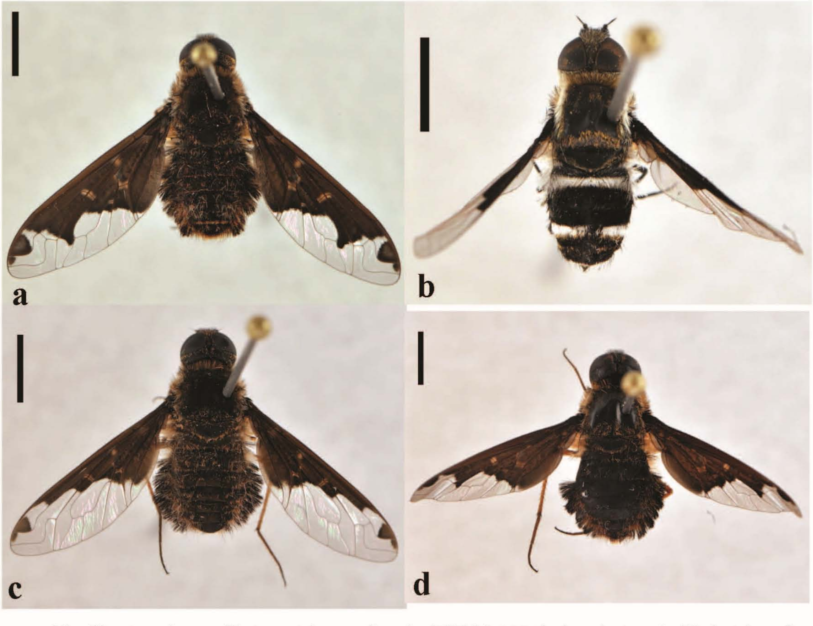

Figure 12. *Hemipenthes*. **a** *H. jaennickeana*, female (CNIN 1137) dorsal view **b** *H. lepidota*, female (CNIN 200) dorsal view **c** *H. scylla*, male (CNIN 725) dorsal view **d** *H. sinuosa*, female (CNIN 1134) dorsal view. All scale bars: 3 mm.

Hemipenthes lepidota **(Osten Sacken, 1886b)**

Figure 12b

Material examined. EAM: Apr (1 M), Aug (1 F); CHU: Apr (1 F, 3 M), Aug (1 M); EEO: Jul (1 F, 4 M), Aug (1 F); REC: (1 M); REE: Apr (11 F, 2 M), Aug (1 F); RLC: Jun (1 F), Jul (3 F); RPA: Apr (1 F), Sep (4 F), Oct (2 F).

Known Nearctic records. Canada (Alberta); Mexico (Baja California, Baja California Sur, Coahuila, Chihuahua, Guerrero, Morelos, Puebla, San Luis Potosí, Sonora, Tamaulipas); USA (Arizona, California, Colorado, Idaho, Louisiana, Nevada).

Comments. This species is abundant in the rainy season in most of the Nearctic region but has not been collected in many states of Mexico or the USA where it probably is present.

Hemipenthes scylla **(Osten Sacken, 1887)**

Figure 12c

Material examined. REC: Apr (23 M), Aug (7 M); REE: Feb (5 M), Apr (2 M); RLC: Mar (8 M), Jul (8 M), Sep (9 M).

Known Nearctic records. Mexico (Coahuila, Morelos, Guanajuato, Sonora); USA (Arizona, Texas).

Comments. Males of this species are abundant all year long but females are unknown. There is no explanation for this lack of females in the collections. Extreme sexual dimorphism and misidentification of females can be dismiss, since there is no *Hemipenthes* species from which only females are known. One possible explanation is that females life span is too short and therefor encounter probabilities are low. Distribution is discontinuous with populations present in central and northern Mexico and the southern USA; it is unknown whether this species is present in between these areas.

Hemipenthes sinuosa **(Wiedemann, 1821)**

Figure 12d

Material examined. REC: Apr (3 F); REE: (Feb (1 F), Apr (2 F); RLC: Jul (1 F, 1 M), Sep (1 M); RPA: Sep (2 F).

Known Nearctic records. Mexico (Coahuila, Morelos); USA (Alabama, Arizona, Arkansas, Connecticut, Delaware, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Minnesota, Mississippi, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin).

Known host. *Neodiprion sertifer* Geoff. (Diprionidae).

Comments. *Hemipenthes sinuosa* is only known from Morelos in the center of Mexico and Coahuila in the northeast, but can be found almost in all of the USA. It is clearly undersampled in Mexico.

Genus *Lepidanthrax* Osten Sacken

Remarks. Forty seven of the 52 species of *Lepidanthrax* are from the Nearctic region. Hall (1976) published a revision of this genus including keys for species.

Lepidanthrax arizonensis Hall, 1976

Figure 13a

Material examined. EEO: Mar (1 F); Oct (2 M).

Known Nearctic records. Mexico (Coahuila); USA (Arizona).

Comments. *Lepidanthrax arizonensis* has a restricted distribution, being present only in Arizona and Coahuila, but probably is also present in Chihuahua, Texas and New Mexico.

Lepidanthrax disiunctus (Wiedemann, 1830)

Figure 13b

Material examined. REC: Aug (2 F, 1 M).

Known Nearctic records. Mexico (Coahuila, Distrito Federal, Guerrero, Veracruz); USA (Arizona).

Comments. The distribution of *L. disiunctus* has its northern extreme in Arizona and its southern extreme in Oaxaca, in the southeast of Mexico. It seems this species is rarely collected, but widely distributed.

Lepidanthrax hesperus Hall, 1976

Figure 13c

Material examined. EAM: Apr (2 M); CHU: Apr (2 F, 5 M); ROR: Apr (1 F, 3 M), May (1 F, 1 M); RPA: Apr (1 F, 14 M).

Known Nearctic records. Mexico (Baja California, Coahuila, Sinaloa, Sonora); USA (Arizona, California, New Mexico, Texas).

Comments. This record is the first in northeastern Mexico.

Lepidanthrax hyposcelus Hall, 1976

Figure 13d

Material examined. RLC: Sep (4 F, 15 M).

Known Nearctic records. Mexico (Coahuila, Guerrero, Morelos, Puebla).

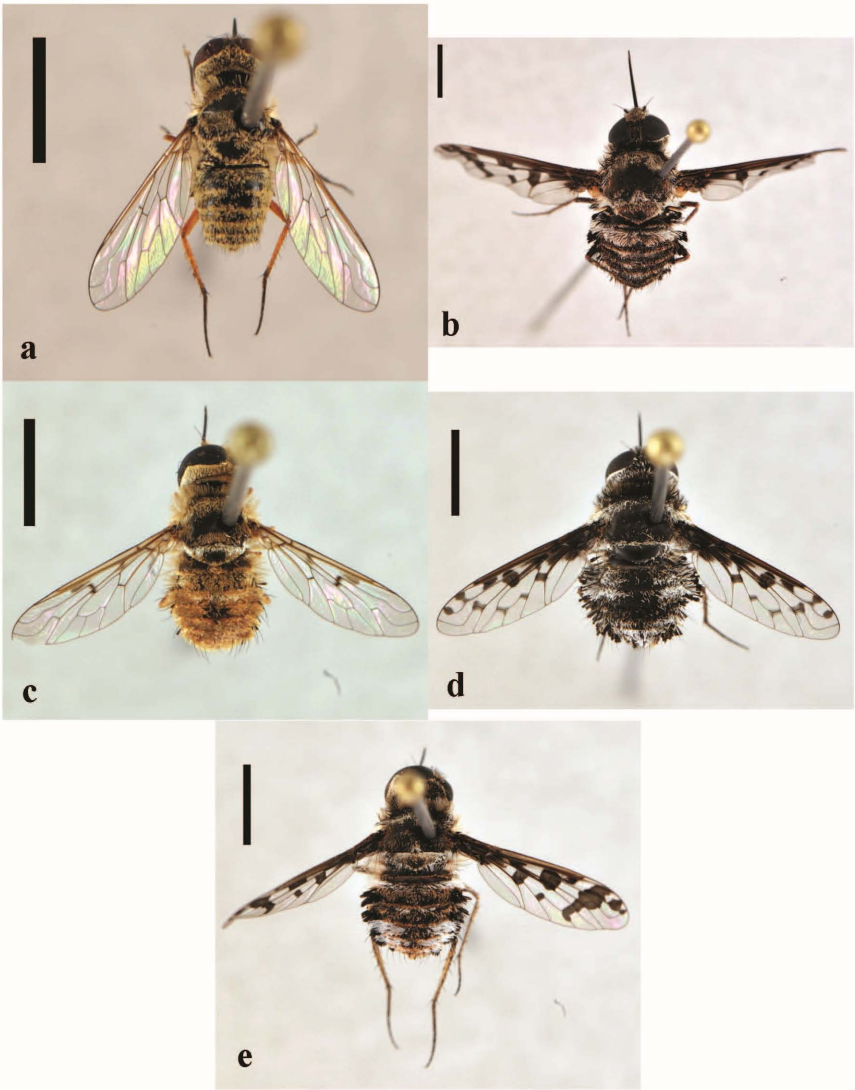

Figure 13. *Lepidanthrax*. **a** *L. arizonensis*, female (CNIN 1352) dorsal view **b** *L. disiunctus* female (CNIN 334) dorsal view **c** *L. hesperus*, male (CNIN 1339) dorsal view **d** *L. hyposcelus*, male (CNIN 369) dorsal view **e** *L. proboscideus*, male (CNIN 357) dorsal view. All scale bars: 3 mm.

Comments. *Lepidanthrax hyposcelus* is endemic to Mexico, previously only known from the southwest of the country; this record extends its distribution to the northeast of the country.

Lepidanthrax proboscideus (Loew, 1869)

Figure 13e

Material examined. ECA: Sep (1 F, 2 M); EEO: Apr (1 F), Aug (1 F, 1 M), Oct (4 F, 15 M); ROR: Sep (2 M); RPA: Sep (2 M), Oct (1 M).

Known Nearctic records. Mexico (Baja California, Baja California Sur, Coahuila, Durango, Guerrero, Morelos, Sonora); USA (Arizona, California, Nevada, New Mexico, Utah).

Comments. *Lepidanthrax proboscideus*, *L. fuscipennis* Hall, 1976 and *L. disiunctus* are the only species of this genus distributed in both the Nearctic and Neotropical regions. Of these *L. proboscideus* extends as far as El Salvador, the most southern distribution for a Nearctic species of this genus. This is the first record of this species in the northeast of Mexico.

Genus *Neodiplocampta* Curran

Remarks. *Neodiplocampta* is a small American genus, more diverse in the Neotropical than the Nearctic region. Hull and Martin (1974) described seven of the 16 species and published a key for all species of the genus.

Neodiplocampta (*Neodiplocampta*) *miranda* Hull & Martin, 1974

Figure 14

Material examined. CHU : Aug (1 F); EEO: Aug (1 F, 1 M); ROR: Jul (1 F); Oct (1 M); RPA: Aug (1 F, 2 M).

Known Nearctic records. Mexico (Coahuila, Guerrero, San Luis Potosi, Sinaloa, Sonora); USA (Arizona, California, Florida, Texas).

Comments. *Neodiplocampta* (*N.*) *miranda* and *N.* (*Agitonia*) *sepia* Hull, 1966 are the only two species distributed in both biogeographic regions (Nearctic and Neotropical). This species is distributed from the south of the USA to Nicaragua, but has not been collected in most Mexican states. This lack of records is possibly due its low abundance.

Genus *Paravilla* Painter

Remarks. Fifty five of the 58 species of the genus are Nearctic. All species of *Paravilla* collected in Coahuila were exclusively collected in the summer months from April to July. Hall (1981a) reviewed this genus and presented a key for species and description of new species.

Figure 14. *Neodiplocampta* (*N.*) *miranda*, female (CNIN 225) dorsal view. Scale bar: 3 mm.

Paravilla edititoides (Painter, 1933)

Figure 15a

Material examined. EAM: Jun (1 M); CHU: Apr (1 F), Jul (2 F, 1 M); ECA: Apr (1 F, 1 M), Jul (1 M); EEO: Apr (1 F, 10 M), May (1 F, 2 M), Jul (9 M); REE: Apr (1 M); RLC: Jun (2 F, 5 M), Jul (1 F); ROR: Jul (1 F, 3 M); RPA: Oct (1 M).

Known Nearctic records. Canada (Saskatchewan); Mexico (Chihuahua, Coahuila, Durango, Jalisco, México, Zacatecas); USA (Arizona, Colorado, Idaho, Kansas, Montana, Nebraska, New Mexico, Oklahoma, Utah, Texas, Wyoming).

Comments. This species is very abundant and present in most of North America, from Canada as far as Jalisco in central Mexico.

Paravilla flavipilosa (Cole, 1923)

Figure 15b

Material examined. CHU: Apr (1 M); Jul (1 M); ECA: Apr (1 M); EEO: Apr (7 M), May (11 M); ROR: Apr (2 M); RPA: Apr (1 M).

Known Nearctic records. Mexico (Baja California Sur, Coahuila, Nuevo León); USA (Arizona, California, Colorado, Texas).

Comments. *Paravilla flavipilosa* is abundant and restricted to the south of the USA and north of Mexico.

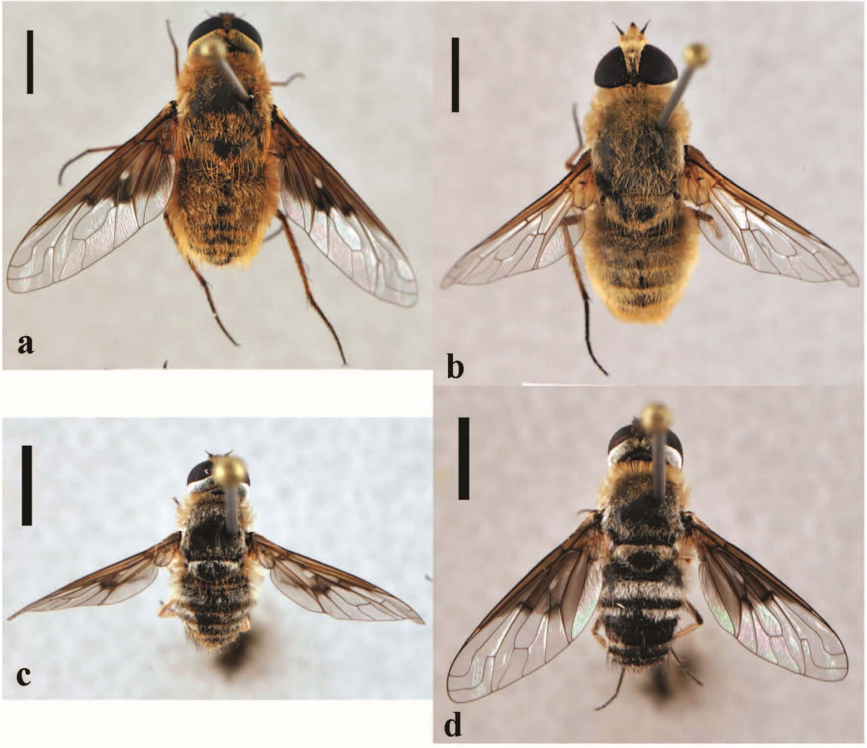

Figure 15. *Paravilla*. **a** *P. edititoides*, male (CNIN 1272) dorsal view **b** *P. flavipilosa*, male (CNIN 1125) dorsal view **c** *P. parvula*, female (CNIN 884) dorsal view **d** *P. separata*, female (CNIN 898) dorsal view. All scale bars: 3 mm.

Paravilla parvula Hall, 1981a

Figure 15c

Material examined. EAM: Apr (1 F); CHU: Apr (1 M); RPA: Apr (7 F, 13 M).

Known Nearctic records. Mexico (Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Nuevo León, San Luis Potosí, Sonora, Zacatecas), USA (Arizona, New Mexico, Texas, Utah).

Comments. *Paravilla parvula* is relatively well collected in northern and central Mexico. Its distribution also includes the south of the USA but no farther north than Utah.

Paravilla separata (Walker, 1852)

Figure 15d

Material examined. CHU: Apr (1 F); EEO: Apr (3 F); REE: Apr (5 F, 3 M); RPA: Apr (1 M).

Known Nearctic records. Canada (Ontario, Manitoba); Mexico (Coahuila); USA (Alabama, Florida, Georgia, Iowa, Kansas, Michigan, Minnesota, Mississippi, Nebraska, Ohio, South Dakota, Wisconsin).

Comments. *Paravilla separata* is present mainly in the eastern half of the USA, and southeastern Canada. This record in Coahuila represents the southern extreme of the distribution of this species, and is the first in Mexico. It may also be present in Tamaulipas and Nuevo León but doubtfully in the northwest of Mexico.

Genus *Poecilanthrax* Osten Sacken

Remarks. Four species from this mainly Nearctic genus are recorded in Coahuila for the first time. Painter and Hall (1960) published a review of *Poecilanthrax* with a key and images of the species.

Poecilanthrax effrenus (Coquillett, 1887)

Figure 16a

Material examined. EAM: Apr (1 F, 1 M), Jun (1 F, 1 M), Sep (1 F); CHU: Jun (1 F); ROR: May (10 F, 5 M), Jul (2 F, 3 M), Aug (1 M); RPA: Jun (4 F, 1 M), Jul (6 F, 6 M), Aug (1 F, 1 M), Sep (4 F), Oct (2 F, 1 M).

Known Nearctic records. Mexico (Baja California Sur, Chihuahua, Coahuila, Sonora, Tamaulipas); USA (Arizona, California, New Mexico, Oklahoma, Texas).

Comments. This record fills a gap in *P. effrenus* distribution between northwest and northeast populations of Mexico. This species is probably present in Baja California and Nuevo León, but has not yet been recorded.

Poecilanthrax fasciatus Johnson & Johnson, 1957

Figure 16b

Material examined. EAM: Sep (1 M); CHU: Oct (1 M); ROR: Oct (1 M); RPA: Oct (1 M).

Known Nearctic records. Mexico (Coahuila); USA (Colorado, Kansas, Texas).

Known host. *Chorizagrotis auxiliaris* Grote (Noctuidae).

Comments. *Poecilanthrax fasciatus* is collected in Mexico for the first time, and this extends the southern limit of this species distribution.

Poecilanthrax hyalinipennis Painter & Hall, 1960

Figure 16c

Material examined. EAM: Mar (3 M), Oct (1 F); CHU: Oct (1 M); ROR: Oct (4 M); RPA: Sep (1 F), Oct (2 F, 6 M).

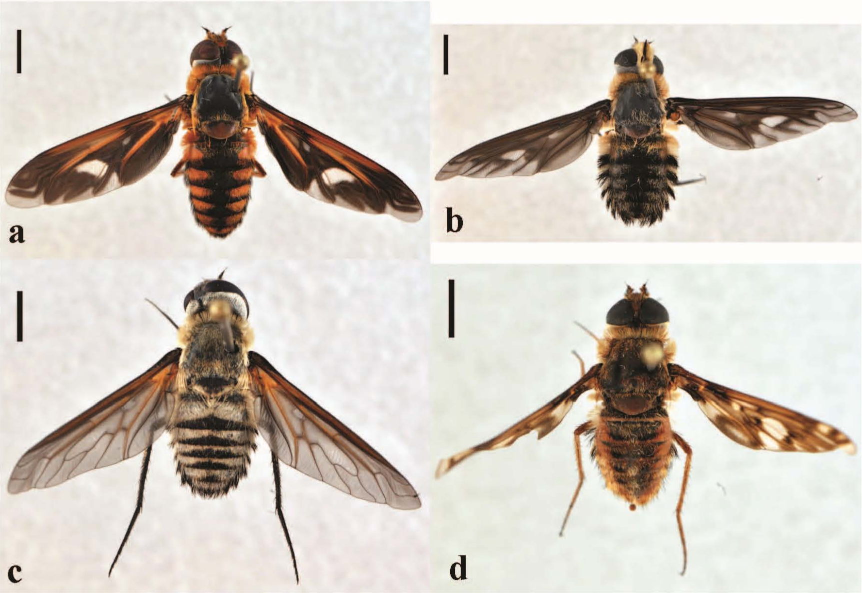

Figure 16. *Poecilanthrax*. **a** *P. effrenus*, female (CNIN 1380) dorsal view **b** *P. fasciatus*, male (CNIN 218) dorsal view **c** *P. hyalinipennis*, female (CNIN 1365) dorsal view **d** *P. poecilogaster*, male (CNIN 1356) dorsal view. All scale bars: 3 mm.

Known Nearctic records. Mexico (Coahuila); USA (Arizona, California, Nevada, Utah).

Comments. This record extends the distribution of *P. hyalinipennis* into the northwest of Mexico. Considering its distribution in the USA, this species may also be present in the northeast of Mexico.

Poecilanthrax poecilogaster (Osten Sacken, 1886b)

Figure 16d

Material examined. REE: Apr (2 M).

Known Nearctic records. Canada (Alberta, Manitoba, Ontario, Saskatchewan); Mexico (Coahuila, Morelos, Nuevo León, Sonora); USA (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Utah).

Comments. Most of the records in the USA and Mexico of this rarely collected but widespread species are from Pacific Coast states, although, there are records from Nuevo Leon and Coahuila in northeast Mexico.

Genus *Rhynchanthrax* Painter

Remarks. Of the seven species of this exclusively Nearctic genus, six are present in Mexico, with *R. maria* (Williston, 1901) and *R. nigrofimbriatus* (Williston, 1901) being endemic to this country. Only *Rhynchanthrax parvicornis* (Loew, 1869) has not been collected in Mexico, but it is distributed across the southern USA and may also occur in the north of Mexico.

Rhynchanthrax capreus (Coquillett, 1887)

Figure 17a

Material examined. CHU: Apr (1 M), Aug (13 F, 6 M), Jul (12 F, 6 M), Sep (1 F, 3 M).

Known Nearctic records. Mexico (Coahuila); USA (Arizona, California, Colorado, Nebraska, Nevada, New Mexico, Utah).

Comments. This is the first record of this species in Mexico. *Rhynchanthrax capreus* is the only species occurring in the northwest of the USA, while the other species in the genus are present mainly in the south and east of the country. This species may also be present in the northwest of Mexico (Baja California, Sonora, Chihuahua).

Rhynachantrax texanus (Painter, 1933)

Figure 17b

Material examined. EEO: May (1 M); RLC: Jun (1 F, 11 M), Jul (3 M).

Known Nearctic records. Mexico (Coahuila, Sonora); USA (Kansas, New Mexico, Texas).

Comments. This is the most eastern record in Mexico for this species. In the USA it is distributed in the southern-center of the country, but in Mexico it has been collected in Sonora so it probably also occurs in Arizona.

Genus *Thyridanthrax* Osten Sacken

Remarks. *Thyridanthrax* has twice as many species in the Palearctic region as in the Nearctic and Neotropical regions combined. All 12 species in North America are present in the USA with five also in Mexico. These are the first records of this genus in Coahuila. The distribution of *T. selene* (Osten Sacken, 1886b) and *T. pallidus* (Coquillett, 1887) are very similar, being present in all of the southern USA and probably also in all of northern Mexico, although they have been only collected in Sonora and Coahuila to date. Both species are rare and were collected only in April.

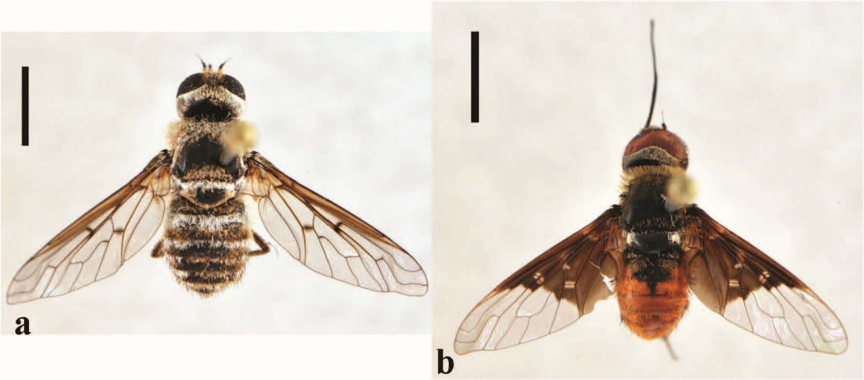

Figure 17. *Rhynchanthrax*. **a** *R. capreus*, female (CNIN 940) dorsal view **b** *R. texanus*, male (CNIN 263) dorsal view. All scale bars: 3 mm.

Thyridanthrax pallidus (Coquillett, 1887)

Figure 18b

Material examined. REE: Apr (4 F, 1 M).

Known Nearctic records. Mexico (Coahuila); USA (Arizona, California, Nevada, Texas, Utah).

Comments. This represents the first record of this species in Mexico.

Thyridanthrax selene (Osten Sacken, 1886b)

Figure 18a

Material examined. EAM: Apr (1 M); REE: Apr (2 F, 2 M).

Known Nearctic records. Mexico (Coahuila, Sonora); USA (Arizona, California, Texas).

Comments. This is the most eastern record in Mexico.

Genus *Xenox* Evenhuis

Remarks. Of the five species that constitute this genus, four are present in Mexico.

Xenox xylocopae (Marston, 1970)

Figure 19

Material examined. ECA: Sep (1 M).

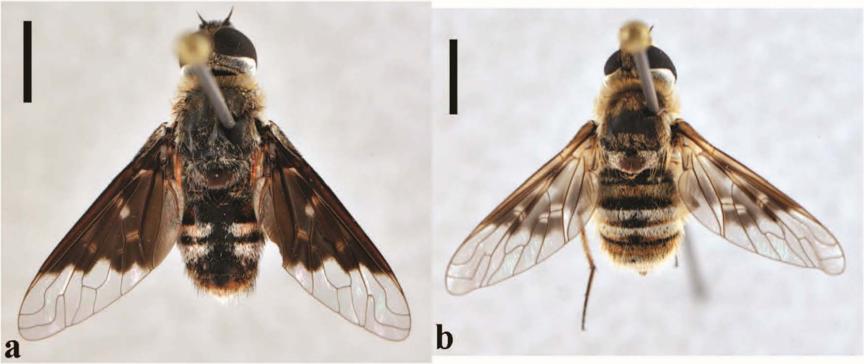

Figure 18. *Thyridanthrax*. **a** *T. selene*, male (CNIN 182) dorsal view **b** *T. pallidus*, female (CNIN 1162) dorsal view. All scale bars: 3 mm.

Figure 19. *Xenox xylocopae*, male (CNIN 1165) dorsal view. Scale bar: 3 mm.

Known Nearctic records. Mexico (Chihuahua, Coahuila, Sonora), USA (Arizona, New Mexico, Texas).

Known host. *Xylocopa micheneri micheneri* (Hurd) (Apidae) as reported by Minckley (1989).

Comments. *Xenox xylocopae* appears to be restricted to the northeast of Mexico and south of the USA. Three of the other species also have restricted and separate distributions: *X. delila* Loew, 1869 is present in the northwest of Mexico and California; *X. nigritus* (Schaeffer, 1768) occurs from the northeast of Mexico (Veracruz and Tamaulipas without overlap with *X. xylocopae*) to South America; and *X. tigrinus* (De Geer, 1776) is present in the eastern USA and southern Ontario. Only *X. habrosus* (Marston, 1970) has a distribution overlapping with the other four species, being present in all of Mexico and the southwest of the USA.

Discussion

The data presented here increase the knowledge of Bombyliidae in Mexico but also reveals the deficiencies in sampling of the family in the country. The species list for the state increased three-fold, which demonstrates the lack of knowledge of the Bombyliidae fauna in this region. Almost all states of Mexico are in a similar situation but northern states appear to have higher diversity and should be priorities for sampling. Hull (1973) identified the northwest of Mexico as a species concentration area of Bombyliidae, but the northeast portion of the country may have the same species richness. Diversity of this family in the north of Mexico is probably much higher than recorded, as indicated by the richness in the south of USA which has similar environmental characteristics but much better sampling. Therefore northeast Mexico is possibly one of the most under sampled areas in the Nearctic region for Bombyliidae, given the great diversity of this family in the area, combined with the size of this part of the country. The study of Bombyliidae in the northern states of Mexico should be more of a priority than field work in the center or the southern states.

Most of the species collected in this study have a broad distribution in the USA but Mexican records are isolated. There are probably more species yet to be recorded from Coahuila and other Mexican states, especially species present in southern border states of the USA. Some species are recorded only from Coahuila in the northeast of Mexico but are also present in the northwest of the country. More studies are required to determine if these species have a disjunct distribution or if any are represented by distinct, cryptic eastern and western species.

Cuatro Ciénegas' biological and conservational importance has long been recognized for reptiles (McCoy 1984), birds (Contreras-Balderas 1984), plants (Pinkava 1984, Villarreal and Encina 2005), snails (Hershler 1984), Crustacea (Cole 1984) and particularly fishes (Minckley 1984), but little is known of other groups like insects. The insects contain 53% of the described species in the planet (Chapman 2009), so their distribution and diversity should be considered for conservation and natural reserve design. The diversity of insects, especially of Bombyliidae and similar arid-regions-diverse groups, increases the conservational value of Cuatro Ciénegas.

Conclusions

The data presented here indicates the significance of Cuatro Ciénegas for Bombyliidae diversity. Comparison with other nearby areas should be undertaken to confirm whether this area really is richer for this family. Data also reveal that true species richness of Bombyliidae is much higher than previously recorded. This could also be true for other insect groups. More funding should be destined for faunistic studies of megadiverse groups with ecological importance such as Diptera, Coleoptera, Hymenoptera and Lepidoptera. The information obtained from these studies might be used first to quantify the species richness and species exchange between areas (beta diversity) (Whittaker 1972) and later to propose conservation management schemes.

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CAPITULO 2

ARTÍCULO ENVIADO A REVISIÓN

Patrones de diversidad y uso de recursos de insectos antófilos en Cuatro Ciénegas, Coahuila, México.

Este capítulo está en formato de manuscrito para la revista *Environmental Entomology*

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Diversity and resource use patterns of anthophile insects in Cuatro Ciénegas, Coahuila, Mexico

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Abstract

Bees and flies are the main pollinators that maintain plant diversity and crop production. Studies on pollinator communities have focused on bees, but community structures of bees and flies may be different. We describe and compare the diversity and resource use patterns of six Apoidea and two Diptera anthophile families in Cuatro Ciénegas in the northeast of Mexico. We sampled two distinct geographic units (Valley/Mountains) and two seasons (rainy/dry). We identified the spatial and temporal patterns in species composition and abundance of these families. We compared the diversity of each family between locations and seasons. The spatial and temporal patterns in species composition, diversity, and resource use were different for each family. As a general pattern diversity was higher during the rainy season. Only fly families and Andrenidae presented different species composition between seasons, in contrast with the rest of Apoidea. Two bee families visited more plant species per insect species during the rainy season, whereas flies visited the same number of plant species in both seasons. Apidae, Megachilidae, and Bombyliidae visited more plant species in the mountains; and the other families presented no differences. The differences between community structures of each group may be caused by the distinct life histories, resource needs during the larval stage and foraging behaviors. These differences are relevant in management and conservation programs that could benefit one group of pollinators but harm others with different responses. The traits of some families indicate their value as potential pollinators.

Keywords: Apoidea, Syrphidae, Bombyliidae, dessert fauna, community structure.

Insect pollinators have a central role in ecosystems maintaining their plant diversity (Kearns 2001), but also increasing the production of agrosystems especially of fruit crops that depend on these insects (Morandin and Winston 2006, Klein et al. 2007, Garibaldi et al. 2013). Since the end of the past century, a decrease in pollinator abundance has been recognized, known as the pollinator crisis (Kearns et al. 1998, Kevan 1999), although its existence has been questioned (Ghazoul 2005). The decrease has been reported mainly for the bees, which are considered the most important group of pollinators (Watanabe 1994, Klein et al. 2007, Potts et al. 2010, Aebi and Neumann 2011, Brittain and Potts 2011, Winfree et al. 2011). However, the relative importance of honey bees as pollinators is still questioned (Breeze et al. 2011, Ollerton et al. 2012). Garibaldi et al. (2013) found that visitation rate of insects different to honey bees is more important to fruit set than that of honey bee. The importance of the pollinator guild and the possibility of their decrease impel the study of their communities and the factors that affect them.

Most of the studies on pollinator communities have been focused on bees (Steffan-Dewenter and Tscharntke 2001, Steffan-Dewenter et al. 2001, 2002; Gathman and Tscharntke 2002, Steffan-Dewenter 2003, Steffan-Dewenter and Kuhn 2003, Potts et al. 2003a, 2003b, 2005; Kearns and Oliveras 2009) and only some include Syrphidae (Diptera) (Steffan-Dewenter and Tscharntke 1999, Branquart and Hemptinne 2000, Ebeling et al. 2008, Fründ et al. 2010, D'Amen et al, 2013). Other Diptera have been excluded from many analyses, although other families besides Syrphidae can be as important and efficient pollinators as bees (Motten 1986, Orford et al. 2015) or even the main pollinators as it is the case of Ceratopogonid midges in cocoa crops (Adjaloo and Oduro 2013). Also, flies are the main pollinators in high latitudes and altitudes (Kevan and Baker 1983, Kearns 1992, Eiberling and Oiesen 1999, Ssymank et al. 2008).

If bees' populations are declining, flies with similar functional attributes could fill the niche of the declining bees (Orford et al. 2015). However, there is evidence in Europe of the decline of pollinator flies (Biesmeijer et al. 2006). For most tropical America the condition of populations of flies is unknown and responses to ecological conditions and anthropogenic pressures could be different between flies and bees (Kearns 2001, Orford et al. 2015). Little is known about the differences in community structure, response to environmental variables or resource-use patterns between bees and flies, or even between the families of Apoidea. Diversity and resource-use patterns present great variation between taxa, geographic areas and ecosystems (McCall and Primack 1992, Fründ et al. 2010) so generalizations may not be always correct. Even if flies are not as efficient pollinators as bees, they use the same resources and their communities affect each other (Larson et al. 2001). Understanding the functioning of pollinator insect communities helps in management and conservation programs, especially in the agricultural field.

This study analyzes the anthophile insect communities in Cuatro Ciénegas in the northeast of Mexico. The Cuatro Ciénegas Valley is recognized as a unique environment for its particular geological history (Moreno-Letelier et al. 2012). It is surrounded by seven mountain ranges, including Sierra La Madera in the northwest of the valley. The valley and the mountains have distinct environments, which may be reflected in differences in the communities of pollinators. The aim is to describe and compare the diversity and resource use patterns of six bee and two fly families. To achieve this, the following questions are formulated: a) Are there spatial or temporal patterns in the abundance, species composition or diversity of these families or patterns in the number of plant species visited by these insects?; b) How similar are these patterns among families? Because of the heterogeneity of the environment in this desert area, we expect to find spatial and temporal patterns in all traits for all families, but because of the differences in life histories and specialization, these patterns will be different for each family. An additional objective is to determine if the Cuatro Ciénegas Valley represents a discrete geographical unit, distinct from Sierra La Madera for these insects, distinguishable by the species composition.

Materials and Methods

Study area and sites. The Cuatro Ciénegas municipality is located in Coahuila state in the northeast of Mexico (Figure 1). The Cuatro Ciénegas basin has unique geological and biological histories. The region was isolated from the Atlantic Ocean by the rise of the Sierra Madre Oriental in the Middle Eocene (40 Ma). When the ocean withdrew, part of the water remained trapped in the Valley (Moreno-Letelier et al. 2012). The subterranean water emerges and forms ponds which make this region different from the surrounding desert areas and nearby mountains. Its isolation also provides a high degree of endemism, unique worldwide (Souza et al. 2012). Sierra la Madera is a 3000 m height limestone formation with a northeast-southeast aspect, that limits the Cuatro Ciénegas Valley to the northwest. The mountains act as a barrier for the humidity from the Gulf of Mexico making the lower portions dryer (Villanueva-Díaz et al. 2008). Desert scrub can be found in the lower parts of the mountains, with submontane forest, chaparral, pine-oak forest present as altitude increases and pine forest at the peaks. It presents a high diversity and endemism and a good conservation condition with low human activity (Arriaga et al. 2000).

Seven sampling trips were carried out during 2012 and 2013 with a total of 63 field work days in eight sites (Table 1, Figure 1). The criteria for site selection were the presence of water and flowers, the distances between sites to be larger than foraging distances (Gathman and Tscharntke 2002) and owners' permits. Four sites within the Valley of Cuatro Ciénegas and four sites in Sierra La Madera were selected. Sites span an altitude range from 713 to 1790 m a.s.l. Sampling included three trips during dry season (Dry 1: Feb. 21– Mar. 1, 2012; Dry 2: Apr. 2–Apr. 12, 2012; Dry 3: Apr. 22–May. 3, 2013) and four trips during rainy season (Rain 1: Aug. 20–31, 2012; Rain 2: Sep. 24–Oct. 5, 2012; Rain 3: Jul. 2–12, 2013; Rain 4: Oct. 22–31, 2013). All sites were sampled every trip, with the exceptions of REE (see table 1 for site codes) that was sampled twice (Dry 2, Rain 1), site REC that was sampled three times (Dry 2, Dry 3, Rain 1), also as site RLC (Rain 2, Rain 3, Rain 4).

Sampling and identification. Sampling was made in different times from 8:00 to 18:00 h in the various sites, according to site accessibility. For standardization and comparison purposes, the interval from 10:00 to 15:00 h was selected for the analysis, as all samplings coincide in this interval. During sampling all observed adults of Apoidea, Bombyliidae and Syrphidae were collected with an aerial net. For each specimen collected the hour and substrate or species of plant visited were recorded, the plants were also collected for their taxonomic identification. Insects were identified with specialized keys: Apoidea (Michener 2000), Bombyliidae (Hall 1981) and Syrphidae (Vockeroth and Thompson 1981). The identification of plants and unknown insect species were made by specialized taxonomist (see Acknowledgments). When identification was not possible, specimens were assigned to a morph. Bombyliidae specimens were deposited in the Colección Nacional de Insectos of the Instituto de Biología, UNAM (CNIN-IBUNAM); Apoidea and Syrphidae specimens were deposited in the Museo de Zoología at the Facultad de Ciencias, UNAM.

Species richness estimation. To evaluate the effectiveness of sampling and to reduce the sampling bias, of each insect family the species richness were estimated with the Chao1 nonparametric estimator (Colwell and Coddington 1994) using SPADE (Chao and Shen 2010). The CI of the estimations were calculated from the SE obtained from bootstrapping. Estimations were log-transformed so the lower bound of the interval was, at least, the number of observed species (Chao and Shen 2010).

Diversity analysis. The Shannon-Wiener indices (H') were estimated with the Chao and Shen (2003) method based on the proportion of *singletons* (species with just one record) in the sample. This method of estimation has been tested with good results in simulations and with real data (Chao and Shen 2003, Beck and Schwanghart 2010). The values of H' were estimated for each family in both locations and both seasons with SPADE (Chao and Shen 2010). The SE and the CI for the estimations were calculated by bootstrapping.

The value of H' is a measure of entropy and indirectly of diversity. It is expressed in *nats* (when the logarithmic base used to calculate it is e), which is an adimensional unit (Moreno et al. 2011). Its value, even if useful for comparison between communities, lacks of biological meaning and its interpretation is complicated. The diversity was expressed as the effective number of species (ENS) (Jost 2006). The ENS is calculated as $\exp(H')$. The ENS and its CI were calculated from the estimated H' for each family. The overlaps between the 95% intervals were inspected to compare the diversity between seasons and locations. Factorial ANOVAs for the species richness, diversity, and number of plants visited by species of each family were made, with location, season and its interaction as predictive factors. No interaction between location and season was found for any group ($p > 0.05$), so results for each factor are presented independently.

Resource-use patterns. The number of plant species visited by each family was estimated, for both season (dry/rainy) and both locations (Mountains/Valley), with the same method as the used for the estimation of the species richness of insects. The number of plant species visited by each family of insects, in both seasons and in both locations, was adjusted by the number of species of each family of insects; this value represents the number of plant species visited by a single species of each family of insects. The adjusted values of number of plant species visited were compared between locations and seasons, by inspecting the overlap of the CI to determine significant differences.

Spatial-temporal community structure. To analyze the variation in composition and abundance of species a Principal Component Analysis were performed with CANOCO 4.56 (Ter Braak and Smilauer 2009). The ordination axes were calculated with the composition and abundance of the species of each family. As species abundance was biased with many rare and a few abundant species, the data of species abundance were log-transformed:

$$Y' = log(A * Y + B)$$

where $A = 1$ and $B = 1$. In this way the ordination was not dominated only by abundant species (Leps and Smilauer 2003). The ordination diagrams were drawn with the two first axes in a sample-distance focus scale. Over these diagrams, the categorical variables for location (sites in the Valley/sites in the Mountains) and season (samplings of dry season/samplings of rainy season) were projected as points. The distance between two points in the ordination diagram represents the difference in composition and species proportion in that variable category. Spatial structure was recognized if Valley sites appear together with each other and separated from Mountain sites. In the same way, temporal structure was recognized if dry and rain samplings differentiated from each other.

Results

Insect species richness and sampling effort. A total of 4074 insects of 227 species were collected. The most abundant and species-rich family was Bombyliidae with 100 species and 52% of the specimens. Syrphidae had 15% of the specimens in 29 species. Ninety-eight taxa composed the Apoidea (Andrenidae, 18; Apidae, 60; Colletidae, 16; Halictidae, 30; Megachilidae, 43; Melittidae, 2), that represented the 33% of the insects collected. The species richness estimation indicated a total of 263 species (Table 2), so 86% of the estimated species in the area were collected. Syrphidae sampling was the least effective, but 75% of the estimated species of these family were collected. The best sampled family was Melittidae with 100% of their species collected. The completeness of the lists of the other taxa was in between these values (Apidae 79%, Andrenidae 83%, Megachilidae 85%, Halictidae 86%, Colletidae 88%, and Bombyliidae 96%), so the sampling effort was adequate.

Spatial and temporal patterns of diversity. For five families there were not significant differences in species richness between seasons and locations. Andrenidae and Colletidae were richer in the rainy season and in the Valley, and Melittidae presents two species and just seven specimens in the Mountains and none in the Valley (Table 2).

In general, Diptera families were more diverse than Apoidea families (Table 2). Bombyliidae was the most diverse group whereas Colletidae and Melittidae were the least diverse of the families. There were no significant differences between the diversities of Andrenidae, Apidae, Halictidae, and Megachilidae. Andrenidae and Colletidae presented a temporal diversity pattern, being more diverse during the rainy season. The other groups were equally diverse between seasons. Nevertheless, the total diversity was significantly higher during the rainy season. Regarding spatial diversity patterns, the total diversity in the Valley and the Mountains were not significantly different, but Diptera groups and Melittidae were more diverse in the Mountains. Apidae was the only family significantly more diverse in the Valley than in the Mountains.

Patterns of plant visitation. Estimation of the number of plant species visited was higher for Bombyliidae than any other group (± SE) (97.1 ± 12.2), followed by Megachilidae (77 ± 23.2), Apidae (68.1 ± 5.6) and Halictidae (60 ± 21). But when the number of plant species was adjusted by the per insect species, then Megachilidae was the family that visited more plant species per insect species (4.4 ± 1.33) and Bombyliidae occupied the last place (0.89 ± 0.11) (Table 2). In general, insects visited more plant species per insect species in the rainy season than in the dry season (Table 2). Andrenidae was the only family that visited more plants per insect species in the dry season. Diptera, Colletidae, Halictidae, and

Melittidae showed no significant differences in the number of plant species visited between seasons. Apidae and Megachilidae visited more plant species per insect species during the rainy season. Apidae, Megachilidae, Mellitidae, and Bombyliidae visited significantly more plants species per insect species in the Mountains than in the Valley. The other families presented no spatial patterns in resource use. But the general pattern for the total data showed that more plant species per insect species were visited in the Mountains than in the Valley.

Spatial-temporal structure of abundance and composition of insect species. PCA ordination diagrams of sites (Figure 2) showed that for Andrenidae, Apidae, Halictidae, and Bombyliidae the Valley and Mountains represented discrete geographic units, distinguishable by the species and their abundances in each location. Regarding temporal structure, species composition and abundance of Andrenidae, Bombyliidae, and Syrphidae differed between seasons (Figure 2). In this way, Andrenidae and Bombyliidae presented both spatial and temporal structure. On the other hand, Megachilidae and Colletidae did not present spatial or temporal structure, as species composition and abundance of these families were similar between seasons and locations. Melittidae data were not enough to construct an ordination diagram, therefore, we excluded this family of this analysis.

There were marked differences in the temporal structure of the communities of Diptera and Hymenoptera families. First, Bombyliidae and Syrphidae presented temporal structure but Andrenidae was the only Apoidea family with such structure. Second, the variation in species composition between samples of the same season was similar for both seasons in Diptera families; but Apoidea presented more variation between samples in the rainy season than in the dry season.

Discussion

Species richness. It is considered that insects are more diverse and abundant during the rainy season (Janzen 1973). These differences between seasons are explained by the quantity of available resources which gives stability to the ecosystem (Martínez-Falcón et al. 2010). Six of the eight groups analyzed had the same species richness in both seasons. In the Valley the presence of water in all sites throughout the year stabilizes the ecosystems and allows the species to be active. This could be a special characteristic of the region and more insects groups in the area should be analyzed to confirm this phenomenon.

Species richness and abundance of Bombyliidae in this area is remarkable. Cuatro Ciénegas' 109 estimated species for this family represent 28% of the species recorded in the country and 2% of the global diversity (Evenhuis and Greathead 1999, Zhang 2011, Avalos-Hernández et al. 2014). Syrphidae species richness in this area is also important with 18% of the known species of Mexico (Thompson et al. 1976, Papavero and Ibáñez–Bernal 2001, 2003). Species richness of bee families proportional to species recorded in Mexico is not as high as with Diptera diversity. Halictidae is the bee family with the highest proportion of species, representing 10% of the species of Mexico (Ascher and Pickering 2015). On the lowest end of Apoidea, the Andrenidae species of Cuatro Ciénegas represent 3% of the species of the country (Ascher and Pickering 2015). These high species richness of these flies had been found before, Petanidou and Ellis (1993) reported a higher diversity of Bombyliidae and Syrphidae than expected in a Mediterranean ecosystem in Greece, compared with similar ecosystems in California and Chile. Bombyliidae is more diverse and abundant in arid environments, and the north of Mexico is a diversity center for this family

(Hull 1973, Evenhuis and Greathead 1999). On the other hand, Syrphidae is more diverse in the Neotropical region than in the Nearctic region (Vockertoh and Thompson 1981). The higher number of species and abundance of Bombyliidae, compared with Apoidea, in this region, agree with the known biogeographic patterns.

Diversity patterns. Some studies that have found temporal diversity patterns treated bees as a single group (Oertli et al. 2005, Sydenham et al. 2014) and just some authors have analyzed patterns for each family (Richards et al. 2011). Mixing data from Diptera and Hymenoptera is not justified, because of the ecological differences between these taxa, but mixing data from the different Apoidea families is also incorrect. The different patterns can only be perceived if each family is analyzed independently.

Diversity depends on the species richness and evenness of abundances. The differences between the patterns in species richness and diversity show the dominance of some species in a habitat or season. While total species richness is the same in both seasons, diversity is higher in the rainy season which indicates dry season has higher dominance, Andrenidae and Colletidae also present this pattern. Particularly *Perdita* spp. (Andrenidae) are more abundant during the dry season, and scarce in the rainy season, suggesting they are adapted to exploit the conditions of the dry season. In a similar way, differences in richness and diversity show that dominance is greater in the Valley for Diptera. Only Apidae has more diversity and less dominance in the Valley. This is an interesting result since *Apis mellifera* L. is the most abundant species of Apidae with 273 specimens collected in the Valley and 73 specimens in the Mountains. Even with this high abundance of *A. mellifera*, dominance in the Valley is lower than in the Mountains, indicating the high diversity and evenness of species of this family in the Valley.

The higher diversity in the rainy season could be explained by the increase in resources, especially plants. Bee diversity is known to be affected by the plant diversity that is higher during the rainy season (Ebeling et al. 2008, Kearns and Oliveras 2009). The diversity of bees is also directly related to the complexity of the landscape (Steffan-Dewenter et al. 2002). This could increase the diversity in the Mountains that present more complex topography and habitat heterogeneity than the Valley. Spatial patterns are also consistent with the supposed negative relation between the diversity of pollinators and disturbance (Scriven et al. 2013) and between diversity and isolation (Steffan-Dewenter and Tschamtke 1999). The disturbance is higher in the Valley because of the higher human population, tourism, and water extraction for human use (Arriaga et al. 2000). Another alluded factor affecting diversity is the level of competition between pollinators (Heithaus 1979). Differences between diversity patterns in each group may be because of the different responses to these factors, or that they are affected by different factors which may be related to resource availability for the immature stages. All the insects included here use flowers as the principal resource for adults but larval stages of Diptera and some parasitic bees depend on other resources.

Temporal patterns in resource use. The diversities of most animals are correlated with the diversity of plants (Fründ et al. 2010). For nectivores flowering plants are the most important resource and the number of flowering plants affects their diversity (Steffan-Dewenter and Tscharntke 2001, Steffan-Dewenter et al. 2002, Potts et al. 2003b, Ramírez

2004, Kremen et al. 2007, Ebeling et al. 2008, Kearns and Oliveras 2009). Other important plant community characteristics are the quality of flowers (Potts et al. 2005) and flower cover (Hoiss et al. 2012), which are related to pollinator abundance. The number of plant species present in each site was not measured, only the plants visited were recorded. Because of the sampling method a causal relation between the diversities of plants and insects cannot be tested, but this approach permits to compare the patterns of resource use between groups.

The pattern of frequency in plant visits is community specific. McCall and Primack (1992) reported that in some communities frequency is higher during summer while in others insects visit more plants during spring. Flower resource used by insects has temporal patterns because the foraging behavior (Steffan-Dewenter and Kuhn 2003), the flower visit frequency (McCall and Primack 1992), and the number of plants visited (Heithaus 1979) varies between seasons. Plant visit preferences changes with the season as a response to resource availability (Heithaus 1979, Branquart and Hemptinne 2000). Interaction network also changes between seasons, *Copestylum* (Syrphidae) network is nested during the rainy season and stochastic during the dry season (Martínez-Falcón et al. 2010).

Combining diversity, species composition and resource-use patterns, we found that some families show the capacity to modify their foraging behavior according to seasonal changes. Species richness and diversity of Apidae, Halictidae, Megachilidae and both families of Diptera are the same in both seasons. Halictidae, Syrphidae and Bombyliidae visit the same number of plants in both seasons. But Apidae and Megachilidae visit more plant species per insect species in rainy season. Apidae and Megachilidae also present a similar species composition between seasons (Figures 2b,c). This means that for these two families, the same species are visiting more plants depending on the season. Andrenidae presents an interesting pattern, it visits more plant species per insect species during the dry season, but species richness and diversity are higher during the rainy season. But contrary to Apidae and Megachilidae, Andrenidae species composition is different between seasons (Figure 2a). These changes in foraging behavior could be provoked by the abundance and quality of the resource and the capacity of the species of each family to shift or increase the number of plants they visit. If the resource is scarce or plants offer less nectar and pollen, then insects need more floral visits per plant or to visit more plants to fulfill their requirements, but insects need to be capable of visiting different plant species according to the season. Some pollinators change their preferences if the resource is scarce while other keep feeding on the same plants (Fründ et al. 2010). So the differences between temporal diversity patterns of insect and number of plants used may reflect the capacity of Andrenidae, Apidae, and Megachilidae to adapt to different conditions and use the available resources. This has implications for the efficiency of these families as pollinators since the same number of species could visit and potentially pollinate more plants. On the other hand, Bombyliidae pollination requires more diversity and abundance to be effective. Motten et al. (1981) showed that *Bombylius major* L. (Bombyliidae) can be an effective pollinator of *Claytonia virginica* L., the lower carrying capacity of pollen of this fly, compared with the carrying capacity of bees, is compensated with its high abundance. The high abundance, species richness, diversity and number of plant species visited by Bombyliidae could make them important pollinators in this system, but pollination efficiency measurements are required to confirm this.

The differences in resource-use patterns between families may be related to the mean foraging distances that each group travels and taxon-specific foraging preferences. The foraging distance varies between months because bees travel more distances if the resource is scarce (Steffan-Dewenter and Kuhn 2003). Foraging distances also vary between taxa, solitary bees forage nearer their nest than social bees (Gathman and Tschamtke 2002). Foraging distances of pollen collectors are larger than nectar collectors because pollen is less abundant than nectar (Steffan-Dewenter and Kuhn 2003). These functional traits could predict the number of plant species that an insect visit and its potential as pollinator; to answer this, is necessary to find the correlation between resource use and these traits.

Spatial patterns in resource use. Apidae, Megachilidae, and Bombyliidae visit more plants per insect species in the Mountains. As with the temporal resource use patterns, plant diversity and foraging behavior could explain the differences between locations. But in the spatial context, the altitude has to be considered. Like most insects, pollinator diversity decreases at high altitudes (Gimenes 2002, Rahbek 2005, Fischer et al. 2011), but altitude also affects the composition of the communities (Hoiss et al. 2012) and the insect-plant interactions (Ramos-Jiliberto et al. 2010). It is also known that at higher altitudes pollinators visit fewer plant species (Ramos-Jiliberto et al. 2010). But pollinator flies abundance has been reported to increase with altitude in alpine communities of Norway (Lázaro et al. 2008) and in lowlands of Tasmania where flies dominate from as low as 700 m (Hingston and McQuillan 2000). The pooled data indicated that insects visit more plant species per insect species in the Mountains. No group visited more plant species per insect species in the valley, possibly because the plant species richness was higher in the Mountains.

Apidae, Megachilidae, and Bombyliidae have the same number of species in the Valley and Mountains but visit more plant species in the Mountains. Species composition of Bombyliidae and Apidae differ between locations so it may be argued that the species of the Mountains have different foraging behavior than those in the Valley. But the composition of species of Megachilidae was similar in the Valley and in the Mountains. This suggests that Megachilidae species are changing their resource use according to the traits of the mountains ecosystems, in a similar way they do in the rainy season as discussed above. Other families like Andrenidae, Colletidae, Halictidae and Syrphidae do not make this shift and visit the same number of species in the Valley and the Mountains.

Although in general the patterns differ between families, there are some similarities in the resource use patterns between these insects. Apidae and Megachilidae have similar temporal resource use patterns between them but different from other Apoidea. Colletidae, Syrphidae, and Halictidae present no patterns in the number of plants visited between seasons or locations. Bombyliidae present the same temporal pattern of resource use as Syrphidae and Halictidae, but the same spatial pattern as Megachilidae and Apidae. Regarding pollination, Megachilidae could be the most efficient pollinator as its species can increase the number of plants they visit if the diversity of plants is higher. It is also noteworthy that even if Apidae is more diverse in the Valley, the number of plant species per insect species visited by this family is higher in the Mountains, so increasing the diversity of this family not necessarily increases the plants visited and pollinated.

Spatial and temporal patterns in species composition. Temporal differences in species composition of pollinators are common (Heithaus 1979, Petanidou and Ellis 1993, Branquart and Hemptinne 2000, Scriven et al. 2013). Possibly related to the diversity and abundance of plants, as pollinators use different plants in each season (Branquart and Hemptinne 2000, Potts et al. 2003b). The temperature may also cause different species composition because small bees cannot live in cold weathers (Stone 1993). Diptera families' patterns support these ideas but all bee families, except Andrenidae, have similar species composition in both seasons. The stability of the Valley ecosystem, due the constant presence of water and the stable conditions around the ponds, may be playing an important role in these patterns, combined with the specialization level. If insects are generalist or their feeding plants are abundant then the composition of species is similar between sites and seasons. On the other hand, specialization promotes a more marked temporal structure because insects are linked to their feeding plant, as reported for Bombyliidae in Egypt (El-Moursy et al. 1999). This suggests that Andrenidae, Bombyliidae, and Syrphidae present higher specialization than the other families.

Species composition of two sites can be similar due the spatial closeness between them, but also due the environmental similarities. Aizen and Feinsinger (2003) reported the same composition of bee species in separate sites with the same degree of disturbance, this indicates that species composition is better predicted by conditions than by distances. Spatial patterns of species composition show that the Valley and the Mountains are independent geographic units, but not for all groups. Colletidae, Megachilidae, and Syrphidae do not present such distinction between locations. So, the isolation degree of the Valley varies for each taxa studied.

The difference between flies and bees community structures could be explained be their distinct life histories. Bees depend, as larvae and adults, on flower resources while Bombyliidae and specially Syrphidae present a diversity of habitats as larvae (predators, parasites, scavengers). This relates plant communities more closely to bee than to fly communities. Although some Syrphidae species present aquatic larvae (*e.g. Eristalis*), interestingly all the Syrphidae species collected have terrestrial larvae, so the water bodies are not particularly important for abundance patterns of this family in this region. Abundance and quality of nesting sites also affect species composition of bees but not of flies (Steffan-Dewenter et al. 2001, Potts et al. 2005). Finally, mimetism could also be affecting these fly communities. Bombyliidae and Syrphidae are mimics of Hymenoptera, but the similarities are higher in Syrphidae (Gilbert 2005). Since mimics must coexist with their models in order to receive a benefit, the structure of Diptera communities may be related with that of their hymenopteran models.

This is the first study that compares the insect fauna of the Cuatro Ciénegas Valley with the surrounding mountains. Ordination diagrams show that the Valley of Cuatro Ciénegas and the Sierra la Madera are distinct geographic unit for four of the seven families included in this analysis. Many endemic species of bacteria, plants, and some relatively well-known animal groups are recorded within the valley (Cole 1984, McCoy 1984, Villarreal-Quintanilla and Encina-Domínguez 2005, Souza et al. 2012). The same may occur for other insect groups. For now, it is not possible to affirm that the valley species are endemic because sampling is scarce in the country.

To conclude, we found the existence of temporal and spatial patterns in the diversity and use of flower resources of anthophile insects. These patterns are different for each family analyzed. The study confirms that community structure of Diptera and Apoidea families differ from each other and even between the families of each group, so observed patterns in some bee family or group cannot be generalized to flies or other families of Apoidea. Further studies are required to determine the exact causes of these differences. Even if bees are the main pollinators, flies visit a different set of plants (Ssymank et al. 2008). A management plan that considers only bees or even just a family or species (*e.g. Apis mellifera*) may affect negatively other benefic insects. Besides, the loss of plant diversity may not affect all pollinators in the same way or even may benefit some of them by reducing competition. Given the importance of flies, studies on pollinator ecology must include them together with bees.

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Table 1. Sampling sites characteristics. Vegetation according to Pinkava (1979, 1984).

Site (Code)	**Location geographic coordinates**	**Altitude (m a.s.l.)**	**Vegetation**
Rancho Pozas Azules (RPA)	Valley 26°49’39” N 102°01’24” W	713	Halophile, Aquatic and subaquatic, Transition.
Ejido Antiguos Mineros (EAM)	Valley 26°46’58” N 102°00’20” W	725	Halophile, Aquatic and subaquatic, Transition.
Rancho Orozco (ROR)	Valley 26°52’18” N 102°05’17” W	740	Halophile, Aquatic and subaquatic, Transition, Desert shrub.
Churince (CHU)	Valley 26°50’30” N 102°08’10” W	768	Gypsophile, Halophile, Aquatic and subaquatic, Transition, Desert shrub.
Ejido El Oso (EEO)	Mountains 27°03’08” N 102°13’35” W	1085	Desert shrub, Chaparral.
Rancho El Espejo (REE)	Mountains 27°13’19” N 102°30’19” W	1425	Desert shrub, Chaparral.
Rancho La Casita (RLC)	Mountains 27°06’45” N 102°23’40” W	1630	Desert shrub, Chaparral.
Rancho El Chupadero (REC)	Mountains 27°10’07” N 102°34’26” W	1790	Desert shrub, Chaparral.

Table 2. Estimated species richness (S Est) (± SE), estimated diversity as effective number of species (ENS) (± SE) and plant species used by Insect species (PSU/IS) (± SE) of each family by locations and seasons are presented.

	Hymenoptera						Diptera		Total
	Andrenidae	Apidae	Colletidae	Halictidae	Megachilidae	Melittidae	Bombyliidae	Syrphidae	
N	214	625	57	246	193	6	2126	607	4074
S Est.	18.2 (± 1.8)	43 (± 8.1)	8 (± 2.2)	23.3 (± 4.1)	17.5 (± 2.6)	2 (± 0.4)	109.5 (± 4.3)	39.3 (± 8.9)	263.4 (± 14)
Mount.	6.3 (± 0.7	17 (± 4.5)	4 (± 0.3)	22 (± 7.1)	14.5 (± 1.3)	2 (± 0.4)*	87.1 (± 8.2)	27.3 (± 4.1)	190.1 (± 16)
Valley	11.5 (± 1.3)*	44.3 (± 9.6)	9 (± 4.4)*	20 (± 5.5)	14 (± 4.5)	0	80.7 (± 8)	33.5 (± 10.6)	232.7 (± 26.1)
Dry	6 (± 0)	22.3 (± 4.1)	2 (± 0)	17.3 (± 4.1)	13.5 (± 3.2)	1 (± 0)	80.3 (± 8.9)	30 (± 6.7)	182 (± 16.3)
Rainy	15.5 (± 2.2)*	46 (± 12.9)	8 (± 2.2)*	17 (± 2.9)	17 (± 4.5)	1 (± 0)	85.1 (± 5.0)	26 (± 7.2)	217.1 (± 16.4)
ENS	7.9 (± 0.65)	10.2 (± 0.69)	5.7 (± 0.53)	9.8 (± 0.82)	9.82 (± 0.75)	2.0 (± 0.65)	51.3 (± 1.16)	13.4 (± 0.65)	101.9 (± 2.15)
Mount.	7.8 (± 2.18)	6.6 (± 0.68)	3.3 (± 0.53)	5.7 (± 1.04)	9.7 (± 0.93)	2.0 (± 0.65)*	39.1 (± 1.44)*	14.6 (± 0.85)*	78.0 (± 2.4)
Valley	6.2 (± 0.48)	10.0 (± 0.78)*	4.2 (± 0.86)	8.4 (± 0.97)	8.0 (± 0.85)	0	31.6 (± 1.11)	9.6 (± 0.80)	71.4 (± 1.95)
Dry	4.2 (± 0.27)	9.1 (± 0.90)	2.0 (± 0.12)	7.1 (± 0.87)	10.8 (± 2.14)	1.0 (± 0)	37.6 (± 1.50)	9.2 (± 0.67)	69.1 (± 2.19)
Rainy	13.0 (± 1.58)*	9.5 (± 0.80)	5.2 (± 0.66)*	9.7 (± 0.95)	8.9 (± 0.75)	1.0 (± 0)	39.2 (± 1.11)	11.8 (± 0.82)	83.1 (± 2.28)*
PSU/IS	1.13 (± 0.18)	1.58 (± 0.13)	3.16 (± 1.11)	2.58 (± 0.90)	4.4 (± 1.33)	1 .0 (± 0.20)	0.89 (± 0.11)	1.32 (± 0.16)	0.49 (± 0.03)
Mount.	0.87 (± 0.21)	2.83 (± 0.53)*	2.75 (± 1.05)	1.09 (± 0.49)	3.52 (± 1.02)*	1.0 (± 0.20)*	0.87 (± 0.13)*	0.95 (± 0.12)	0.54 (± 0.05)*
Valley	1.22 (± 0.16)	0.84 (± 0.10)	1.17 (± 0.24)	1.43 (± 0.53)	1.25 (± 0.19)	0	0.37 (± 0.07)	0.85 (± 0.16)	0.17 (± 0)
Dry	2.0 (± 0.48)*	0.82 (± 0.03)	2.25 (± 0.65)	1.21 (± 0.39)	0.81 (± 0.21)	1.0 (± 0)	0.46 (± 0.09)	0.82 (± 0.10)	0.26 (± 0.03)
Rainy	0.58 (± 0.02)	1.25 (± 0.14)*	2.44 (± 1.03)	2.44 (± 1.14)	5.76 (± 2.58)*	1.0 (± 0)	0.76 (± 0.09)	1.23 (± 0.31)	0.50 (± 0.05)*

Asterisk indicate significant differences ($P < 0.05$) between seasons or locations, the asterisk marks the significant higher value.

Figure 1. Location map of samplings sites within Cuatro Ciénegas region.

Figure 2 a-c. PCA ordination diagrams based on composition and abundance of each family analyzed. Samples (circles in a-g) from Dry (white) or Rainy (black) seasons and sites (circles in h-n) from Valley (white) and Mountains (black) are added. Squares position indicates the mean species composition of all samples from that season (Dry or Rain in a-g) or all sites from that location (Valley or Mountains in h-n). Explained variances are shown in each axis. a-g: temporal structure; h-n: spatial structure. a, h: Andrenidae; b, i: Colletidae; c, j: Megachilidae; d, k: Apidae; e, l; Halictidae; f, m: Bombyliidae; g, n: Syrphidae. See table 1 for site codes.

Figure 2 d-g. *Cont*.

Figure 2 h-k. *Cont*.

Figure 2 l-n. *Cont.*

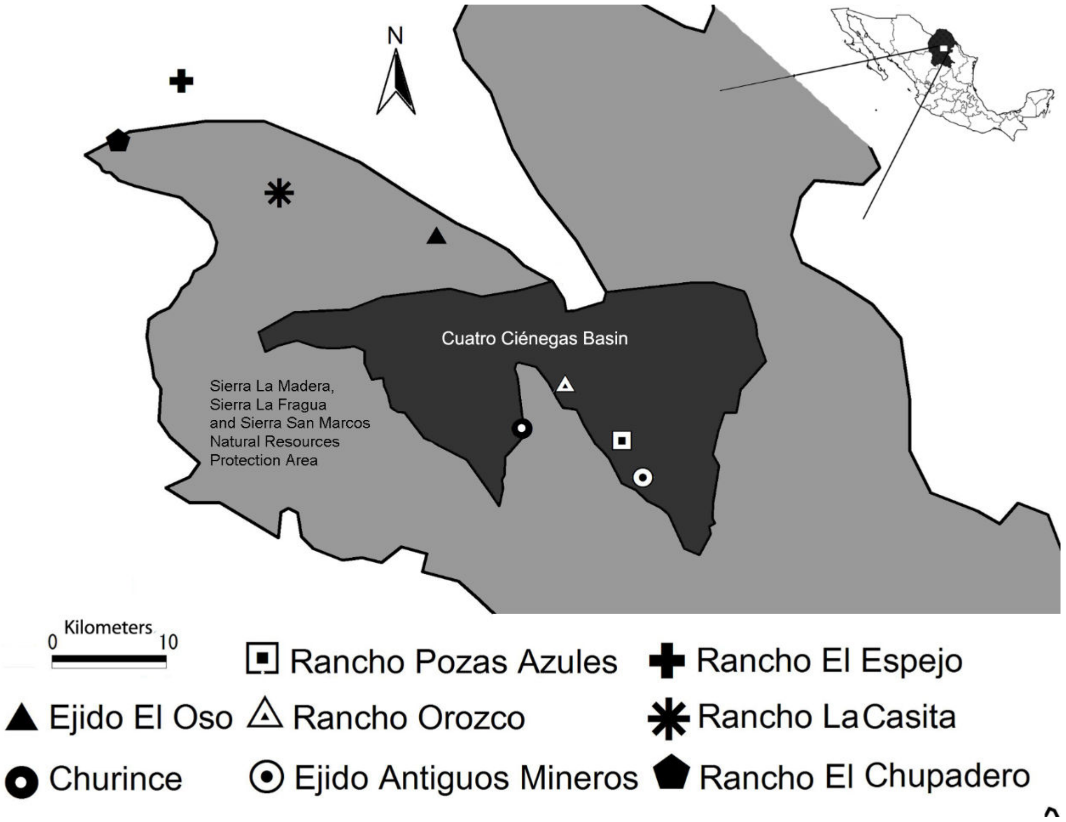
N
Cuatro Ciénegas Basin
Sierra La Madera,
Sierra La Fragua
and Sierra San Marcos
Natural Resources
Protection Area
Kilometers
0
10
Rancho Pozas Azules
Rancho El Espejo
Ejido El Oso
Rancho Orozco
Rancho La Casita
Churince
Ejido Antiguos Mineros
Rancho El Chupadero

Figure 1.

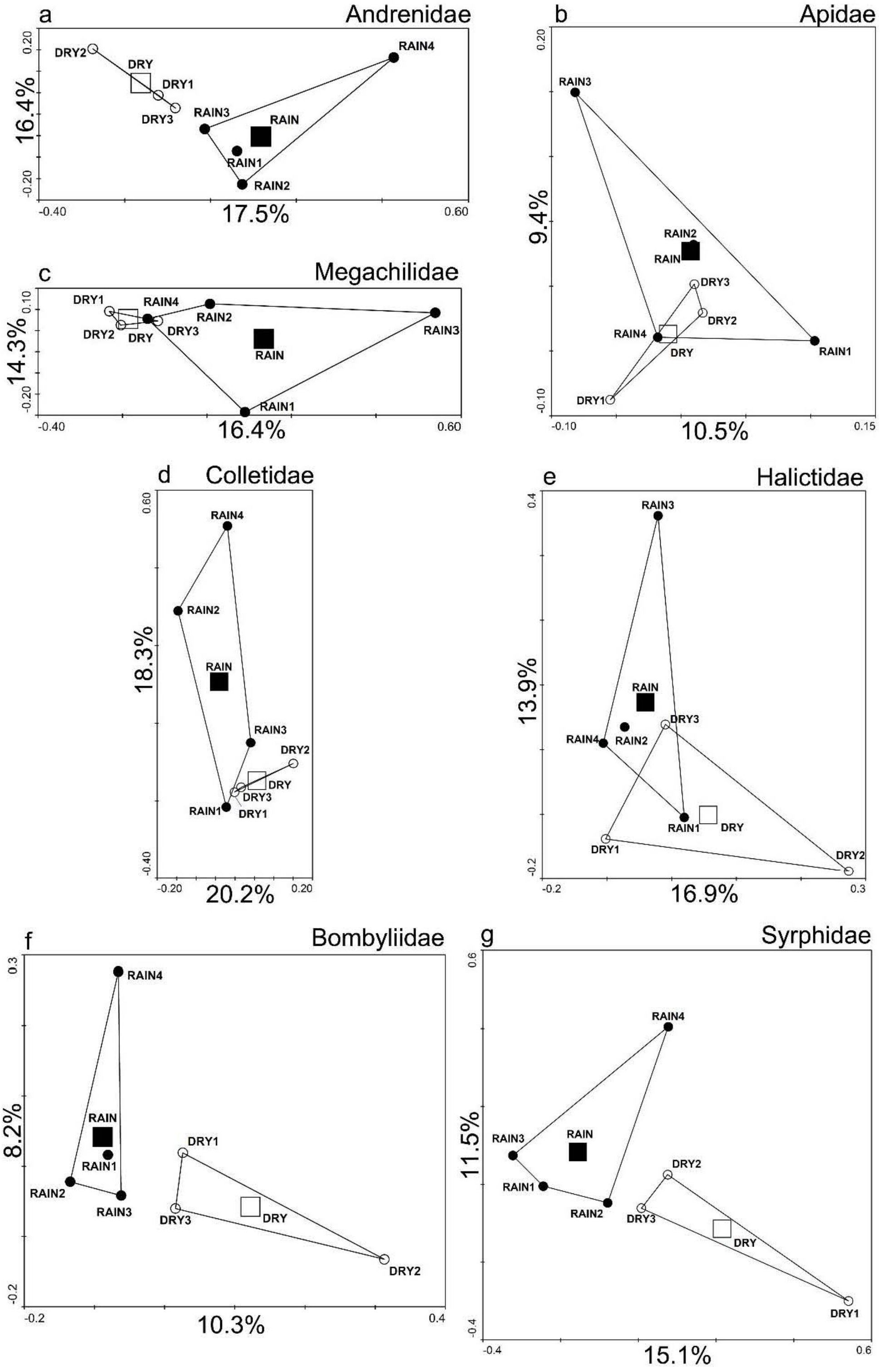
a
Andrenidae
DRY2
DRY
DRY1
DRY3
RAIN3
RAIN
RAIN1
RAIN2
RAIN4
0.20
-0.20
16.4%
-0.40
0.60
17.5%
b
Apidae
RAIN3
RAIN2
RAIN
DRY3
DRY2
RAIN4
DRY
RAIN1
DRY1
0.20
-0.10
9.4%
-0.10
0.15
10.5%
c
Megachilidae
DRY1
RAIN4
RAIN2
DRY2
DRY
DRY3
RAIN
RAIN3
RAIN1
0.10
-0.20
14.3%
-0.40
0.60
16.4%
d
Colletidae
RAIN4
RAIN2
RAIN
RAIN3
DRY2
DRY
DRY3
RAIN1
DRY1
0.60
-0.40
18.3%
-0.20
0.20
20.2%
e
Halictidae
RAIN3
RAIN
DRY3
RAIN4
RAIN2
RAIN1
DRY
DRY1
DRY2
0.4
-0.2
13.9%
-0.2
0.3
16.9%
f
Bombyliidae
RAIN4
RAIN
RAIN1
RAIN2
RAIN3
DRY1
DRY3
DRY
DRY2
0.3
-0.2
8.2%
-0.2
0.4
10.3%
g
Syrphidae
RAIN4
RAIN3
RAIN
RAIN1
RAIN2
DRY2
DRY3
DRY
DRY1
0.6
-0.4
11.5%
-0.4
0.6
15.1%

Figure 2 a-g

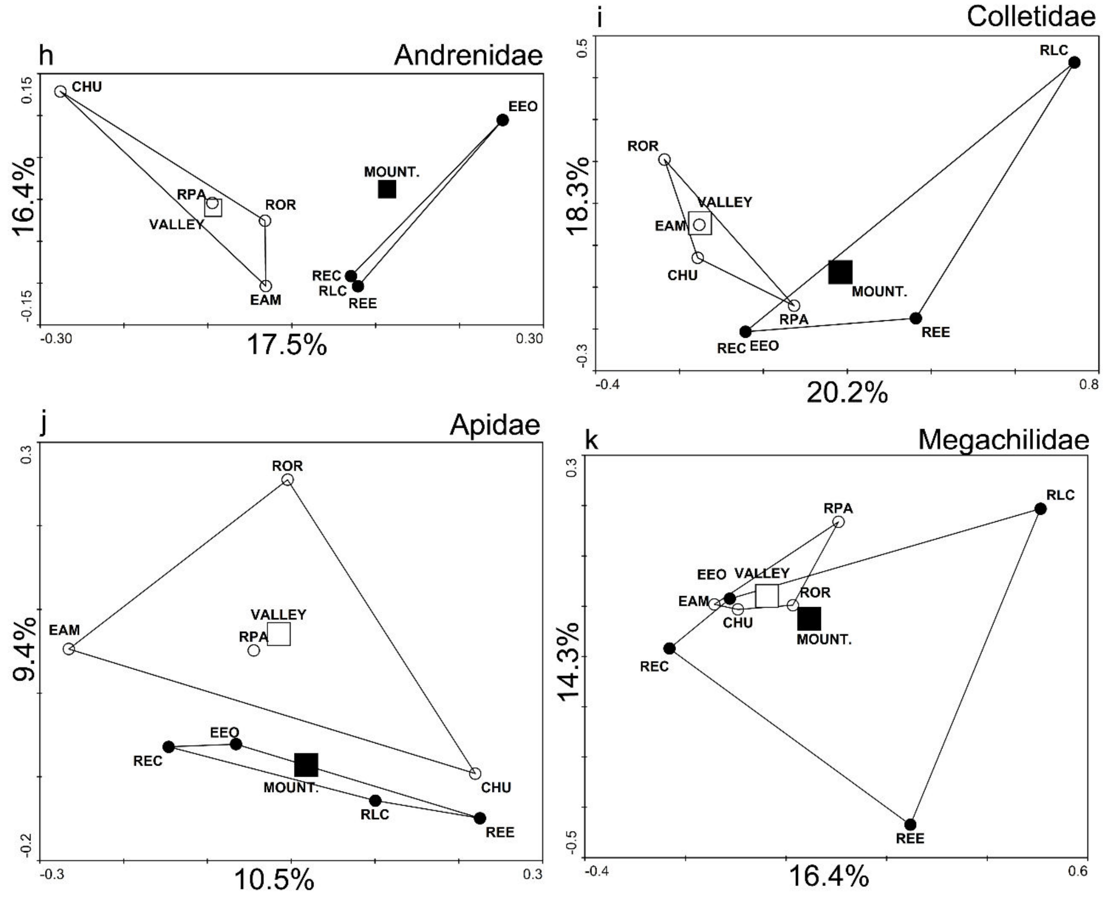
h
Andrenidae
0.15
16.4%
-0.15
-0.30
17.5%
0.30
CHU
RPA
VALLEY
ROR
EAM
EEO
MOUNT.
REC
RLC
REE
i
Colletidae
0.5
18.3%
-0.3
-0.4
20.2%
0.8
RLC
ROR
VALLEY
EAM
CHU
MOUNT.
RPA
REC
EEO
REE
j
Apidae
0.3
9.4%
-0.2
-0.3
10.5%
0.3
ROR
VALLEY
RPA
EAM
EEO
REC
MOUNT.
RLC
CHU
REE
k
Megachilidae
0.3
14.3%
-0.5
-0.4
16.4%
0.6
RPA
RLC
EEO
VALLEY
EAM
ROR
CHU
MOUNT.
REC
REE

Figure 2 h-k

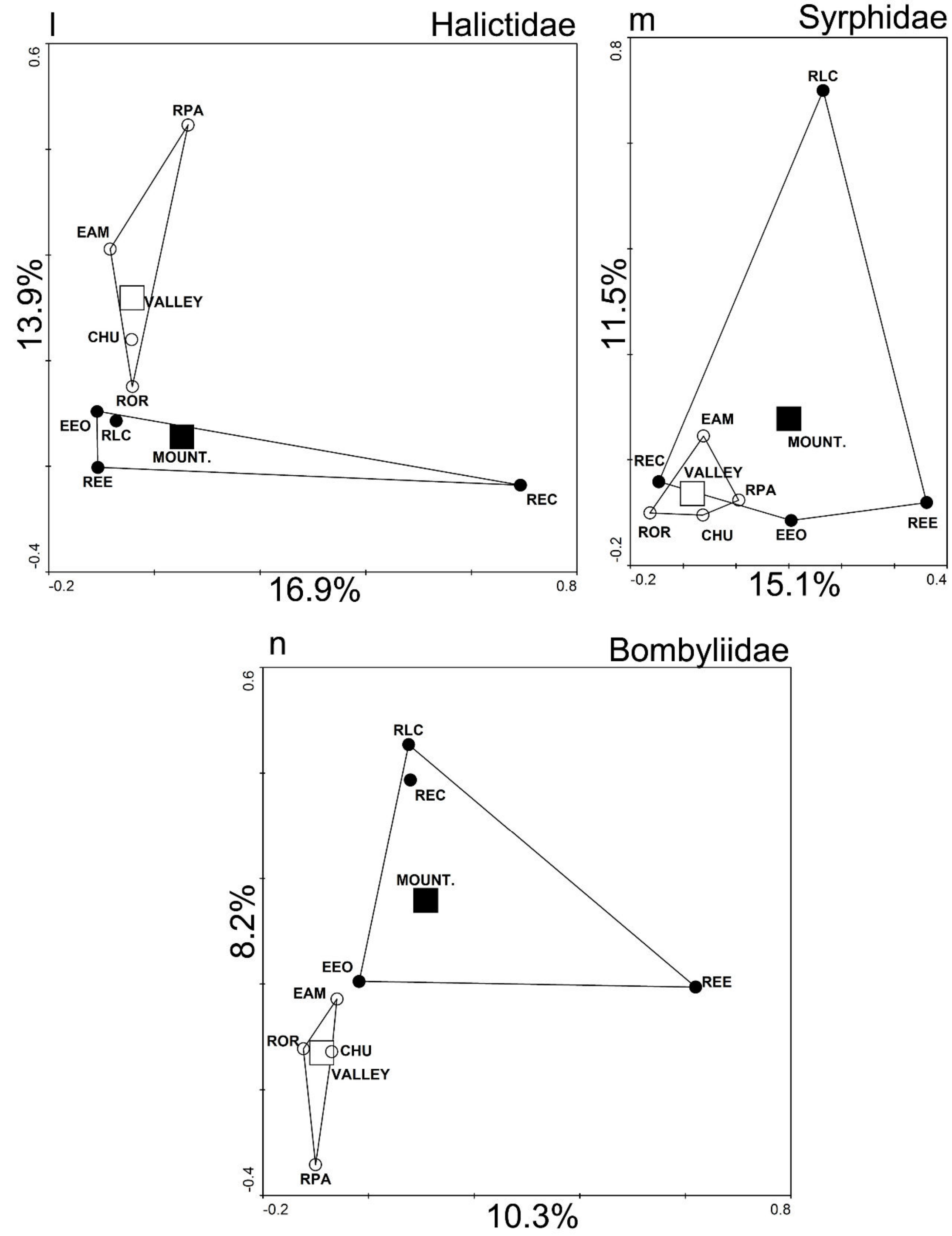
l
Halictidae
0.6
-0.4
13.9%
-0.2
0.8
16.9%
RPA
EAM
VALLEY
CHU
ROR
EEO
RLC
MOUNT.
REE
REC
m
Syrphidae
0.8
-0.2
11.5%
-0.2
0.4
15.1%
RLC
EAM
MOUNT.
REC
VALLEY
RPA
ROR
CHU
EEO
REE
n
Bombyliidae
0.6
-0.4
8.2%
-0.2
0.8
10.3%
RLC
REC
MOUNT.
EEO
REE
EAM
ROR
CHU
VALLEY
RPA

Figure 2 l-n

CAPITULO 3

ARTÍCULO ENVIADO A REVISIÓN

Efecto negativo de la abundancia de abejas sobre la abundancia de moscas miméticas sugiere competencia entre miméticos y sus modelos

Este capítulo está en formato de manuscrito para la revista *Ecological Entomology*

Negative correlation between the abundance of bees and the abundance of mimetic flies suggests competition between mimics and their models

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ABSTRACT

1. A community of Batesian mimics could be affected by the community of their models. Here we evaluated the relation between the abundance and species richness of mimetic flies and the abundance and richness of their bee models. We also analyzed the correlation between the abundance of the mimics and their similarity with their models.

2. Bees and flies that visit flowers, Syrphidae and Bombyliidae, some of which are mimetic of bees, were collected in the region of Cuatro Ciénegas, Coahuila in the northeast of Mexico. Mimetic species and their similarity degree were defined with morphometric techniques and discriminant functions.

4. A negative relation between the abundance of model bees and the abundance of mimetic flies was found, but no relation was detected between model bees and non-mimetic flies. This proves that mimetic interactions affect the community of mimetic flies and suggests a competition interaction between mimics and models.

5. The similarity degree of mimics with their models is negatively correlated with mimics' abundance. This supports the multi-model hypothesis for imperfect mimicry, which states that some mimics imitate more than one model, with an intermediate morphology; thus receiving protection in the presensce on any of their models and being more abundant than mimics that imitate a single model..

6. No relation was found between the species richness of models and richness of mimics, possibly because the number of species involved was low.

7. The mimetic interaction between pollinator insects affects their abundances and potentially the efficiency of pollination service they provide.

Keywords: Syrphidae, Apoidea, mimetic interactions, community ecology, imperfect mimicry, Cuatro Ciénegas.

INTRODUCTION

Batesian mimicry is a strategy in which a species without a defensive mechanism, called mimic, copies the warning signal of an aposematic species with such mechanism, called model (Speed, 1999; Ohsaki, 2005; Ceccarelli & Crozier, 2007). Flies of the families Syrphidae and Bombyliidae are presumably mimics of bees and wasps (Howarth *et al.*, 2000, 2004; Penney *et al.*, 2012). Mimetic interactions have supposedly evolved by natural selection due to an increase in mimic fitness by the similarity with the models (Speed, 1999; Holen & Johnstone, 2006; Ries & Mullen, 2008; Savage & Mullen, 2009; Pfennig and Kikushi, 2012a). This interaction can be analyzed from diverse ecological and ecolutionary perspectives. One approach is the study of the effect of mimicry on the structure of the communities of mimics and models (Alexandrou *et al.*, 2011).

The morphological similarity is essential for the Batesian mimicry theory. Higher similarity implies a better protection for the mimic (Wickler, 1968; Harper & Pfennig, 2007; Pfennig & Kikuchi, 2012a, b). However, the so-called imperfect mimics present a low similarity with the models. The multi-model hypothesis (Edmunds, 2000; Howarth *et al.*, 2004) suggests that imperfect mimics evolved to have an intermediate morphology between different models and receive the benefit of the similarity in the presence of any of these models. The presence of imperfect mimics allows a higher ratio of mimics to any single model, because mimics do not depend exclusively on the abundance of any model.

Besides morphological similarity, the Batesian mimicry requires three conditions to be effective (Wrickler, 1968; Joron, 2009): 1) The models must be more abundant than the mimics. This allows the predators to learn the warning signal. 2) Mimics and models must coexist in space and time. In the case of anthophile flies and bees, this condition may lead to an increase in the competition for flower resources. This competition can be reflected in the abundance patterns of mimics and models. 3) Predators must have the ability to learn. Such ability is affected by the similarity degree between models and mimics (Darst, 2006).

To examine the effects of mimicry on the community structure of models and mimics, we first determine (1) which species of Bombyliidae and Syrphidae are mimics of bees in Cuatro Ciénegas region? With the mimics and their models defined, then we test the multi-model hypothesis prediction that mimic-model ratio should be higher for imperfect mimics than for good mimics. For this, we ask, (2) how the similarity degree of the mimics with their models and the abundance of the mimics are related? If the good mimics receive more protection, then the abundance of mimics will be positively related to the similarity degree with their models. But if imperfect mimics receive more protection by imitating different models, then the abundance of mimics will be negatively related to the similarity degree with their models. Lastly, we examine, 3) how is the relation between the abundance and species richness of the model species and the abundance and richness of the mimetic species? If a higher abundance of models provides more protection to the mimics, then the abundance of bees will be positively related to the abundance of mimetic flies. Also, as the diversity of bees represents the array of potential forms to be imitated by the flies, then the diversity of mimics will be positively related to the diversity of models.

METHODS

Study area. The municipality of Cuatro Ciénegas in Coahuila in the northeast of Mexico is a region with unique geological and biological characteristics. The region was isolated from the Atlantic Ocean when the Sierra Madre Oriental appeared in the mid-Eocene 40 Ma. When the ocean withdrew some of the water remained trapped in the valley of Cuatro Ciénegas (Moreno-Letelier *et al.*, 2012). This water emerges as ponds, which make different this region from the nearby desert areas, and produces a high degree of isolation and endemicity, unique worldwide, similar to that in the Galápagos Islands (Souza *et al.*, 2012). Sierra La Madera is a limestone mountain range with northeast-southeast orientation. This range acts as a barrier for the humidity from the Gulf of Mexico, which makes lower portions dryer (Villanueva-Díaz *et al*., 2008). In the lowlands, the vegetation is desert shrubs and in highlands, submontane forest, chaparral, and pine-oak forest are present, with pine forest in the peaks.

Eight sampling sites were selected within Cuatro Ciénegas municipality. Four sites in the Cuatro Ciénegas Valley: Churince (CHU), Rancho Orozco (ROR), Rancho Pozas Azules (RPA), and Ejido Antiguos Mineros (EAM); and four sites in Sierra La Madera northwards the Valley: Ejido el Oso (EEO), Rancho El Espejo (REE), Rancho El Chupadero (REC) and Rancho La Casita (RLC). Sites cover an altitude range from 713 to 1790 m.a.s.l. Details of the location and characteristics of the sites can be checked in Ávalos-Hernández *et al.* (2014). We selected the sites by two criteria: 1) the presence of flowers, which are associated with the studied insects and in turn associated with water bodies; and 2) the distances between sites should be greater than foraging distances of these insects (Gathman & Tscharntke, 2002). We made seven sampling trips in 2012 and 2013. Four sampling trips in dry season: Dry 1 (February 21–March 1, 2012), Dry 2 (April 3–12, 2012), Dry 3 (April 22–May 3, 2013), and Dry 4 (October 19–November 4, 2013); and three trips during rainy season: Rainy 1 (August 20–31, 2012), Rainy 2 (September 24–October 5, 2012) and Rainy 3 (June 3–15, 2013). In each trip, we sampled seven or eight sites. Due to the difficult access, sites REE, RLC, and REC were sampled three times, REE in Dry 1 and 2, and in Rainy 1;

REC in Dry 2 and 3 and in Rainy 1; while RLC was sampled in Dry 4 and Rainy 2 and 3. A total of 69 samples were taken.

Sampling. Collects spanned from 8:00 to 18:00 h in the various sites, according to site accessibility. For standardization and comparison purposes the interval from 10:00 to 15:00 h was selected for the analysis, as all samplings coincide in this interval. During each sampling, we collected all observed bees and the flies of Bombyliidae and Syrphidae. We recorded the sampling time and plant or substrate of each specimen. For the taxonomic determination, we used specialized keys for Apoidea (Michener, 2000), Bombyliidae (Hall, 1981; Hall & Evenhuis, 1981) and Syrphidae (Vockeroth y Thompson, 1981) and assistance of a specialist for each group of insects and plants.

Morphometric analysis and mimetic complex determination. We took digital photographs of dorsal and lateral views of 20 specimens from 57 species (six Apidae, 32 Bombyliidae, one Colletidae, two Halictidae, six Megachilidae and 10 Syrphidae) with a Nikon Dx10 camera and a macro lens 105 mm. The analysis included all species with a length of at least 1 cm. Each image included a scale in mm. From the images, we made the following measurements: body length (BL); wing length/BL ratio; abdomen circularity; thorax wide/head wide ratio; thorax length/abdomen length ratio; average and standard deviation of wing luminosity; average and standard deviation of level of red, green and blue (RGB) in the abdomen; average and standard deviation of abdomen luminosity. We measured luminosity values and RGB levels in Adobe Photoshop®, and the other measurements with the software ImageJ (http://imagej.nih.gov/ij/). Antenna length is recognized as an important character to distinguish between flies and bees (Bain *et al.*, 2007). In a preliminary analysis flies and bees were completely separated by this character and no mimetic complex were defined. In order to form mimetic associations, we excluded the antenna length from the analysis.

We applied a discriminant function analysis to the biometric data of both fly families paired with each bee families separately. The functions assigned each specimen to a group according to the Mahalanobis distance in the morphometric space of that specimen to the nearest centroid of a species, which is the average morphology of the species (Penney *et al.*, 2012). We checked for analysis assumptions, such as no collinearity between variables, no correlation between means and variance within groups and covariance homogeneity between groups. The model was evaluated with auto values and Wilks lambda of the discriminant functions. These two techniques show that all variables contribute to the classification of the specimen. Also, we made cross-validation in which each specimen is classified with a function estimated with data from all other specimens, except the test specimen. Each discriminant function analysis produced: a) a classification matrix in which each specimen was assigned to a species according to their scores in the discriminant function; b) a posterior probability for each specimen of belonging to each species; and c) the Mahalanobis squared distances between each specimen and the centroid of each species, and between the species centroids. We considered the distances between the species centroids in the morphological space as a measurement of morphological similarity between species.

We considered a mimetic association between a fly and a bee species if at least one of these conditions were met: 1) if a fly specimen was classified as a bee or vice versa or; 2) if a fly specimen obtained a posterior probability of belonging to a bee species equal or higher to 0.10 or vice versa. All mimics and models associated were considered a mimetic complex. Each group formed by mimics and their models was considered a mimetic complex.

Similarity-abundance correlation. We used a Kendall (Ʈ) rank correlation test to estimate the correlation between the abundance of mimics and the similarity degree to their models. The abundance of each mimic was adjusted relative to their model abundance (mimic abundance/model abundance). The Mahalanobis distances between centroids of the mimic and the model species were used as a similarity measure.

Effect of the model community on the mimic community. We test the effect of the abundance of models on the abundance of mimics with GLMs. For each mimetic complex, we constructed a model with the abundance of mimics as the response variable. Predictive variables were: Location (Mountains, Valley), Season (Dry, Rainy), Number of plant species visited by mimics of focus complex, Abundance of models of focus complex, Abundance of other flower visitors (mimics and models of other complexes, non-mimetic flies, and non-model bees).

Abundance of mimics of complex i = b_0 + b_1 Location + b_2 Season + b_3 Number of plant species visited by mimics of complex i + b_4 Abundance of models of complex i + b_5 Abundance of other flower visitors

We also used the abundance of non-mimetic flies as a response variable to test if the abundance of models has an effect only on their mimics or on all flies in general. The same predictive variables were included in this model but Abundance of models included bees of all complexes, the number of plant species was only those used by non-mimetic flies and the abundance of other flower visitors included mimetic flies of all complexes and non-model bees.

Abundance of non-mimetic flies = b_0 + b_1 Location + b_2 Season + b_3 Number of plant species visited by non-mimetic flies + b_4 Abundance of models + b_5 Abundance of other flower visitors

We estimated the effect of species richness of models on the species richness of mimic and non-mimic flies with two models. In the first one, the response variable was the species richness of mimetic flies and the predictive variables were Location, Season, Number of plant species visited by mimics, Species richness of models and Species richness of other insects (non-mimetic flies and non-model bees).

Species richness of mimics = b_0 + b_1 Location + b_2 Season + b_3 Number of plant species visited by mimics + b_4 Species richness of models + b_5 Species richness of other insects

The second model had as response variable the species richness of non-mimetic flies and the same predictive variables but the number of plant species visited corresponded to those used by non-mimetic flies and the species richness of other insects included mimetic flies and non-model bees.

Species richness of non-mimetic flies = b_0 + b_1 Location + b_2 Season + b_3 Number of plant species visited by non-mimetic flies + b_4 Species richness of models b_5 Species richness of other insects

As dependent variables are count data these were fitted to a GLM with Poisson error distribution. We checked for models assumptions of homogeneity of variance and normal distribution of residuals with a residual vs fitted graph and a Normal Q-Q plot. As overdispersion was present, we made a quasipoisson adjustment (Ver Hoef & Boverg, 2007). All analyses were made with R version 3.2.3 (R Core Team, 2015).

RESULTS

Mimetic complexes. Five species out of Syrphidae were defined as mimics of nine species of bees (Table 1). *Copestylum anna* Williston and *C. lentum* Williston had one model each, the other three species imitated more than one species of bees. Five of the nine species of model bees belonged to Apidae, three to Megachilidae and one to Halictidae. *Apis mellifera* L. was the model of four Syrphidae species. None Bombyliidae presented enough morphological similarity to be classified as a mimetic species.

Mimics abundance and similarity degree. There were 15 possible mimic-model combinations within the five complexes (Table 2). In nine of these pairs, the model was more abundant than the mimic. The proportion of mimics with their models presented a positive correlation with the Mahalanobis distance in the morphological space (Ʈ = 0.472, $P = 0.015$). This means that more similar mimics were less abundant than imperfect mimics.

Effect of the abundance of models on the abundance of mimics. The abundance of models was negatively related with de mimics abundance in complexes B, C, and D (significance level $P < 0.1$) (Table 3). The abundance of mimics of complexes A and E presented no relation with the abundance of the models. No relation was found between the abundance of mimics and the abundance of other flower visitors. The abundance of non-mimetic flies did not present a relation with the abundance of other insects that visit flowers. The number of plant species visited was positively related to the abundance of mimics and non-mimetic flies. Regarding location, complexes B, C and D were more abundant in the Valley, in contrast with non-mimetic flies that were more abundant in the Mountains. No-mimetic flies were more abundant during Rainy season but mimics of complexes B, D, and E were equally abundant in both seasons. The variable Season was not included for complexes A and C because no specimen of these complexes were collected during the rainy season. Whereas for complex E the number of plant species visited was excluded because all specimens were collected on the same plant species.

Effect of the species richness of models on the species richness of mimics. The species richness of models and other insects were neither related to the species richness of mimetic flies nor with the species richness of non-mimetic flies (Table 3). The richness of mimetic and non-mimetic flies had a significant positive relation with the number of plant species visited. Besides, the species richness of mimetic flies was higher in the Valley and in the dry season, this pattern was not present in the non-mimetic flies.

DISCUSSION

Mimetic complex delimitation. Similarity measurement is fundamental in mimicry studies because it is the way a mimetic interaction is identified and the mimic and model defined. The simplest method to measure similarity is by personal criteria of the researcher or volunteers (Bain *et al.*, 2007), but this method is subjective and non-replicable. Howarth *et* *al.* (2000) take into account, besides the expert opinions, phenology and distribution data to define mimics and models. Other studies measure the similarity between mimics and models from the perspective of birds, supposedly the main predators of flies, through conditioning and experimentation (Dittrich *et al.*, 1993; Green *et al.*, 1999; Stoddard, 2012). Morphometric techniques and multivariate analyses are an objective and practical alternative to quantify the similarity (Bain *et al.,* 2007; Penney *et al.*, 2012), particularly discriminant analysis. Some of the bee species that appeared here as similar to flies are not evident models from the human perspective (*v. gr.*, *Agapostemon*), but the closeness to the flies in the multidimensional morphological space suggests the interaction. The method applied here takes into account the most conspicuous morphological characters of these insects and gives a similarity measure technique that can be used in other analysis.

Is worth noticing the absence of mimetic species from Bombyliidae, which are commonly known as bee flies. In the morphometric space generated for this study, no Bombyliidae species was close enough to bees to be considered a mimic. These could be because of the strictness of the method or because the species included here are not mimics of bees. The similarity of bombylid species with bees is more general than specific. They do not present yellow and black bands, as Syrphidae do, and their wings frequently are pigmented. Despite the common name and the intuitive similarity with bees and wasps, is questionable if Bombyliidae are really mimics of Hymenoptera. Bombyliids can be imperfect mimics and yet receive a benefit from the interaction. Experiments similar to those in Howarth *et al.* (2000) with bird and images could be useful to determine if these flies are really mimics of bees from the predator perspective.

Relation between the abundance of mimics and similarity degree. A higher mimic-model abundance ratio prevents or delays the predators to learn the warning signal. Then, more abundant mimics undergo a higher evolutive pressure to be similar to their models (Harper & Pfennig, 2007; Pfennig & Kikuchi, 2012a). Some anecdotal field observations (Dittrich *et al.*, 1993; Edmunds, 2000) assert that less similar mimics are more abundant that more similar ones, and our results support those observations. This indicates first, that similarity has a relation with the abundance of the mimics. It also supports the multi-model hypothesis of imperfect mimicry (Edmunds, 2000). Additional evidence for this is that most mimetic flies in this study imitate more than one bee species. The higher abundance of imperfect mimics can be explained if they do not depend on the abundance of a single model, or if they have other defense mechanisms besides mimicry (Gilbert, 2005). These results oppose to those of Penney *et al.* (2012) who did not found a correlation between abundance and similarity degree of flies and wasps.

Relation between the abundance of models and the abundance of mimics. Wallace's original theory of mimicry establishes as a rule of mimicry that models must be more abundant than their models (Wallace, 1867; Joron, 2009). In this way, the encounter rate between predators and models is higher than between predators and mimics. As mimic abundance increases the protection disappears (Joron and Mallet, 1998). Experiments with artificial prey and birds (Lindström *et al.*, 1997) and with bees in controlled conditions (Huheey, 1980), as well as computer simulations (Turner *et al.*, 1984), have shown that if models are more abundant mimics suffer less predation. Field studies give conflicting evidence, while Howarth *et al.* (2004) found a positive relation between the abundance of mimetic flies and their models, other field observations do not support this pattern (Dlusski, 1984; Dittrich *et al*., 1993; Azmeh *et al.*, 1998; Howarth *et al.*, 2000).

An explanation for these high abundances of mimics in relation to their models is the presence of alternative preys that reduce the pressure on mimics (Luedeman *et al*., 1981; Dlusski, 1984, Getty, 1985; Sherratt, 2003). This implies that if other non-mimetic species are excluded from the analyses (*v. gr.*, Howarth & Edmunds, 2000), results would be not conclusive and the effect of mimicry could not be estimated. Here we include all species not involved in the mimetic interaction from the same taxonomic groups, this allows us to establish if patterns of mimics and models communities are due the mimicry interaction or another ecological trait of these species.

We presented evidence that the community of models affects the community of mimics because only the abundance of bee models has a relation with the abundance of mimetic flies; neither the abundance of non-mimetic flies nor the abundance of non-model bees affect mimics' abundance. This relation between models and mimics was negative in three of the five mimetic complexes. In this flower-visiting insects system, the competition between mimics and models for the flowers could be playing an important role in the community structure of models and mimics. Pfennig and Kikuchi (2012b) considered the presence of competition between models and mimics to explain imperfect mimicry. They propose that mimicry applies pressure for morphological convergence while competition promotes divergence. The negative relations between the abundances of models and mimics found here suggest competition. Additional evidence of this is that the species richness of plants visited is the most important variable to explain the species richness and abundance of mimics, indicating the importance of flowers to these insects, resource that is shared with the bees.

In the studied system, we see that mimetic complexes B, C, and D that present a negative relation between abundances of mimics and models are also more abundant in the valley than in the mountains (Table 3). All bees (models and non-models) are also more abundant in the valley (934 specimens) than in the mountains (407 specimens). Non-mimetic flies are the only group with the opposed pattern being more abundant in the mountains (Table 3). This difference by location of the abundances of mimetic and non-mimetic flies could be due the differences in available resources. Base resources were not measured in this system, but in a previous study (Ávalos-Hernández *et al*., unpublished data.) is reported that species richness of Syrphidae and the number of plant species they visit are the same in the mountains and in the valley. So there is no difference in species richness of Syrphidae between the valley and the mountains, but the abundance of mimetic species is higher at the valley and of non-mimetics species is higher in the mountains. This shows that the mimicry interaction affects the community of these flies and suggests a complex interaction between models and mimics. An explanation for these results in that mimetic Syrphidae are more abundant in the valley because their models are more abundant there and mimics need to coexist with their models, nevertheless competition with their models reduces the abundance of mimics. On the other hand, non-mimetic Syrphidae do not need to coexist with the bees and avoid competition with them, which is why these non-mimetic flies are more abundant in the mountains, where bees are less abundant.

Regarding temporal patterns, there are also differences between mimetic and non-mimetic flies. Non-mimetic are more abundant during the rainy season (Table 3) while mimetic flies are more abundant in the dry season. Even when complex B, D, and E present no significant differences in abundance between the rainy and the dry season, all three have more specimens in the dry season. This is clear with *C. marginatum* Say from complex D with 134 specimens from dry season and just 26 specimens from the rainy season, but variation in samples of the dry season is so high that the difference is non-significant. Mimics of complexes A and C were collected only during the dry season. In a general way, mimics are more abundant in dry (257 specimens) than in rainy season (73 specimens). Then, as the location does, the season also have a different effect on mimetic and non-mimetic flies.

Relation between species richness of models and species richness of mimics. It was expected that a higher richness of model species would be positively associated with more mimic species because more diversity of models means more forms to imitate. No relation was found between the species richness of mimics and models. This could be due the low richness values of both groups. However, congruent with the abundance patterns more mimetic species were found in the dry season and in the valley, and no differences between locations or season were found in the non-mimetic flies. With these results, we suggest that location and season affect differentially the species richness of mimetic and non-mimetic Syrphidae.

Once we have determined that abundance of mimics and models has a negative relation the next step is to determine if this represents a competitive interaction. For this, we are measuring the resource use overlap between mimics and models to see if the overlap is higher between mimics and models than between mimics and other bees.

Few studies focus on mimicry at a community level in the field, compared with experimental or controlled condition studies (Ruxton *et al.*, 2004). With field data here we show that there is an effect of the model community on the mimics' community, but not in the community of non-mimetic flies. In addition, we tested two predictions of the Batesian mimicry theory. As predicted by the multi-model hypothesis of imperfect mimicry (Edmunds, 2000; Howarth *et al.*, 2004; Gilbert, 2005) the more dissimilar mimics were the more abundant. The relation between the abundances of models and mimics is inconsistent with the predictions of the traditional theory of mimicry. The abundance of mimics decreases as the abundance of model increase, possibly due the competition between mimics and models for flower resources. This relation is not present for non-mimetic flies. Anthophilous mimetic flies present an opportunity to explore a complex interaction that includes mimicry and competition. This has relevance not only in the field of community ecology theory but also in pollination ecology. The negative relation between the abundance of models and mimics could be reciprocal, so the presence of mimetic flies reduces the abundance of model bees, which in turn affects pollination.

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Contribution of authors

O. Ávalos-Hernández and Z. Cano-Santana are responsible for the project design and paper writing. Data collection and analysis was done by O. Ávalos-Hernández.

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Table 1. Mimetic species founded with a discriminant function analysis with 15 characters descriptive of size, form, and color.

Complex	**Mimic**	**Model(s)**
A	*Copestylum anna* Williston	*Centris* sp.
B	*Copestylum caudatum* Curran	*Anthophora* sp. 1, *Apis mellifera, Agapostemon* sp. 1
C	*Copestylum lentum* Williston	*Apis mellifera*
D	*Copestylum marginatum* Say	*Anthophora* sp. 2, *Apis mellifera, Agapostemon* sp. 1
E	*Palpada mexicana* Macquart	*Anthophora* sp. 2*, Apis mellifera, Centris* sp., *Tetralioniella* sp., *Megachile* sp. 1*, Megachile* sp. 2, *Megachile* sp. 3

Table 2. Abundance of mimics and models and distances in the morphological space. Mahalanobis distances between species centroids were obtained from the discriminant function analysis.

Complex	**Mimetic species**	**Model species**	**Mimic abundance**	**Model abundance**	**Mahalanobis distance**
A	*Copestylum anna*	*Centris sp.*	26	24	34.557
B	*C. caudatum*	*Apis mellifera*	94	237	14.301
B	*C. caudatum*	*Anthophora* sp. 1	94	31	38.429
B	*C. caudatum*	*Agapostemon* sp.	94	35	20.538
C	*C. lentum*	*A. mellifera*	29	237	13.584
D	*C. marginatum*	*A. mellifera*	160	237	10.167
D	*C. marginatum*	*Anthophora* sp. 2	160	35	19.038
D	*C. marginatum*	*Agapostemon* sp.	160	35	18.554
E	*Palpada mexicana*	*A. mellifera*	21	237	7.371
E	*P. mexicana*	*Centris* sp.	21	24	34.586
E	*P. mexicana*	*Tetralioniella* sp.	21	31	13.845
E	*P. mexicana*	*Anthophora* sp. 2	21	35	12.561
E	*P. mexicana*	*Megachile* sp. 1	21	35	12.774
E	*P. mexicana*	*Megachile* sp. 2	21	19	17.494
E	*P. mexicana*	*Megachile* sp. 3	21	76	15.162

Table 3. General linear models of abundance and species richness of mimetic and non-mimetic flies of Syrphidae. Exponentiated coefficients are presented for models of each mimetic complex and non-mimetic flies. Abu. Mod., Abundance of model bees; Abu. Other, Abundance of other flower visitors; Sp. Rich. Other, Species richness of other flower visitors; Sp. Rich. Plants, Species richness of plants visited; Sp. Rich. Mod., Species richness of model bees. V, higher value of response variable in Valley; M, higher value of response variable in Mountains; R, higher value of response variable in Rainy season; D, higher value of response variable in Dry season ($^{+}$ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Response	**Predictors**					**Null deviance / Residual deviance**
Abundance	**Location**	**Season**	**Sp. Rich. Plants**	**Abu. Mod.**	**Abu. Other**	
Copestylum anna (A)	1.35		20.953***	1.229	0.0997	131.502 / 11.213
C. caudatum (B)	3.369*** (V)	1.502	3.653***	0.951^{+}	0.999	254.712 / 33.971
C. lentum (C)	4.142* (V)		7.014***	0.805**	0.988	112.263 / 17.374
C. marginatum (D)	2.524^{+} (V)	2.138	2.886***	0.851*	0.985	470.70 / 150.06
Palpada mexicana (E)	1.457	0.98		0.944	1.013	76.837 / 73.045
Non-mimetic Syrphidae	0.66^{+} (M)	0.546** (R)	1.671***	1	1.01	289.46 / 128.73
Species Richness				**Sp. Rich. Mod.**	**Sp. Rich. Other**	
Mimetic Syrphidae	1.486* (V)	1.666* (D)	1.723***	0.977	0.969	89.775 / 34.512
Non-Mimetic Syrphidae	0.853	0.963	1.462***	1.006	0.972	87.125 / 57.712

DISCUSIÓN GENERAL

En este trabajo se describieron las comunidades de abejas y moscas que visitan flores en Cuatro Ciénegas, Coahuila. Se encontraron patrones de diversidad y uso de recursos los cuales son diferentes para cada familia, y se evaluó el efecto del mimetismo sobre la comunidad de miméticos. Para el estudio de las comunidades biológicas se debe seguir una secuencia, en primer lugar es necesario conocer sus componentes. Una vez que se tienen las especies que componen una comunidad se pueden describir los patrones de diversidad, abundancia u otras propiedades de las comunidades. Por último, se puede analizar los factores que afecten estos patrones, como en este caso el mimetismo.

Las comunidades son sistemas complejos de diversos elementos, que son las especies que las conforman. Para estudiar estas comunidades agrupamos a estas especies en conjuntos naturales o artificiales para ordenarlos y así poder analizar o comparar entre conjuntos o entre comunidades. La delimitación de dichos conjuntos determina los patrones que se encuentran en las comunidades y puede llegar a afectar las conclusiones. Los estudios sobre comunidades de insectos polinizadores generalmente tratan a las abejas como un grupo homogéneo (Oertli *et al.*, 2005; Sydenham *et al.*, 2014). En el capítulo 2, se encontró que cada grupo taxonómico tiene sus propios patrones de diversidad y de uso de recursos. Por esa razón, los estudios de las comunidades de insectos que visitan flores deben considerar las diferencias entre familias o incluso a niveles más bajos de clasificación. Posteriormente, en el capítulo 3, se encontró que dentro de cada taxón hay subgrupos cada uno con sus propios patrones, en este caso los Syrphidae miméticos tienen patrones de abundancia diferentes a los no miméticos. Entonces, los grupos de especies que se formen para los análisis dependerán del grado de detalle que quiera obtenerse. Por un lado, si se utilizan grupos muy incluyentes como todas las abejas, se perderá información importante como las diferencias en el uso de recursos que tiene cada familia. Pero por otro lado, si se separan en varios grupos, el estudio se hace muy complejo y las conclusiones muy específicas para cada grupo pequeño de especies. Separar los resultados por familia resultó eficiente para describir los patrones con el detalle requerido para este estudio.

Los resultados confirman que las moscas que vistan flores deben incluirse en los estudios de insectos polinizadores. En primer lugar, en el capítulo 1 se encontró que estas comunidades no están bien conocidas ni descritas y que su diversidad es mayor a la previamente considerada para el estado de Coahuila. Esto se puede ver por la proporción de nuevos registros que se obtuvieron para Bombyliidae. En el capítulo 2, se encontró que la abundancia y diversidad de Bombyliidae es mucho mayor a la de las abejas, y que los patrones de diversidad y uso de recursos de Diptera son diferentes a los de las abejas. Esta gran abundancia de moscas es relevante porque la eficiencia de estos insectos como polinizadores depende de su abundancia (Motten *et al.*, 1981) ya que transportan menos polen que las abejas. La abundancia de Bombyliidae en Cuatro Ciénegas lo hace un grupo de polinizadores potencialmente importante. También, en el tercer capítulo, se encontró una relación negativa entre las abundancias de Syrphidae miméticos y abejas modelo. Esto nos lleva a la conclusión de que tanto Syrphidae como Bombyliidae tienen un efecto directo o indirecto sobre la polinización, ya sea por la abundancia relativa o por las interacciones de mimetismo con las abejas. La inclusión de Diptera que visitan flores es relevante en estudios de comunidades de polinizadores.

Las diferencias entre las familias en los patrones espacio-temporales de la diversidad y uso de recursos indican que cada comunidad tiene un funcionamiento diferente. Existen diversos factores que afectan de forma diferente a cada comunidad como pueden ser las respuestas a las condiciones ambientales. Los resultados muestran que el mimetismo es uno de estos factores que afectan el funcionamiento de las comunidades al modificar la abundancia y posiblemente el uso de recursos. De esta forma, el mimetismo puede modificar procesos ecológicos como la distribución espacial y temporal de las especies, la sucesión, la dominancia o la exclusión de algunas especies. La interacción mimética también puede relacionarse con procesos evolutivos como es el aumento en la especialización de los polinizadores. Esto es porque, si el mimético y el modelo compiten por el recurso floral, entonces una estrategia sería especializarse para reducir el solapamiento del uso de recursos. Esto también puede favorecer la especiación si distintas poblaciones, separadas en tiempo o espacio, se especializan en visitar flores de plantas diferentes. El reconocimiento de las diferencias entre la estructura de las comunidades de polinizadores y el efecto del mimetismo sobre estas, permitirá tomar en cuenta esta interacción para generar planes de manejo de polinizadores, dirigidos a un grupo en específico.

El mimetismo se ha estudiado poco a nivel de comunidad (Ruxton *et al*., 2004). Los estudios se enfocan en especies particulares. Además, los estudios del mimetismo en campo también son raros, ya que es más práctico realizar experimentos con presas artificiales en condiciones controladas y depredadores entrenados (Kauppinen y Mappes, 2003; Aronsson y Gamberale-Stille, 2012). El enfoque que se planteó aquí con buenos resultados, fue ver el efecto del mimetismo sobre la comunidad de miméticos mediante la comparación de las comunidades de especies miméticas y no miméticas de un mismo grupo taxonómico. Para ello se tuvo que definir a las especies miméticas y sus modelos. Este es el paso más importante de cualquier estudio de mimetismo y frecuentemente no se le da importancia o se suponen a las especies como miméticas (Heal, 1981, 1982; Howarth y Edmunds, 2000; Howarth *et al.*, 2004). Aquí se presentó un método práctico para definir especies miméticas y sus modelos y cuantificar la similitud morfológica entre ellos. Este método es modificación del empleado por Penney *et al.* (2012) y podría seguir empleándose para estudios posteriores con insectos miméticos.

A partir de los resultados que indican una posible competencia entre modelos y miméticos se está trabajando para profundizar en la relación entre el mimetismo y la competencia entre moscas y abejas. Esta idea del mimetismo y competencia como fuerzas contrarias ya la había presentado Pfennig y Kikuchi (2012a) como una explicación al mimetismo imperfecto. Ellos plantean a la competencia como una fuerza para la divergencia morfológica y al mimetismo como una fuerza para la convergencia. El enfoque que se propone en el presente trabajo es que el mimetismo ente moscas y abejas promueve la coexistencia, pero el uso del mismo recurso (las flores) por ambos grupos, genera competencia. Por lo tanto, se propone analizar las diferencias en el uso de los recursos entre moscas miméticas y no miméticas. En particular en el grado de solapamiento del uso de recursos entre miméticos y modelos, así como el grado de especialización de miméticos y no miméticos.

Derivado de este trabajo se propone muestrear más estos insectos, en particular en estados fronterizos cercanos a localidades o áreas bien muestreadas en EE.UU. donde se sepa que existe diversidad alta. Esto permitirá completar las listas de especies de los estados del norte del país. También se propone estudiar más a fondo la capacidad de algunos grupos de modificar sus patrones de uso de recursos y así aumentar las plantas que visitan de acuerdo a la disponibilidad de estos en cada ambiente o temporada, un rasgo deseable de un buen polinizador. Un proyecto interesante sería buscar si esta capacidad está relacionada con otros rasgos funcionales o morfológicos. De esta forma se podría predecir qué familias o taxones tiene potencial de ser polinizadores eficientes.

Con base en los resultados obtenidos en la tesis, así como en la discusión sobre los mismos, se puede concluir lo siguiente.

1. Las moscas miméticas que visitan flores y las abejas modelo son un buen sistema para estudiar una interacción compleja donde interviene la necesidad de coexistencia del mimetismo con la exclusión competitiva por las flores. A partir de este sistema se puede estudiar la evolución del mimetismo imperfecto por fuerzas contrarias.
2. La entomofauna de la zona norte del país tiene una diversidad mucho mayor a la reportada hasta ahora.
3. Cuatro Ciénegas presenta una diversidad alta para estos insectos en relación a la diversidad del país. Al igual que con otros grupos esta zona es de relevancia biológica y debe estar sujeta a medidas de conservación.
4. Los estudios de ecología de comunidades de abejas debe considerar las diferencias entre las familias, ya que estas presentan patrones diferentes y las conclusiones obtenidas con un grupo no pueden generalizarse a los demás.

5. Las moscas por su abundancia y diversidad son polinizadores potenciales de gran importancia. Estudios sobre la ecología de la polinización deben incluir a este grupo de insectos para estar completos.
6. El mimetismo afecta tanto a las comunidades de miméticos como a las de los modelos. Los patrones de abundancia y diversidad son diferentes entre moscas miméticas y no miméticas del mismo grupo taxonómico.
7. La abundancia de las moscas miméticas tiene una relación negativa con la abundancia de abejas modelo; esto sugiere una interacción competitiva, pero más estudios son necesarios para confirmar esta aseveración.

La estructura de una comunidad se define por muchos factores, como los estocásticos, las particularidades de cada especie y las interacciones entre las especies y de estas con el medio. Cada interacción tiene una mayor o menor importancia en la estructura de la comunidad. En el sistema de moscas miméticas y abejas, el mimetismo es una interacción que sí afecta a las comunidades. La disyuntiva que se presenta en estos insectos entre la competencia y la necesidad de coexistir por el mimetismo apenas comienza a ser estudiada. Aquí se abordó desde la perspectiva de las comunidades pero podría abordarse a nivel de poblaciones o con un enfoque experimental. Este sistema de moscas miméticas y abejas modelo representa un campo de investigación con potencial para las teorías ecológicas tanto de competencia como de mimetismo.

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